vation biologists could agree on priorities, it is unlikely they would match either public sentiment or current endangered-species laws. These laws, rightly or wrongly, work to protect species regardless of their appearance, taxonomic rank, or economic utility.

The authors have obviously been prompted by the editors to make practical suggestions to foster conservation. Millar and Libby make several intriguing suggestions, including the establishment of large-scale and spatially integrated networks of "genetic management systems" aimed at species with broad ranges that have not yet become rare or threatened. Falk and the Center for Plant Conservation summarize many other recommendations in their appendix on "Genetic sampling guidelines for conservation collections of endangered plants." These guidelines have the virtues of being specific and simple (sample 10 to 50 individuals from each of 3 to 5 populations, modified for life history, pattern of distribution, and so on) and will likely be widely applied. With such simple rules of thumb, however, it will be tempting to sidestep the tedious steps recommended by many authors to measure and assess population parameters and genetic variability prior to designing sampling schemes. In addition, a formulaic approach ignores the specific complexities emphasized as important by many of the authors.

Despite controversies over such technical issues of implementation, the authors all agree we must vastly expand our conservation efforts. This volume has greatly advanced the field by crystallizing the genetic issues and providing a convenient and authoritative source for those practicing in the emergency wards of conservation biology.

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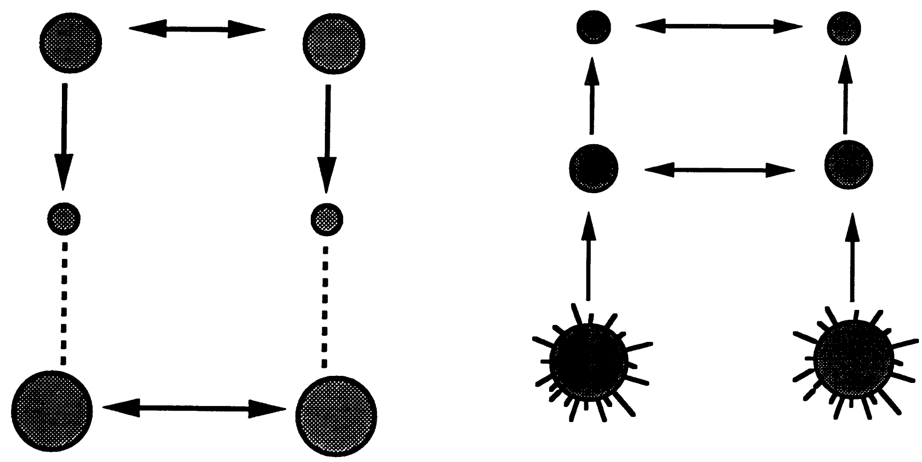


Sketches of two hypotheses according to which removal of herbivores from a community would have little effect. *Left*, " 'The world is green' hypothesis of Hairston *et al.* (1960). Solid lines indicate strong interactions, and dashed lines indicate weak interactions. Predators compete and limit [folivores], which then do not limit plants, and, in consequence, the plants do compete. Granivores, frugivores, and nectarivores do compete, however, because seeds, fruits, and nectar are in limited supply." *Right*, " 'The world is prickly and tastes bad' hypothesis of Murdoch (1966). . . . Plants are difficult to eat, and so the availability of digestible, accessible plants limits herbivores (which compete), and these, in turn, limit carnivores (which also compete)." A survey of data "unequivocally rejects" both hypotheses. "Herbivore removals *do* have effects." [From *The Balance of Nature*]

Big Questions in Ecology

The Balance of Nature? Ecological Issues in the Conservation of Species and Communities. STUART L. PIMM. University of Chicago Press, Chicago, IL, 1992. xiv, 434 pp., illus. $62; paper, $26.95.

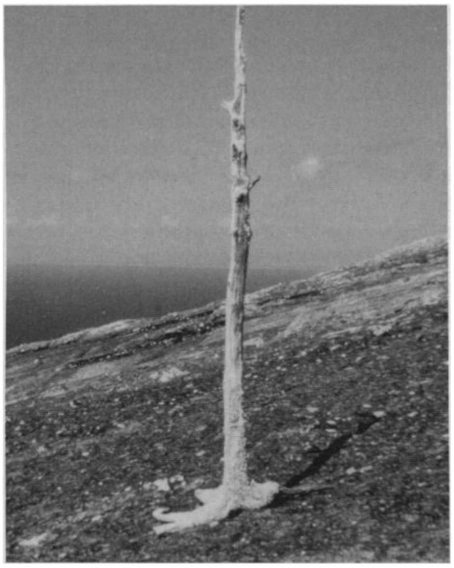
This is a wondrous book, filled with fascinating questions and sweeping patterns based on huge statistical data sets. It deals with the big questions in ecology. How quickly will species recover following catastrophes? Can we predict which species are particularly vulnerable to extinction? Which species will succeed if they are introduced into communities? Its tack is to get far back and squint and see what stands out.

