

## Pursuit of a Possible Dream<sup>1,2</sup>

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In his own research Hairston has attacked the seemingly impossible with aplomb and has attained considerable success with some pioneering field experiments on competitive interactions among salamanders. His research has been a model and inspiration for many students of salamander natural history who have come after him. This logistically intractable group of animals has traits that are nearly the opposite of those looked for in an ideal experimental animal: terrestrial species are active on the surface only on moist nights; not all individuals are typically active at one time; their food is mobile; they eat what they can catch except perhaps at times of excess, when they are more selective; their pace of life is extraordinarily slow (rendering breeding or growth experiments difficult because of the time involved); they are difficult to mark as individuals; and their retreats cannot usually be determined without disrupting the microstructure of their habitat. Nevertheless, salamanders increasingly tease the creative imaginations of young researchers, who are taking their questions about life history, foraging or defensive behavior, and competitive interactions into the field to answer by controlled experimental and observational techniques.

Over the last two decades research on salamanders has taken its place in generating and testing ecological and behavioral theory, a fact that Hairston acknowledges but does not discuss since much of this research does not contribute directly to his main topic. He focuses on competition and predation as agents in structuring salamander guilds. His book is not a comprehensive review of salamander ecology but a selection of work relevant to this focus. Hairston uses salamanders to emphasize the importance of experimentation for deciphering community structure rather than using them to develop an understanding of how their communities evolve. While he succeeds in making an eloquent and successful plea for experimental studies, he fails somewhat in providing a coherent picture of salamander communities and their evolution.

The tension between an "observational" and "experimental" approach to testing theories in community ecology centers on the adequacy of the controls used: even field experiments can be rigorously controlled whereas comparative observations usually leave much to doubt in the adequacy of their controls. Theoretically, either approach can be equally as rigorous as the other. In practice, an observational approach may be more difficult in terms of finding the appropriate controls, but if Hairston is right that the experimental work on sunfish he cites is the best to date in showing that competition can lead to niche partitioning, then experiments have yet to prove their superiority in furthering our understanding of community structure. Some observational studies have been as strong as these experiments in suggesting that niche differences have been the result of competition.

Hairston begins with a theory and selects works that bear on it: the method which philosophers used to tell scientists to use. My preference is to synthesize what is now known about the biology and develop or reject theories from this knowledge. I admit the difficulties in acquiring the necessary basis for this approach, though. Ideally, the interaction is two-way, with data suggesting theory and theory suggesting data to collect. I have found this approach successful and see some of it in Hairston's own work, which does

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<sup>2</sup>Community Ecology and Salamander Guilds.

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rely a great deal on good 'old-fashioned' natural-history observations. Unfortunately, much of the real flavor of his published research dims in this pursuit of a somewhat outdated theoretical ideal.

Hairston aims his critique at the theoretical school initiated in 1957 by Mac Arthur. Prior to this time ecological theory was either vague or limited by the ability to formulate experiments to test theories. What happened in the 1960's was a rediscovery of the method of Darwin and other keen naturalists -- the use of the comparative approach to gain insight into the evolutionary mechanisms responsible for the observed patterns. In addition to the verbal arguments used prior to this time, theories incorporated mathematical models that could make quantitative predictions of what should be seen in nature if the models were correct. An orgy of going out to collect the relevant data resulted in a great deal of poor natural history, because many of these new-style 'naturalists' ignored all but the factors relevant to test a theory. Sloppy theories which fail to make explicit all of their underlying assumptions, combined with sloppy data collected to test these theories, do not render the approach invalid or even less powerful than the experimental approach to theory-testing and -development which Hairston favors. In trying to resurrect this older approach to community ecology, Hairston glosses over or ignores the limitations and difficulties with experiments. The experimental approach works more easily in the laboratory, where all relevant aspects of a (more artificial) system can be monitored.

