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Ecological Communities

Conceptual Issues and the Evidence



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Edited by

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This book is dedicated to
RICHARD P. SEIFERT
whose critical experiments
with natural communities
are a model for
contemporary ecology.

Preface

Ecological communities are groups of species living closely enough together for the potential of interaction. Various levels of ecological effect might result from interactions that do occur, from slight, intermittent influences to intense, enduring ones that are so profound as to lead to regulation of the interactant populations. We organized a symposium, held on March 11, 12, and 13, 1981, at Wakulla Springs, Florida, to emphasize the tremendous range of possibilities for organization and working of different communities; this book is the result. Species might compete with, prey upon, parasitize, or infect one another, or even aid one another mutually. However, all possible interactions do not occur, and those that do need not be intense or persistent and need not be cybernetic, nor need they have enduring evolutionary effect. One possibility that we expect to obtain fairly commonly is the community with so few strong interactions that organization arises primarily from mutually independent autecological processes rather than from synecological ones. Such communities would not be holistic entities, but rather just collections of relatively autonomous populations in the same place at the same time. Independent coexisting populations would likely be exposed to some of the same exogenous forces, such as the weather, but equally likely their reactions to externalities would be sufficiently different to make knowledge of each species' autecology necessary to an understanding of the group as a whole. Thus, good population ecology is a basis for good community ecology.

The contemporary questions in community ecology concern the existence, importance, looseness, transience, and contingency of interactions. Which interactions actually occur? How do interactions vary among species, environments, and locales? What fraction of ecological interactions between species have any enduring influence upon morphology, behavior, or reproductive phenotype? How do different kinds of interactions among a group of coexisting species—predation, disease, competition, etc.—meld for some net influence? The most profound issue of contemporary ecology, indeed the issue that may most distinguish ecological phenomena from those of finer levels of biological organization, stochasticity, makes deductive answers to all of these questions doubly

difficult to find. Are interactions among species substantially changed by externally imposed fluctuations in exogenous factors such as the weather or casually associated predators? What influence does the inexorable wander of climate have on interactions with subtle effects, which may take many generations to work their influence on species?

The key to resolving these conceptual issues is evidence. We have emphasized evidence as a topic of this symposium because community ecology does not have a strong tradition of using the diversity of evidence that has been so powerful in other disciplines. Sciences that have progressed rapidly (physics, chemistry, molecular biology) have made great use of sorts of evidence that ecology has not, of vigorous hypothesis testing and experimentation. Vigorous hypothesis testing maximizes the potential of falsifying ideas. In contrast, much of community ecology has often been content with generalized mathematical theory and passively (rather than experimentally) collected observations. Most important, mainstream community ecology has accepted confirmatory evidence almost exclusively. One conventional approach to community ecology is to seek corroboration in broad patterns among species for the generalized theory of competitive relations among species. Confirmation of the orthodox "neo-Malthusian" view, that interspecific competition for limited, depletable resources is the prime factor in community organization and evolution, has been inferred from observational data of many sorts, e.g. from relative abundances of species, their taxonomic mixes in communities, their relative morphologies, etc. (Hutchinson, 1978).

Certainly, rapidly progressing sciences have used confirmatory evidence too, but of a fundamentally different sort than is traditional in community ecology. In physics, E. Rutherford's experiments showing heterogeneous scattering of alpha particles by metal foil corroborated a planetary, non-homogeneous model of the atom. In molecular genetics, experiments showing semi-conservative reduplication of DNA corroborated the double-helix model of the genetic material. The fundamental difference is that these classic corroborations were of surprising, "risky" theoretical predictions, whereas those in conventional community ecology are not. "Riskiness" of a theoretical prediction is a characteristic argued by Karl Popper to be a key to vigorous science, and we agree. The risk of a theoretical prediction increases with the number of distinct, possible, qualitatively contrary outcomes for an experiment. *A priori*, alpha particles could have been scattered homogeneously, to imply a very different sort of atomic model from that implied by Rutherford's experiment. Before the experiments, replication of DNA could have been found to be at either extreme, conservative or semi-conservative, or some fraction in between. The important feature of the experiment was that it had tremendous potential to falsify the double-helix model.