Pimm begins by breaking ecological stability into five related parts: stability in the strict sense, resilience, variability, persistence, and resistance. He defines each, gives the units in which each is measured, and then sets about presenting data sets that show how each form of stability is influenced by various biological attributes of species and the way they are dynamically imbedded in multi-species and multi-trophic-level communities. The problem, of course, is that phenomena that occur on such large spatial and temporal scales do not lend themselves to experimental manipulation. Like cosmologists, ecologists must rely on mathematical extrapolation. Yet unlike the situation in cosmology, the equations governing the dynamics of interacting species are only caricatures. The ecologist concerned with the big picture is faced with huge scales, complex interactions, and unknown relationships. Pimm is undaunted and seeks patterns.

Sure enough, patterns emerge. Yet, as Pimm often points out, the large scatter about most of the plots relating his various stability measures to suspected individual characteristics (for example, body size, reproductive rate, population density) or the way a species is linked to others (number of trophic levels, number of prey species) suggests that ecology still has a lot to learn about these stability measures. Perhaps we have not yet identified some of the most pivotal influences. One possibility, not discussed much here but emerging as a contender, is that the stability properties of a particular species's population are affected at least as much by the abundance of habitat space and the arrangement of habitat patches in space as by the population densities of species with which the species interacts or the temporal variability of the climate. Could it be, for example, that the relatively common population cycles of species in the arctic and subarctic zones have less to do with classical predator-prey dynamics as a driving force than with the fact that in the boreal zone a large continuous expanse of homogeneous habitat still exists and that this allows dispersal to act in nonlinear ways?

The exposition dealing with temporal variability (chapters 3 through 6), its detection and interpretation, is lucid and up-to-date. The complications inherent in time-series analyses based on few data points are not likely to be resolved soon. The synthesis of meta-studies on introduced species is also extremely useful. Pimm compares this empirical literature with simulation models that also show that species-rich, highly connected communities are harder to invade. One small quarrel concerns the cause of this result. The notion (p. 185) that "the more competition, the less likely a species will be able to invade" implicitly invokes the idea that under high competition the invader is less likely to displace the resident than vice versa. But why? Competition would work in both directions and the models do not build any priority effect for residents into the pairwise descriptions of species interactions that form their core. How does this priority effect for residents emerge? Pimm's answer seems to beg the question.

The subtitle "Ecological Issues in the Conservation of Species and Communities" suggests that broad-based general models like those Pimm reviews will have utility in directing management plans for conservation. As Pimm notes in a chapter on the limitations of such models (curiously placed near the very end of the book), this is a



"Devastation caused by introduced rabbits on Round Island," Mauritius. "Goats, sheep, and rabbits are capable of causing severe damage to habitats. . . . On oceanic islands where these herbivores have destroyed the native habitat, complete reptilian or avian communities have been affected." [From *The Balance of Nature*; photograph from Ian Atkinson]

contentious issue. Some would argue that the only purpose of general models, at least in ecology, is to point out the kinds of possible ways in which nature could work. When it comes to determining how nature actually does work and managing nature at these high levels of biological organization (communities and ecosystems), empiricism, they would argue, is a more practical and fruitful guide.

On the other hand, recent experience provides at least one counter-example. Usually, even in ecological management, we must begin to answer a question with a guess. The nature of government is that we, as scientists, usually are not called in until there is some urgency. We must guess before the facts are all in. Later, we can refine our guesses by collecting more data and making our models more specific and detailed. The case of the federally listed and endangered northern spotted owl is a prime example. Russell Lande presented a very general model in *American Naturalist* in 1987. This model, really not owl-specific at all, predicted an extinction threshold such that, if habitat abundance was fragmented and reduced below it, the young searching for suitable territories amid a matrix of unusable habitat would likely die. Extinction of the metapopulation would be almost guaranteed, even though the available habitat might be sufficient to support many individuals.