With admirable stubbornness Hairston tries and succeeds in convincing us that one of the most intractable of experimental animals I know of can be naturally manipulated to test ecological theories. This is an important achievement. The theoreticians who have relied primarily on comparative data collected easily and quickly in brief bursts of activity are shown to have no basis for not doing experiments. Comparative data are quick to gather, analyze and publish whereas adequate experiments require much labor and years of waiting before the results can be usefully published even in preliminary form. The years of the 1960's were ones of academic growth in the sciences but also with the prospect of accommodating the baby boom; a lot of money finally became available and there seemed to grow an urgency to obtain tenure or degrees before funding ran out. Moreover, the physical sciences were achieving more prominence; the more precise and analytical, the more like the physical sciences ecology could be made, the greater its chance to capture the attention of other scientists. Physicists or mathematicians joining ecology became more common as the former recognized that the latter could be nearly as rigorous a science; ecology was no longer thought to fall into that ambiguous region between the soft and hard sciences.

Unfortunately, all aspects of biology belong to that messy region because biological systems, particularly ecological ones, have histories which influence the present state of the system at least as much as do basic principles. The basic mechanism of the evolution of living systems is natural selection, which is historical by nature. Evolutionary history had to enter ecology and it did so in a haphazard way. Hairston does not address this aspect, which is peripheral to the antagonism which has existed between the theoretical and experimental schools of community ecology in the past several decades. Systems ecology, another approach to understanding communities, is essentially ignored in this work, in particular because it has little bearing on the way one taxonomic guild contributes to community structure.

Although Hairston's arguments are reasonable, their restricted focus limits the value of his critique of community ecology because these issues, although not yet relegated to history, are slowly becoming so as new ideas wiggle into the field. The work has considerable historical interest but does not integrate enough of what might be important in the near future. In particular he neglects the more evolutionary approaches that offer a somewhat different way of attacking community structure than he covers here and hints of which would have added to the value of this treatise. Hairston's choice of theories is broad, particularly as some have not used salamanders as tests, but his review is not very thorough and is somewhat biased as a result. For example, the most convincing work that he cites on niche partitioning has admitted flaws (cf. Maiorana 1977) and yet he does not use this to demand more thorough work to justify this approach. Somehow one gets the

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feeling that poor experiments are superior to poor observations; such a viewpoint can be dangerous in the advancement of a field where first principles are not well established and where the basis for evaluation is still so primitive.

The main models which Hairston critiques are the following:

--*Limiting similarity and Hutchinsonian ratios:* Hutchinson's use of a few examples to suggest a mathematical theory of limiting similarity inspired Mac Arthur and Levins' more theoretical attempt several years later. Unfortunately, Hutchinson's production of a 'magic' number based on 13 observations misled the gathering of inappropriate data to test the underlying mechanism of limiting similarity. It is not the ratio of size difference that is of importance but the overlap of the size distributions of two species (Maiorana 1978a). Because size variation is more difficult to obtain either from the field or from the literature, this point has remained understudied despite its central place in theory for over two decades. Data I have been collecting (now thousands of congeneric pairs) support these theories and negate the conclusions derived from the null tests used by Roth (1981) and Simberloff and Boecklen (1981).

An important point that has been overlooked in interpretation of these 'null tests' is that size displacement is only one of the multiple niche axes that species use to be different. Unless one also knows about other possible axes in niche space along which species may diverge, values of complete or almost complete overlap may be causally irrelevant to tests. How does one decide from simple size data without insight into the natural history of the species concerned? A compilation derived from taxonomic description of species indicates that the problem may not be as formidable as it could be; indirect evidence, if voluminous enough and not extrapolated beyond its limit, can give insight into communities. Museums were once the depositories of much information on community structure and they still house in dusty tomes and specimens a great deal of information of potential importance to community studies in a way which Hairston does not recognize.