In community ecology, we have learned that there is little general risk for the orthodox competition theory in broad interspecific patterns in nature; the gamut of possible patterns are all seen as supporting the theory. Classic examples of this approach are the inference that competition, albeit in different forms, causes the different shapes of observed relative abundance curves of species in large samples. In this volume, Colwell and Winkler correctly point out that correlations of dispersal success with taxonomy can result in morphological patterns among species that do not reflect the effects of interspecific competition on character displacement. This is a result adumbrated by Grant and Abbott (1980). Thus, interspecific patterns alone are no risk for competition theory, and conversely, interspecific patterns are only the softest corroboration of the theory. Without hard evidence on the existence of interspecific competition, its intensity, endurance, and ability to overcome the influences of other factors, and most importantly, without hard evidence on the ability of competition to cause morphological differences between species, the first link in the necessary chain of evidence for establishing competition-caused character displacement as a general property of communities is missing. Equally important, hard evidence is needed on how other factors, such as dispersal, can modify any previous interspecific patterns among species. Although hard evidence on these crucial questions has not yet been produced, we hope that the acute scrutiny that this particular facet of community ecology receives in this volume will stimulate critical studies.

Of course, that much evidence in community ecology to date is but "soft corroboration," with little potential to falsify theory, does not mean that the theory is incorrect, only that the evidence is flimsy. The difficulty of experiments on communities, deriving from the large number of simultaneously relevant variables, the sometimes vast scale, and often long periods of time that must be accommodated for meaningful data, means that passively obtained observational data will continue to play a role in our science. So, one of our major goals for this symposium is to include discussions of the most critical possible means of dealing with non-experimental data, of tests that can potentially falsify theoretical predictions, even when manipulation and experimentation are impossible.

However, we believe that the most powerful means of critically testing propositions in community ecology is just that which has proven most powerful in other fields, experimentation. However, doing experiments in ecology is not just like doing them in other fields. Community ecology's uniqueness lies in the extraordinary diversity, variation, and heterogeneity of its objects of study, and in their historical legacy accumulated through evolution. Individual organisms, populations, species, and communities all are many orders of magnitude more variable internally than are the objects studied in physics, chemistry, or molecular biology, and the art

in our science must reflect the difficulty of dealing with this variability. Differences among individuals such as age, sex, and nutritional condition are extremely important to how populations function, and likewise up through communities and ecosystems. Slight differences among species in trophic habit, ecological amplitude, and life history greatly affect the likelihood, intensity, and persistence of interactions among species. Most challenging, the stochasticity of the external environmental further varies population and community behavior. The same species in different environmental circumstances may have quite distinct ecology and influences upon other species. These contingencies mean that powerful experiments in community ecology must take into account autecology and natural history. Knowledge of autecology and natural history concerns species particulars and idiosyncracies, and only with this knowledge can experiments in community ecology reflect the actual influences of interactions among species.

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*Tallahassee, Florida
May 1982*

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Introduction

An Overview: Real and Apparent Patterns in Community Structure

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"Two noticeable characteristics of papers recently published are the widespread interest in field quantitative methods in the study of population density, rates of spread, fluctuation, reproduction, feeding, or mortality; and an increasing awareness of evolutionary dynamic problems such as selection and competition. At the same time there is a general adoption and a tightening up of the statistical treatment of ecological data, which, though entirely sound and necessary, would become a partly bad feature if it tended to exclude the equally valuable type of observations on the pattern of nature, and the habitats and distribution of animals, that ecologists and naturalists can contribute." (Elton, 1947)

INTRODUCTION

In 1944, the British Ecological Society held a symposium on "The Ecology of Closely Allied Species," at which Lack, Elton, Varley, and others used various lines of evidence to argue that competition is a major factor in structuring plant and animal communities. Others argued to the contrary, with Diver contending that "the mathematical and experimental approaches had been dangerously oversimplified and omitted consideration of many factors [including] sources of energy and their relative availability, predator attack, mobility, population structure and growth, individual growth rate and bulk, relation of life cycle to annual cycle, range of tolerance, means of dispersal, and the like" (Anon., 1944). He concluded "there was little direct evidence that cohabitation or separation of related species was determined by space and food, since other factors usually kept populations below the point at which serious pressure was developed." Broadly similar themes dominated the celebrated Cold Spring Harbor Symposium in 1957, with some arguing that density-dependent effects arising from biological interactions are of predominant importance in setting population levels, while others argued the importance of the density-independent regulatory effects caused by the weather and other

