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COMMUNITY ECOLOGY OF SALAMANDERS[1]

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Salamanders (Amphibia: Caudata) are often dismissed, even by biologists, as interesting oddities: small, unobtrusive animals, seemingly far-removed from the mainstream of vertebrate evolution and largely irrelevant to ecosystem function or to the development of ecological theory. In this slim volume, one of our preeminent ecologists has gone far toward correcting this inaccurate view.

N. G. Hairston is uniquely well-qualified for the task he has set for himself. It is only a slight exaggeration to state that Hairston and an outstanding cadre of his former graduate students (including D. E. Gill, K. C. Nishikawa, M. T. Southerland, S. G. Tilley, and H. M. Wilbur) have virtually defined experimental salamander ecology. Because a number of the other important researchers in this area (notably R. G. Jaeger and his coworkers) have employed approaches that are consistent with those of the Hairston "school," experimental salamander ecology forms a relative cohesive whole.

This book is, however, much more than a mere compilation of what is known about the community ecology of salamanders, for Hairston is a man with a mission: to call into question the entire body of concepts that constitutes current community ecology. Community theory, which emerged some 25 years ago with the seminal theoretical papers by R. H. MacArthur, R. Levins, and their coworkers, is considered by Hairston (p. 201) to be "unacceptable . . . too many facts must be ignored." Hairston's chief weapon in his assault on current community theory is the controlled field experiment ("the hallmark of acceptable scientific procedure" [p. 35]). Although he acknowledges at one point that field experiments do not necessarily succeed, he proceeds as if they are the only way to study ecology. Alternative approaches (such as descriptive studies, analysis of patterns of correlation, observation of uncontrolled "natural experiments," etc.) are dismissed as providing, at best, "weak inference" (p. 173). Many readers of *Evolution* may find this dichotomy between "good" and "bad" science to be overstated and needlessly stark. For all their clarity and rigor, field experiments are impossible or impractical to apply to a great many important problems. The reader is referred to T. W. Schoener's (1983) review for a more measured, though still very favorable, assessment of the role of field experiments in ecology.

Hairston begins with a very useful historical review of the development of community theory and a spirited critique of that theory's untested, and often patently unrealistic, assumptions. Although I would agree that much of current community theory seems to be a mathematical colossus that totters on empirical feet of clay, Hairston sometimes seems to go too far in his attempt to paint an unrelievedly bleak picture of the current state of affairs. As an example, he criticizes the well-known "guild concept" introduced by R. B. Root some 20 years ago, because guild specification is rather arbitrary and because not all members of some guilds can be shown to compete. But the value of the guild concept is that it focuses attention on species that exploit similar resources in similar ways, regardless of taxonomic affinity. One can then ask: which, if any, members of a particular guild compete with one another? Admittedly, "similar" is a vague term, and the question of whether two sympatric species of salamanders, both of which feed on terrestrial invertebrates, should be assigned to the same or different feeding guild can only be answered after one has defined what is meant by a similar food resource. Are all forest-floor invertebrates to be considered one general type of food, or do we wish to define different invertebrate taxa (or size classes) as forming the resource bases for different guilds? The point is that the investigator is the one who must set the limits of guild membership in any specific case. Some guild members may compete intensively at all times; others may compete weakly or intermittently; and some may not compete at all. That such a range of interactions is in fact revealed in the studies of salamanders reported by Hairston is hardly an indication that the traditional guild concept is "wrong" or useless—only that it is not restricted to species that show strong competition.

Chapter 2 contains a review of equilibrium and stability in natural populations. Here, Hairston argues persuasively that terrestrial salamanders are more likely than most other organisms to satisfy the assumption of equilibrial population levels that underlie many mathematical models of ecological communities.

In Chapter 3, Hairston presents a well-organized summary of life histories in the three major ecological groupings of North American salamanders: pond-breeding species, fully terrestrial species, and stream-side species. Much of the material in this chapter will be familiar to specialists, but others may be surprised to learn, for example, that most species of salamanders lack an aquatic larval stage or that well over half of the world's salamander species occur only in the New World tropics.

Chapters 4, 5, and 6 summarize the results of field experiments aimed at clarifying the role of interspecific competition (and, to a lesser extent, predation) in salamander communities associated with freshwater ponds, terrestrial sites, and streams, respectively. Although results vary somewhat from one group of species

[1] *Community Ecology and Salamander Guilds.* N. G. Hairston, Sr. Cambridge Univ. Press, N.Y. 1987. x + 230 pp. $54.50.

to another, some general patterns emerge. Intense, density-dependent, interspecific competition or predation (or both) are common in communities of pond-dwelling salamander larvae. Less intense competition, but not predation, occurs regularly in terrestrial salamander communities, but only between morphologically similar species. Streamside salamanders (studies have so far been virtually restricted to *Desmognathus*) show both predatory and competitive interactions, depending mainly on the size differential between coexisting species.

