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Book Review: DESERT MYTH-BUSTERS

THE BIOLOGY OF DESERTS. David Ward. 2009. (The Biology of Habitats series.) Oxford University Press, New York. 304 pp. Softcover, $55; hardcover, $120. ISBN 978-0-19-921147-0 or 978-0-19-921146-3.

Deserts are not places where organisms die; rather, they are places where organisms succeed with less, and thus there is much to be learned from deserts. Indeed, the biotic interactions among desert organisms are rich and varied, as in other systems. (It is also probably true that this is the reason deserts play such a crucial role in many religions—because they allow a focus on what is essential and what is not, but that is the subject of a different review.) David Ward has written a wonderful book on deserts; it is organized around ideas concerning deserts, rather than specific desert systems. Doing it this way allows Ward to choose examples that best illustrate the specific points from the wide variety of desert systems found in the world.

The book begins with the reminder of Dobzhansky that nothing in biology makes sense except in the light of evolution. The first chapter is a general introduction, explaining exactly what a desert is. We all know, of course: some kind of arid place; but the real issue is, what does that mean? The answer is that deserts have both low precipitation and high variation in precipitation. Ward shows that there is strong negative correlation between median annual rainfall and coefficient of variation of rainfall—it is the lack of precipitation, and not high temperature, that makes a desert. He then explains the environmental factors that deny rainfall to deserts.

Chapter Two focuses on abiotic factors. Ward once again emphasizes the temporal and spatial variation in annual rainfall as important characteristics of deserts. In a desert, rain falls in pulses that are patchy in space. In some coastal deserts rain may not fall for long periods of time, but water arrives through fog generated by coastal upwelling (in the Atacama Desert in Chile and Peru, it is claimed that rain did not fall for nearly 400 years). Temperature is also clearly a factor in creating deserts, but there are both cold and hot deserts.

In Chapter Three, Ward considers the adaptations of desert plants to the abiotic environment. Plants can deal with low water in the desert by escaping, evading, enduring, or resisting drought, and there are examples of each. There is correlation between the photosynthetic pathway (C3, C4, or the less common Crassulacean Acid Metabolism [CAM]), plant morphology, and strategy for dealing with drought. Ward separates annual and perennial plants, grasses, and forbs. For the annuals, he spends considerable time on seed germination strategies, including dispersal (asking why long-range dispersal is rare—although he gives much of the answer in the previous chapter about the spatial patchiness of rain), delayed germination, and structure. One cannot address

these trade-offs without thinking of the classic work of Dan Cohen and John Gillespie on mean–variance trade-offs and geometric vs. arithmetic means. For grasses, forbs, and shrubs/perennials he discusses clonality, stomatal opening and closing, and leaf pubescence. In addition, there are geophytes, plants that use underground organs for storage of water (e.g., irises and lilies) and both stem and leaf succulents (e.g. cactus, aloe). Finally, Ward discusses halophytes—plants that adapt to high salt regimes (either through accumulation or storage).

In Chapter Four, Ward considers the adaptations of desert animals to the abiotic environment. Overall, the strategies for dealing with lack of water and temperature are to evade or endure. A simple scaling argument shows the complexity of the problem: a large ratio of surface area to volume will allow easier cooling, but also more rapid water loss. Thus, for example, tenebrionid beetles may develop wax sheaths that allow cooling but insulate for water loss. In general, the evaders are the invertebrates, desert amphibians and reptiles, and the smaller mammals, rodents, and insectivores. In addition to the beetles, Ward discusses a variety of fascinating animals including snails, frogs, gerbils, spiders, and termites. He explains the physiological mechanisms that are used to control heat gain, using dune larks and sandgrouse as examples. Some of the birds and reptiles have glands to sequester salt. Ward includes a brief section on temporary pools and then discusses the endurers, the best known being the camel, oryx, and desert sheep.

In Chapter Five, Ward discusses the roles of competition and facilitation in structuring desert communities. He reviews the theories that place varying weights on resources, tolerance, and density dependence and then turns to the competition between animals, much of which is described using the patch selection theory developed by Mike Rosenzweig, Joel Brown, and Burt Kotler. This theory allows one to take both foraging gain and predation risk into account and thus blend aspects of individual behavior and population ecology. Ward describes experiments designed to test these theories and shows that work still needs to be done; indeed I'd say that there is a great need for some formal statistical modeling and the simultaneous but rigorous comparison of multiple hypotheses. He then turns briefly to keystone species (kangaroo rats are one), apparent competition, and priority effects. These sections are way too brief and the use of Lotka Volterra competition equations to illustrate the priority effect is a somewhat confusing and wrong (but the section is too brief to tell), although the example of ephemeral pools is a good one concerning priority effects.