Because size displacement is a basic element of the guild structure of salamanders (see below), theory that stresses its importance to community structure should not be dismissed as lightly as Hairston has done, particularly considering the lack of thoroughness of his review. My own examination of this literature suggests that a particular compilation of uncontested facts can lead to different conclusions depending on one's initial theoretical orientation (see Maiorana 1978b or 1978c as examples in a different area of ecological modelling).

--*Food webs and trophic structure:* An inevitable and perhaps even defining aspect of a community involves 'who eats whom'. In a perfectly pacific world all individuals would be content to 'soak' up the rays of the sun and leave others in peace. The problem comes when too many try to occupy the 'beaches' of sun absorption and competition exerts its influence. Some 'fight' by building structures to get higher than competitors while others discover they can simply feast on the 'sun bathers' directly (and so predation is born). One of the more striking aspects of my own research on salamander diets was how much it revealed about the behavior of the litter community with which terrestrial salamanders compete and on which they feed. Diets (Maiorana 1971, 1978d) prompted questions about the organization of litter communities (Maiorana 1974) that I am still pursuing. Properly interpreted salamander diets are as valid as pitfall traps in assessing the behavior of fauna within their size range.

Hairston gives only token recognition to the importance of food webs in community structure despite his own seminal contribution to the topic (Hairston, Smith and Slobodkin 1960). At one level of analysis salamander guilds are at the same trophic level, with the minor exception of larger ones eating the smaller ones that happen to cross their path. At another level, the potential for salamander to eat salamander is extremely important to the topic of salamander communities despite Hairston's dismissal at the end (p. 192). Many observations of salamander communities suggest possible predation as an organizing factor even if a larger salamander can only ingest part of a tail. Stomach observations show few examples of 'cannibalism' where lab observations indicate no inhibition of eating another. In his first chapter Hairston only mentions the theoretical work concerning the stability that a food web gives to a community (Cohen 1978, Pimm 1982). He

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is short on his criticism of assumptions of these models despite the fact that the entities that are entered into the analysis do not represent single species or populations. One species can appear on several trophic levels, as do virtually all salamanders. Making evolutionary sense of such a web does mean sorting the elements into independently evolving units. One criticism that Hairston raises for these models (take the competitive interactions of the producers cannot be considered) is probably valid for them but not for other potential models for the evolution of food webs. For example, the competition among terrestrial plants may influence very much the structure of the two main trophic levels that feed upon them (Maiorana 1985, 1990, and in preparation).

--*Loop Analysis*: I find this topic somewhat strange to include in a brief review of community ecological theory relevant to salamanders (an inference based on some non-inclusions), except that Hairston tried to use it to analyze his own data. His very brief critique of this theory and its failure to be incorporated into or to inspire subsequent research seems to toss it into the bin of historical relicts. Might it nevertheless represent a true insight into community structure that can be translated into one that can be obtained in messy but rigorous ways from nature? Can it even be transformed into a feasible lab or field experiment involving some known organism? Hairston gives no hint and I become frustrated because I cannot translate this theory to actuality and yet I have a feeling it has some value even if transmuted.

--*Null Hypotheses*: Although a popular way to criticize another's insight into the structure of ecological communities, the so-called 'null hypothesis' is often not really the null state but an alternative explanation. In a biological system why should randomness prevail over order and can one even demonstrate randomness if one fails to find a difference from an apparently 'null' state for a particular case or even for many? Does such negation prove a mechanism of natural selection invalid? Selection and randomness often lead to the same broad statistical conclusions, so one must manipulate or refine the statistics to prove one or the other case. Take for example the number of herbivore species associated with trees of various geographical ranges in contrast to the number of species of any taxon as a function of area occupied. On log-log plots there appears to be a similar relationship; on arithmetic plots, the predators on trees have an upward swing in numbers while colonizers of islands have a downward swing (Maiorana 1979, and in prep.). Trees with large geographic ranges and abundance get a disproportionate share of herbivores whereas islands became quickly saturated with species in a particular taxon as they increase in size.