environmental factors. The Brookhaven Symposium of 1969 on "Diversity and Stability in Ecological Systems" again drew together many of the contemporary leaders of the subject; I think it gave a less polarized and more synthetic account of the issues, although (as the title itself suggests) there may have been too much of a tendency to view communities as orderly, patterned "systems." The present volume stems from a conference held at Wakulla Springs in 1981, and the same themes still interweave, albeit now greatly enriched by a rapidly expanding body of field observations, carefully planned experimental manipulations in the field and laboratory, and more rigorous techniques of statistical evaluation of the data. Whether these themes are drawing toward their resolution, or whether we are still in the opening passages of the work, is for the reader of this volume to decide.

An eager and naive pattern-seeker might note that these landmark meetings are regularly spaced, with a 12-year period, and might even go on to speculate on the underlying cause of this cycle (12 years is roughly the time from entering graduate school to the tenure decision?). This is silly. The "cycle" does, however, serve to illustrate one central concern of the Wakulla Springs Conference: given some apparent pattern in the organization of an ecological community, does it really derive from biological interactions among and within species? Or is it the sort of coincidence one often finds when the data are few? Or may the investigator have produced it, unconsciously, by making observations or designing experiments to conform to a preconceived notion? Or may the pattern simply be a statistical property of the system—a true pattern, but having no biological significance? Such questions, involving the disentangling of real from apparent patterns, occur in many other areas of science (see, for example, the debate between Arp and Bahcall (1973) on whether there are, or are not, significant spatial associations between astronomical objects with large but different red shifts); the questions are rarely easy to answer.

The apparent 12-year cycle is spoiled by, *inter alia*, the meeting on the "Ecology and Evolution of Communities" held in 1973 as a memorial to Robert MacArthur (Cody and Diamond, 1975a). Unlike the more wide-ranging meetings mentioned above, this one was mainly concerned with those areas, and that style, where MacArthur's own contributions had been so stimulating: field observations and theoretical models aimed at understanding how communities are structured by biological interactions, particularly competition. In some ways, the 1981 Wakulla Springs meeting represents a healthy reaction against too enthusiastic and uncritical an acceptance of some of the "pattern-seeking" field and theoretical studies of the two past decades. One technique, set out in some recent papers in this volume and elsewhere, is to construct "neutral models" or

“null hypotheses,” which aim to elucidate those apparent patterns that might be exhibited when comparisons are made among a given set of communities, assuming that some, or all, classes of biological interactions are absent. Insofar as comparative studies of real communities yield patterns beyond those found in such neutral models, one can be more confident that community structure is indeed being forged by particular kinds of interactions among species. More specifically, neutral models are being employed in an effort to see whether biologically based patterns must necessarily be attributed to competition, or whether predation or other effects (including, I would emphasize, pathogens or parasites) could equally well be the cause.

Although the phrases null/neutral hypothesis/model are characteristic of the relatively recent literature, the essential ideas have been applied in various contexts in community ecology over the years. (Indeed, any assignment of a significance level to a regression line is explicitly a statement about the rejection of a null hypothesis.) Unfortunately, an appropriate null hypothesis is not always easy to construct; in particular, a proper neutral model may require data that simply are not available. It is just as easy—and just as foolish—to construct an inappropriate or misleading neutral model as it is glibly to deduce evidence for competition from data that are susceptible to other interpretations.

In what follows, I briefly outline a miscellany of examples in which (whether or not the contemporary phraseology is employed) neutral models have been used in the hope of elucidating theoretical or empirical aspects of community structure; some of these examples are covered in more detail elsewhere in this volume, although most are not. Most of these vignettes are complex, and do not admit of Manichean division into white-hatted and black-hatted people. To my mind, no simple moral emerges from these tales, other than the broad injunction that alternative explanations in general, and appropriate neutral models in particular, should always be kept in view when experiments are designed or data analyzed.

I must emphasize, most strongly, that the contents of this introductory chapter do not accurately reflect the amounts of time spent on various topics at the conference itself. One of the main aims of the conference was to focus on analytically designed field studies that test theoretical ideas. Many of the papers did just this, presenting interesting and previously unpublished data (as, for example, in the chapters by Lawton, by Strong, by Rey, and by Grant and Schluter). Although such case studies predominated at the conference, and form the bulk of this consequent book, many participants' clearest memories will be of the disagreements—good-humored but nonetheless sharp—over theoretical and methodological issues; my chapter dwells exclusively on these issues.