One of the most interesting and useful aspects of this book is Hairston's detailed discussion and integration of the series of elegant field experiments that he and his students and coworkers have carried out in the southern Appalachians on *Plethodon* and *Desmognathus*. These studies are perhaps unique in their clear design, broad scope, and longevity (some manipulations were continued for as long as eight years). Furthermore, as pointed out forcefully by Hairston, they have indeed provided clear-cut evidence for the existence of interspecific interactions that could not have been obtained in any other way.

Still, in interpreting the outcomes of these now-classic experiments, Hairston is driven to offer ultimate causal explanations that I found curiously "soft," especially in comparison with the rigorous experimental and empirical stance assumed throughout the book. Hairston rightly inveighs against the tendency of some community ecologists to see competition everywhere. Where properly designed field experiments do indeed demonstrate the existence of competition, he argues that aggressive interference, not exploitation (i.e., niche partitioning), is the operative mechanism, at least for terrestrial salamanders. While the evidence for widespread territoriality and aggression among terrestrial salamanders is now quite extensive, Hairston's dismissal of the possibility of competition for food in terrestrial salamanders seems to lack a firm empirical basis. Simply to assert that all six or seven sympatric species in two local salamander assemblages do not partition food because they all appear to prey on the same general class of food items (insects and other invertebrates) is unwarranted. The salamanders in these Appalachian communities encompass a rather wide range of body sizes, and size-specific or taxon-specific prey selection has now been demonstrated in a sufficient number of salamander species that indiscriminate predation cannot be assumed in the absence of specific evidence to the contrary. Diets of sympatric salamander species typically show considerable overlap but also show significant differences, as in fact Hairston and his co-workers found in the diet study they performed (on *P. jordani* and *P. glutinosus*). Of course, the fact that interference competition may exist does not imply that exploitation competition is unimportant (or vice versa); indeed, a likely scenario for small and fairly generalized predators such as terrestrial salamanders is that both kinds of competitive mechanisms operate simultaneously (Schoener, 1983). Furthermore, because the ultimate purpose of interference competition is to assure access to a critical resource, the question remains: what resource is the basis for interference competition? Without presenting supporting data, Hairston suggests that nest sites may be the critical resource that is in short supply for terrestrial salamanders. Almost nothing is known of the detailed nesting requirements of the species in question (as an example, nesting sites of *P. jordani* have never been observed), so this explanation lacks force. Moreover, some terrestrial salamanders (e.g., *P. cinereus*) defend cover objects (which also serve as prey refugia) when surface conditions are dry and prey are scarce but not when conditions are moist and prey are widespread and abundant. *P. cinereus* does not deposit its eggs under such superficial cover objects, so it can hardly be defending nest sites in the situation just described.

Chapter 7 deals with long-term (i.e., evolutionary) changes in salamander communities, with most attention being given to the evolutionary effects of competition. Here, Hairston describes the results of translocation experiments on *Plethodon* that have clearly demonstrated geographical differences in competitive ability. *P. glutinosus* from an area where its distribution has little altitudinal overlap with that of *P. jordani* (a competitor) are competitively superior to *P. glutinosus* from another area, where overlap with *P. jordani* is extensive.

In the final chapter, Hairston suggests that a greater role should be played by salamanders in future ecological research. Reiterating his conviction that current community ecology is seriously (perhaps fatally) flawed, he recommends rigorous experimental testing for the existence of competition in natural communities, with special attention being given to distinguishing the effects of resource competition from those of interference competition and predation. Several specific opportunities for future field and laboratory research on salamanders are described. Finally, Hairston uses existing data and informed speculation to comment on the possible functional importance of salamanders in terrestrial ecosystems. Again, nonspecialists may be surprised to learn just how abundant salamanders are in some temperate zone forests, where they can exceed birds and mammals in numbers and biomass. It is suggested that terrestrial salamanders may play a significant role in cycling mineral nutrients in forests.

This book is essential reading for graduate students and professionals interested in community ecology. Despite a few rhetorical excesses and an occasional failure to back up sweeping statements with empirical data, Hairston has succeeded in writing a compelling, well-integrated exposition that will stimulate discussion and, one hopes, new research. The writing style is a personal one, i.e., blunt and sometimes a bit scornful of opposing viewpoints, but never vituperative in tone. I mention this last point only because it stands in such refreshing contrast to some of the other recent literature on the status of community ecology. I recommend this book highly and regret that its relatively high price will put it out of the reach of many students, who would most profit from owning it.

Literature Cited

Schoener, T. W. 1983. Field experiments on interspecific competition. Amer. Natur. 122:240–285.

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