Hairston recognizes these problems in a vague way and focuses his explicit discussion on an example he could personally discuss with information from salamanders. He picks the annoying case of species per genus. His criticism of assumptions have assumptions of their own which he seems not to recognize. One glaring omission is that of the influence of body size on the number of species per genus, a problem which has been discussed widely and which is related to theories of community ecology not covered here. One can use species-to-genus ratios to prove so many points in community ecology that the ratio has little meaning unless a particular point is being addressed. For example, I can criticize his statement that the species in more speciose genera are more variable geographically in their morphology, ecological tolerances, etc. than are those in monotypic genera. On the single measure of body size (perhaps the most objective and widely available indication of ecological difference we have yet found), one can find the entire spectrum of possible cases for the size diversity at one taxonomic level and that at another, depending on the animals and taxonomic levels chosen for illustration. In pursuit of evidence which vindicates the idea behind Hutchinsonian ratios, I found puzzling the fact that within species insects commonly have a large range of body size but the dispersion of the mean body sizes of species within a genus was often extremely low (Maiorana, in prep.). A distinct body plan can become only so divergent in size before it becomes different enough in shape (for maintenance of functional integrity) to warrant assignment to different taxa. Because insects are extremely variable in body size as species, they cannot diverge much along a size axis; species diverge ecologically in other dimensions. In contrast, taxa with low size variability as species (e.g., birds and mammals) can assort themselves more widely along a size axis.

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Patterns of taxonomic dispersion may be informative when one also considers the biology of the organisms of interest. As Hairston rightly claims, communities and guilds (and even niches which he does not mention) are ambiguous in synthetic or theoretical work because each case is probably differently defined. Is it difficult to talk explicitly and say what we mean? Even *r-K* selection can have slides or dips which can be recognized and described (Maiorana 1976, 1990). One does not have to pigeon-hole every observation neatly into a few categories. Nature is fuzzy in its boundaries. The more important problem is defining the component part of the Earth's ecosystem that one is using in one's analysis. It is perfectly valid to define or delimit this component as one likes to make a point. For example, to find relevant data to test an idea about the evolution of carnivore diversity, I had to define a carnivore in a more limited way than usual, restricting my category to those species that feed primarily on others of their own higher taxon (Maiorana 1991).

I think Hairston's problem here stems from his lack of incorporation of the evolutionary perspective. Communities are the products of natural selection and one cannot experimentally show now the results of a competitive interaction that occurred long ago. How can Hairston's approach find competition between two species that no longer compete because they occupy nonoverlapping areas in niche space? They can still be of the same guild for analysis because they represent an insight into past competition. Living with cats and people stresses the point to me that the entities we classify, somewhat ambiguously and differently, as guilds or communities reflect individual interactions; a behavioral ecologist would give up watching individuals which did not interact. In community ecology identifying these noninteraction parts of guilds may often be possible only by experiment. Lack of interaction can be just as interesting as interaction but the former is more difficult to discuss. To watch and watch and see nothing may eventually translate into a search of the past for the causal explanation. Paleoecology has become a thriving area as ecologists realize that a lot of what they describe now was caused in the past.

The time has come to unscramble a lot of nonsense about community ecology. As humans destroy more area of 'natural habitat' every day than any scientist can survey in a lifetime, we need to develop some perspectives on organismal diversity that can encompass our own selective impact. Perhaps now is a time for a new understanding of community ecology as we realize that humans are a natural product of evolution and proceed along lines predicted from natural selection. The only problem is that we may exhaust the Earth.

Hairston attempts to stir up our thoughts on community interactions. Although he may often be inaccurate, misleading, or simply wrong, he provides a focus of thought, details to tear one's teeth into to wrestle out new ideas. The way he has stimulated a synthesis of a part of my own work in this review is a measure of the impact that this treatise may have. If not aroused, intrigued, exasperated, or even confused, a reader may die of boredom.

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