NUMBER OF SPECIES PER GENUS

At the British Ecological Society meeting in 1944, Elton presented an analysis of 55 animal communities (including some parasite ones) and 27 plant communities, each from a relatively small geographical area. He showed that, in these communities, the average number of species per genus (the " S/G ratio") was markedly smaller than that for faunal lists from any large region, and attributed this difference to "existing or historical effects of competition between species of the same genus, resulting in a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to coexist permanently on the same area of the same habitat" (Elton, 1946).

C. B. Williams (1964), however, subsequently pointed out that it is a property of the statistical distribution of species among genera that, as the number of species and genera in a sample decrease (as they will when one goes from a larger region to a smaller), the ratio S/G will decrease. More recently, Grant (1966b) and Moreau (1966) have sought to find evidence for competition in the smaller S/G ratios observed for birds on islands or in restricted habitats, while Simberloff (1970) has given an incisive analysis (including extensive numerical simulations) to show that just such decreases in S/G with decreasing S are mathematical properties of the S - G distribution.

This cautionary tale is fairly straightforward. Although the observed S/G pattern appears to be just what one would expect if communities are structured by competition, closer examination shows the pattern to be primarily a statistical artifact, a mathematical property of the way the average S/G ratio varies with S . Insofar as the observed S/G patterns do differ slightly from mathematical expectation, the S/G ratios in restricted habitats appear to be relatively high rather than relatively low (the data points tend to lie slightly above the line derived from the null hypothesis); a more full discussion is given by Strong (1980) and by Simberloff in this volume. Notice that, as Simberloff has repeatedly emphasized, the explanation of the S/G pattern by a null hypothesis does not mean that competition is necessarily unimportant in determining which species co-occur in the communities studied by Elton, Grant, Moreau, and others; rather, it means this particular line of inquiry simply sheds little light.

STABILITY AND COMPLEXITY

The idea that complex ecosystems, with many species and a rich web of interactions, should be more stable than simple ones is an intuitively appealing one; it may seem that a community is better able to cope with

disturbance if there are many alternative pathways along which energy and nutrients may flow. Elton (1958) advanced a set of six arguments in support of this notion that complexity begets stability. One of the six was a theoretical argument and consisted of the observation that mathematical models of simple prey-predator associations exhibit instability (Elton had in mind the neutrally stable Lotka-Volterra model for one prey and one predator, and the unstable Nicholson-Bailey model for host-parasitoid interactions). Whatever the status of the other five arguments (May, 1973, pp. 37–40, 173), this theoretical observation is meaningless until one has determined the stability properties of the analogous models with many predators and many prey. Such multispecies models turn out, in general, to be less stable the more species are present. That is, increasing dynamical stability is not a general mathematical consequence of increasing complexity; rather, the contrary is true.

I think this example belongs in a broad discussion of the uses of null hypotheses, because it provides an illuminating instance where an attractive idea was long accepted (and still is in many Introductory Biology texts) on the basis of logically incomplete arguments. Real communities, of course, are not random selections from the universe of general mathematical models, and the current task is to try to understand the special structural features that complex ecosystems may possess to help them reconcile stability with complexity. Are apparently complex tropical ecosystems actually constituted of many loosely coupled subsystems (Gilbert, 1977; Root, 1973)? Do dynamical considerations constrain the length of trophic chains (Pimm and Lawton, 1977; DeAngelis *et al.*, 1978; Lawton and Pimm, 1978)? Is “donor control” (DeAngelis, 1975), or the character of predators’ functional responses (Nunney, 1980), or some other feature, crucial in distinguishing real food webs from those that may seem possible in general? Or may it be that complex ecosystems really are typically more fragile, being found only in environments where disturbances are typically less severe or more localized than is the case for simpler ecosystems (Wolda, 1978; May, 1979)?

The example is also interesting for the light it sheds on the generation of hypotheses, null and otherwise. It is lunacy to imagine that the dynamical behavior of real communities bears anything but the vaguest metaphorical relation to the linearized stability properties of the conventional “community matrix” (Levins, 1975; May, 1973). But analyses of abstract community matrices have led to the generation of new ideas and the framing of testable hypotheses, such as those about the patterns of connectance in real food webs (Yodzis, 1980; Rejmánek and Starý, 1979), about the lengths of trophic chains, about the structuring of communities in terms of subunits or guilds, and so on. Some of this work is developed more fully in the chapters by Pimm, Auerbach, and Lawton.