Lande, the U.S. Forest Service, and other state and government agencies were guided in part by this model in creating a new management plan (published in 1990). This new plan carefully avoids the habitat fragmentation and consequential risk of extinction inherent in the previous policy.

The message is that general and qualitative models will still play a role in understanding important issues in ecology and conservation for some time to come. If you want to hone your intuition about big problems in ecology, Pimm's book is a great place to start. Though the book is not mathematical, Pimm has the professor's ability to distill the workings of complicated models into verbal descriptions that provide the essence, if not the grit. He provides profuse illustrations to explain and develop his points. This will be a entertaining and provocative book for graduate seminars.

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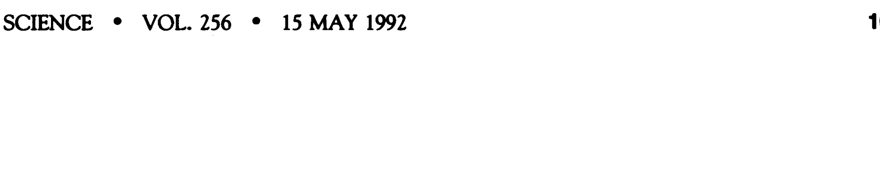
Vertebrate Transitions

Origins of the Higher Groups of Tetrapods. Controversy and Consensus. HANS-PETER SCHULTZE and LINDA TRUEB, Eds. Comstock (Cornell University Press), Ithaca, NY 1992. xii, 724 pp., illus. $95.

Representatives of the major groups of living vertebrates are profoundly distinct from each other, and this fact is traditionally recognized by according these groups the rank of class in the Linnaean taxonomic hierarchy. With the general acceptance of evolutionary thinking in biology during the second half of the 19th century, attention focused on the search for genealogical links between the various classes of tetrapods and between tetrapods and "fishes." Traditionally, paleontologists have sought to identify ancestral groups or even to trace actual ancestor-descendant sequences in the fossil record. In the late 1960s and 1970s, this approach was supplemented by explanatory scenarios for evolutionary transitions in functional terms. More recently, biologists have returned to analyzing the interrelationships of vertebrates, drawing on both morphological and molecular data. The paleontological community has generally been perceived as being rather slow to climb aboard the bandwagon of modern phylogenetic analysis, and some biologists have even come to dismiss fossils as unimportant for phylogenetic inferences. Various recent studies, however, have elegantly demonstrated that phylogenetic relationships are best inferred from simultaneous consideration of both extant and fossil vertebrates.

The present volume comprises a broad spectrum of papers by an international group of experts on the evolutionary transition from aquatic sarcopterygians to tetrapods and the origins of the major taxa of tetrapods. It grew out of a series of seminars presented at the University of Kansas in the spring of 1985; a number of chapters were subsequently added to expand the coverage.

The first five chapters present competing hypotheses concerning the interrelationships of sarcopterygian "fishes" and tetrapods. Among living vertebrates, tetrapods are most closely related to lungfishes, but the picture is much less clear once Paleozoic sarcopterygian "fishes" are also considered. Although the latter are among the most thoroughly studied of all fossil vertebrates, there is still no consensus concerning the relationships of the various major taxa of aquatic sarcopterygians to tetrapods. Chang presents a novel hypothesis of a sister-group relationship between a monophyletic grouping including all aquatic sarcopterygians and tetrapods. This phylogenetic scheme is rendered unlikely by the many derived similarities shared between tetrapods and less inclusive groupings of aquatic sarcopterygians and is rejected by other authors in this section of the volume. Schultze and Vorobyeva provide much new anatomical information on the Devonian Panderichthyidae, based mostly on excellently preserved fossils from Latvia, and argue that panderichthyids are most closely related to tetrapods. Panchen discusses the enigmatic Lower Carboniferous taxon *Crassigyrinus*, which he considers related to anthracosaurian amphibians even though several characters place this taxon close to the base of tetrapod phylogeny. Rather than attempting to examine this problem in an explicitly cladistic fashion, he opts to deliver



"Skeleton of the earliest known reptile, *Hylonomus lyelli*, from the Westphalian B of Joggins, Nova Scotia. Approximately two-thirds natural size." [From R. L. Carroll's chapter in *Origins of the Higher Groups of Tetrapods*]