In Chapter Six, Ward discusses the importance of predation (direct mortality) and predation risk (indirect effects) in structuring desert communities. The latter is "apprehension", a change in behavior related to the risk of predation perceived by the animal. It is in this chapter that the theory of isodars, developed by Mike Rosenzweig and Zvika Abramsky, is explained. Isodars are lines of equal fitness in the phase plane in which one axis is the density of a species in a first habitat and the second axis, the density of the same species in a second habitat, thus showing contours of equal fitness. Isodar theory leads to five different models of density-dependent habitat selection, which differ in qualitative and quantitative features. This theory is illustrated with gerbils. Spiders are used to illustrate the importance of movement and habitat selection (for web building)

and scorpions, the importance of specialization on prey types. Fleas, toads, spiders, and beetles arise in examples of parasitoids and parasites.

In Chapter Seven, Ward continues to make the case that plant–animal interactions in desert communities are important to shaping their structure; i.e., that it is not abiotic conditions alone that determine the biodiversity of arid ecosystems. In particular, he examines and reexamines data on herbivores, with a particularly nice focus on long-term studies. One of the most interesting and important effects is how a selective herbivore affects the relationships between plant functional types described in Chapter Three. For example, in many arid ecosystems, annual species replace perennials following heavy grazing because annuals are more likely to be r-selected species and perennials more likely to be K-selected species. There is a considerable section on pollination, particularly the yucca–yucca-moth mutualism, interesting because yucca moths are the only known pollinators of the yucca, flowers are aborted if too many eggs are laid in them, and cheating has evolved in the system at least twice. A similar system is the senita-cactus–senita-moth mutualism in the Sonoran Desert in the United States. Ward describes some of the theory associated with this system, but the description is particularly dense and I think that it will frustrate most readers. There is a brief section on seed dispersal and predation, followed by a longer section asking, "Are these coevolved systems?", where, in addition to the senita and yucca systems, *Bursera* trees and their leaf beetles, and the dorcas gazelle and lilies are added. For the latter case, a model of optimal foraging by gazelles is briefly described. Although the animals behave in a way consistent with the theory, here—and previously in the book—when describing predictions, Ward writes that, "Gazelles *should* prefer small lilies…" (p. 174, italics added). I would have preferred "are predicted to" because too often individuals who lack an appreciation of theory read the word "should" and conclude that any variation from the prediction disproves the theory. In this case the result is clear and strong, but one must be careful nonetheless.

Chapters Eight and Nine consider larger scales. The former deals with desert food webs and ecosystem ecology and begins by asking, "Can we scale up from two-species interactions to desert ecosystems?" In explaining why the answer is no, Ward reviews the classic food web model of Hairston, Smith, and Slobodkin, putative laws about food webs developed by Joel Cohen, and objections to those laws by Gary Polis, Yoram Ayal, and their colleagues. One of the biggest questions about this issue revolves around cycles that occur in food webs when different life history stages play different roles. For example, gopher snakes eat eggs and young of burrowing owls, while adult owls eat young snakes. It is hard to capture this relationship if "snake" and "owl" are represented by one spot in the food web. Ward then discusses interactions among habitats, and the effects of precipitation, nutrients, disturbances, and decomposition. In Chapter Nine, Ward considers the biodiversity and biogeography of deserts. He shows that regardless of the measure of biodiversity that one uses (local diversity, turnover rates, or regional diversity), one can find deserts where the measure of biodiversity is exceptionally high—deserts are rich places. Community-wide character displacement can take place in deserts.

Chapters 10 and 11, which close the text, are also a pair. The former concerns human impacts and desertification and the latter, conservation of deserts. Here, Ward reviews, through a variety of examples, the paths (overgrazing, erosion due to climate change, anthropogenic effects, soil salinization) that can lead to desertification but argues that grazing is the most important cause of desertification. Furthermore, we need to think of grazing systems as dynamic ones, rather than in a steady state; one of the big challenges is to understand the co-existence of trees and grass. Chapter 10 closes with a discussion about the importance of reversibility when considering our interactions with desert ecosystems. In Chapter 11, Ward argues that deserts should be targets for conservation for a number of reasons, including their unique features, the ecological benefits provided by deserts, and in many cases the relatively pristine nature of deserts. The question then becomes how to proceed with conservation, and Ward discusses the virtues of a focus on species, populations, or habitats. In the course of doing this, we learn that the Succulent Karoo Desert of South Africa and Namibia is the only arid habitat that is considered a formal hot spot of biodiversity. He then discusses restoration ecology in the context of reintroduction, recolonization, and revegetaton. I think that situation of deserts is extremely difficult because it is not clear what the restoration target should be. Ward rightly argues that evolutionary biology should be at the core of thinking about reintroductions and that we should think about genotype by environment interaction—the core of biology—when planning restoration.

Deserts are places where we can often see evolution in action, and David Ward has written a book that is compelling in its breadth and depth of coverage. Buy it, and you will not be disappointed and will be able to come back to it many times and always learn something new and exciting.

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