PATTERNS IN THE RELATIVE ABUNDANCE OF SPECIES

An interesting attempt to employ neutral hypotheses in the exploration of patterns of numbers and relative abundance of species in communities is by Caswell (1976). He begins by attempting to determine the likely distribution of relative abundance of individuals among S species, assuming *no* biological interactions among them. Comparing these "neutral" distributions of species relative abundance with real distributions for birds, fish, insects, and plants in tropical and in temperate zones, Caswell finds real communities to be less diverse (both in the sense of fewer species and in the sense of greater dominance by a few common species) than would be the case in the absence of interspecific interactions. The discrepancy is greatest in the tropics, where biotic effects are thought to be most pronounced. Caswell concludes that the diversity of natural communities may be maintained in spite of, rather than because of, such biological interactions between species. Although it is possible to cavil, on technical grounds, at the appropriateness of the neutral hypothesis used by Caswell to generate interaction-free distributions of relative abundance, his attempt to bring these methods to bear on questions of relative diversity is most original, and deserves more attention than it has received.

One pervasive pattern that has been widely remarked for mature (as opposed to early successional or disturbed) communities of plants, moths, birds, diatoms, and other taxa, is that the distribution of relative abundance is not only lognormal, but is "canonically" lognormal (Preston, 1962; MacArthur and Wilson, 1967). This canonical lognormal is a particular member of the one-dimensionally infinite family of lognormal distributions, corresponding to a particular relationship between the number of species, S , and the variance of the distribution, σ^2 (this relationship is often conveniently parameterized as " $\gamma = 1$ "; for a full discussion, see May, 1975). Another associated pattern, first explicitly remarked by Hutchinson (1953), is that the conventional parameter a (which is essentially an inverse measure of the standard deviation of the distribution of species relative abundance, $a = 0.71/\sigma$) seems always to have a value $a \sim 0.2$. Such generally observed patterns cry out for explanation. I have sought to explain both these phenomena as being no more than likely mathematical properties of any lognormal distribution of species, provided the collection is large enough ($S \gg 1$; May, 1975). While I think it remains true that this "neutral hypothesis" accounts for the roughly constant magnitude of the inverse variance, $a \sim 0.2$, a more careful analysis of the available data by Sugihara (1980) suggests that real distributions of species relative abundance conform to the "canonical" relationship between S and σ more closely than seems explainable by mathematical properties of the distribution alone. Sugihara has, indeed, gone on to advance a pos-

sible biological mechanism underlying the structure of mature communities: the sequential division of niche space by closely related species. This mechanism does lead to expectations of distributions of species relative abundance that are remarkably close to the observed data (Sugihara, 1980).

This is an instructive story. Earlier work took it for granted that the canonical pattern derived in some way from the biological structuring of the community. My subsequent attempt to explain the observed canonical distribution on “neutral” grounds, as being a mathematical property of the essentially randomly determined relative abundance of individuals among a large number of species, now appears to have been too glib; the canonical relationship is obeyed too closely to be explained in this general way. But, as Sugihara emphasizes, the fact that his “sequential niche breakage” model accounts for the observed distributions does not mean it is necessarily correct. It could yet be that a carefully framed neutral model could account for the observed patterns, thus bringing this story full circle for the second time.

SPECIES-AREA RELATIONS

Many authors have studied the empirical relation between the number of species on an island, S , and the area of the island, A . These studies of birds, plants, insects, and other taxa embrace both archipelagoes and other collections of real islands, and assemblies of virtual islands such as ponds, woodlots, or nature reserves. A log-log plot of S against A usually shows a linear relation, of the form

$$S = (\text{constant}) A^z, \quad (1)$$

with z having a value around 0.2–0.3. As pointed out by Preston (1962) and by MacArthur and Wilson (1967), by assuming a canonical lognormal distribution of N individuals among S species, and adding the assumption that N is linearly proportional to island area, A , one can derive equation (1) with $z \simeq 0.25$ for $S \gg 1$ (see May, 1975).

Connor and McCoy (1979) have suggested these observations may be explained by a null model. They observe that z is evaluated as the slope of a regression line, and thus can be expressed as the product of a correlation coefficient (r) and the ratio of the standard deviations of the dependent and independent variables (S_y/S_x). As a null hypothesis, they suggest that both r and the ratio S_y/S_x vary independently randomly between 0 and 1. This hypothesis leads to a relation of the form of equation (1) between S and A , with the regression coefficient z being, on average, the expected value of the product of two numbers each distributed uniformly on the interval 0 to 1, whence $\langle z \rangle = 0.25$. Thus Connor and McCoy's

neutral hypothesis seems to be consistent with the empirical facts, apparently undercutting any need to invoke biological interactions in understanding equation (1).

Sugihara (1981) has, however, noted that the neutral model of Connor and McCoy gives not merely the average value of z , but also the full distribution of z -values that we would expect to see when many such studies are tabulated. Sugihara shows that the z -values actually found in analyses of real data cluster more closely around 0.2–0.3 than does the distribution of values to be expected from the neutral model. Thus, on the basis of this more sensitive test, Connor and McCoy's null hypothesis may be rejected as an explanation for the observed S - A relationships. To put it another way, although the mean value of z predicted by the null model is consistent with the data, the variance in the null model's distribution of z -values is significantly greater than that observed in nature.

There is a useful message here. The null hypothesis cannot be rejected if we look only at the predictions it makes about the average values of a pertinent parameter. But if we probe deeper, looking at the variance or at the full distribution of the relevant parameter values, the actual data can be seen to be too tightly clustered to be consistent with the null hypothesis. This general theme will be heard again, more diffusely, below.

ASSEMBLY RULES AND INDIRECT EVIDENCE FOR COMPETITION OR CONVERGENCE

Many studies seek to show the convergence in the structure of communities in environmentally similar but geographically separated parts of the world. Other broadly related studies aim to find empirical rules governing the incidence of particular species on real or virtual islands of a given size, and governing the assembly of such island communities.

Recently, several people have endeavored to test this work against null models, in order to determine whether the apparent patterns are significantly different from what would be observed if the communities consisted of random collections of species, unstructured by competition or other biological interactions. There is, however, a profound difficulty in the construction of some of these neutral models, which usually are obtained by reshuffling of the observed data. This procedure is open to the objection that, if the real communities have been highly influenced by competition, one cannot construct a truly neutral model by pooling and redistributing the data. The present book contains a good representation of the range of views that are held on this subject, particularly in the chapters by Simberloff, Grant, Gilpin and Diamond, and Colwell and Winkler.

An illustrative example not covered elsewhere in this book is provided by the exchange between Fuentes (1976, 1980) and Crowder (1980). Fuen-

tes (1976) studied the structure of lizard communities in physiognomically similar sites in North and South America, and showed that such communities were more similar to each other than to lizard communities in nearby sites on an altitudinal and vegetational gradient. Crowder (1980) suggested this evidence could not be taken to indicate community-level convergence, because the patterns were not significantly distinguishable from a neutral model that he constructed. But Fuentes (1980) objected, in my view with justification, that “to use the same species and ecospecies numbers I used [in order to construct the so-called neutral model] is to assume my results,” rather than to subject them to an independent test.

Gilpin and Diamond (in this volume) present an illustrative example in which a null model that is constructed by drawing at random (subject to specified constraints) from the pooled data can, in certain limits, lead to nonsense. Suppose one has N islands, on each of which either species A or species B is present, but never both and never neither. If N is large, one would be inclined, intuitively, to regard this “checkerboard” pattern as evidence for competition between species A and B . But it is, of course, desirable to test the pattern against some neutral model, to add rigor to this conclusion. The way neutral models have usually been generated in these contexts is randomly to reshuffle the pool of species, subject to various restrictions. Suppose the set of constraints is that: (i) the number of islands remains equal to the actual number; (ii) the number of species remains equal to the actual number; (iii) each species is present on exactly as many islands as in actuality; and (iv) each island has as many species as does the real island. Although this procedure may appear reasonable, the constraints (iii) and (iv) can have the effect of convolving a lot of biological interactions into the supposedly null hypothesis if the data are in fact strongly structured by competitive or other biological interactions. In the limiting case of the “checkerboard” pattern, these constraints are so severe as to guarantee that the null model is identical with the observed pattern: each island in the hypothetical, “neutrally constructed” archipelago also must have one and only one of species A and B , and in the observed proportions. Clearly one should not reject the hypothesis that competition forged this pattern, but rather should reject, as inappropriate, the construction of the null model.

In this context, the chapter by Colwell and Winkler is illuminating. Using a computer program called GOD, they first generate assemblies of species, whose phylogenetic lineages obey specified rules. Subsets of this “mainland biota” then colonize archipelagoes, as described by a program called WALLACE; in this colonization, competitive interactions may or may not be important, depending on how WALLACE’s rules are specified. Colwell and Winkler can now take the “field data,” thus generated, and can see to what extent the emergent community patterns stand out

against various neutral models. The key difference between this exercise and actual field studies is, of course, that—because GOD and WALLACE are immanent in Colwell and Winkler—they know whether or not their communities really are structured by competitive effects. The gist of their findings is that the conventional neutral models, constructed by reshuffling of the data, are often indistinguishable from the “observed” field data, even when competition has in fact been a strong force in WALLACE’s colonization of the archipelago.

As Simberloff correctly emphasizes in his chapter, in such circumstances we should not give up, but rather should search for some more appropriate way of framing a neutral model. A constructive suggestion advanced by Gilpin and Diamond is to abandon the deterministic kind of model based on averages, and work with the full statistical distribution given by null models (*cf.* Sugihara, 1981). In the “checkerboard” case, the null model would have species *A* present on any island with probability p_A (where p_A is the proportion of the actual N islands on which *A* is found) and species *B* present with probability p_B . This neutral model would thus have a statistical distribution of presences and absences, with some islands having both species, some having one only, and some having none; for large N , the strict “checkerboard” (with one and only one species, *A* or *B*, per island) would then obviously be too patterned to be accounted for on neutral grounds. More generally, Colwell and Winkler’s studies strongly suggest that null tests based on the full statistical distribution of the ensemble of possible models, or at least based on measures of the variance of species’ distribution, are more likely to confirm the existence of underlying biological patterns than are simpler tests based on observed average values (of species per island and so on).

Other chapters offer additional new ideas and new studies aimed at elucidating aspects of the way particular communities are structured. James and Boecklen, for instance, use an innovative statistical analysis to explore the extent to which changes in the population densities of individual species of birds (as observed in a forest site in Maryland over 7 years) are correlated with the morphological relationships among the bird species. In a remarkably exhaustive computer investigation, Schoener compares the actual distribution of size differences among n co-occurring species of hawks ($n = 2, 3, 4, \dots$) with the “null” distribution obtained by considering every conceivable combination of 2, 3, 4, ... species drawn from the global pool. Clearly, the above discussion of indirect evidence for competition does no more than hint at themes and studies that are developed elsewhere in the book.

If, however, the views I have expressed in this section are accepted, it appears that neutral models can be used to confirm the presence of convergence, or of assembly and incidence rules, but that their use in rejecting such patterns will continue to be contentious. The asymmetry arises be-

cause neutral models that give patterns indistinguishable from the real data can always be called into question if they have been constructed by pooling and rearranging the data itself. Given the awkward ambiguities and frustrations inherent in this situation, it is not surprising that feelings sometimes run high!

OTHER COMMUNITY PATTERNS: EFFECTS OF SIZE AND SCALE

It will often be that systematic patterns, in both populations and communities, are apparent if one examines the system on a sufficiently large scale or over a sufficiently long time, but that such patterns do not show up if the study is restricted in space or time. Yet the exigencies of researchers' lives are unfortunately often such that studies must be spatially and/or temporally localized.

One among many possible examples is to be found in studies of coral fish communities. The elegant and careful experimental studies conducted by Sale (1977, this volume) show little evidence of MacArthurian niche structure in these communities. Sale's study sites are, however, about the size of the average seminar room, and it has been argued that such structure is apparent when one looks at the communities over a much larger spatial scale (even stretching, in the studies of Anderson *et al.*, 1981, from the outer Barrier Reef to the Queensland coastline). Likewise, many different views are held about whether intertidal communities are structured by competition or by predation, or whether indeed there is any particular structure (some, but not all, of the views are represented in this volume); again, the answer may depend partly on the scale and detail of the study.

Not only broad questions of scale, but also geographical and climatic details, can be important in forming an appropriate neutral model. Here, one cautionary tale must suffice. Stiles (1977) presented data suggesting that the peak flowering times of the different species within a particular assembly of plants appear to be roughly uniformly spaced, a fact that he argued to be consistent with the notion that the plants have specialized into temporal niches in their competition for pollinators. Poole and Rathcke (1979), however, showed that the distribution of peak flowering times was not significantly different from that generated by the null hypothesis that each species flowers at some random time of the year. But, as pointed out by Cole (1981), there are two pronounced flowering seasons in the region where Stiles's studies were done. Once this fact is taken into account, the flowering peaks are indeed more uniformly spaced than an appropriate neutral model suggests (and the overlap between the peak flowering periods of temporally adjacent species is lower than neutrally explainable). Thus Cole's analysis revives Stiles's conclusions, but now with an added rigor stemming from Poole and Rathcke's constructive criticisms.

PRACTICAL PROBLEMS AND TENTATIVE SCIENCE

Despite recent advances, both in the acquisition of data and in its analysis, I doubt that any multispecies community is sufficiently well understood for us to make confident predictions about its response to particular disturbances, especially those caused by man. Many important practical problems need further ecological studies, of a carefully planned kind, before anything other than crude and tentative generalizations can be made about dynamical behavior in response to perturbation. Unfortunately, in many of these practical situations, decisions must be made today; fishing and whaling quotas will be set for next year, and as habitats are destroyed at an accelerating rate, reserves must be set aside now. The choice in many circumstances is not between perfect and imperfect advice to managers, but between crudely imperfect advice and none at all.

Examples abound. For the multispecies fisheries of the North Sea, the North Pacific, and the Gulf of Thailand, advice based on tentative generalizations and oversimplified models is the best that ecologists can offer. Similarly, the Convention of the Southern Ocean (which aims to enunciate a set of scientific principles as a basis for managing the complex layering of trophic levels from krill to baleen and sperm whales) appeals to broad generalizations; see May *et al.* (1979). In a similar way, plans for the establishment and management of conservation areas and refuges in many different parts of the world rest on guesstimates and principles that are not yet—and may never be—established on an unarguable factual foundation (Soulé and Wilcox, 1980; Jewell, 1981). An instructive example, from a past age, of such practical action based on plausibility rather than certitude is Snow's suspicion that cholera was transmitted by water contaminated with sewage, and his suggestion that the Broad Street pump was the focus of the cholera outbreak in London in 1848. The epidemic stopped soon after the handle was, at Snow's urging, removed from the pump (Winslow, 1943).

In short, in assessing the contributions that ecological theory can make to management decisions, it must be kept in mind that practical decisions are often, of necessity, made in haste and in the absence of full information. This, needless to say, is never an excuse for bad science or overconfident claims based on uncertain knowledge, but it does, in my view, often justify accepting rough and tentative generalizations or patterns that have not been rigorously established.

STUDYING COMMUNITIES

One opportunity that is much neglected by managers of natural resources is the chance to make decisions in such a way as to maximize the flow of information about the system, as a foundation for future management choices. Thus, given that fish and whale quotas are set on the

basis of frankly crude models, different models and recommendations could be made in different geographical areas, so that the management regime assumes some of the aspects of a controlled experiment. The same ideas can be (and to a limited extent are) employed both in establishing reserves and in managing locally abundant populations of endangered or protected animals (see the papers in the volume edited by Jewell, 1981). Snow's suggestion about the pump was a falsifiable hypothesis as well as a public health recommendation.

Both in practical management problems and in academic studies, any attempt to elucidate patterns of community structure must deal with the question of how to delimit the community. Much academic research restricts itself to a particular taxonomic group—birds, or lizards, or insects—instead of first consciously deciding which group of species comprises a coherent and irreducible community. And harvesting studies typically ignore all species that are not exploited, often in ways that are detrimental to the future well-being of the community, harvested and unharvested species alike. Hairston stresses this point later in the book. Recent studies of the structure of communities of seed-eating rodents and ants in desert environments in the American Southwest (Brown and Davidson, 1977; Brown, this volume), and of lizards and birds in the West Indies (Wright, 1979, 1981), are showing the way to a better tradition for the future.

The problem of identifying a coherent community can be exacerbated by a blinkered vision that focuses upon one particular kind of biological interaction to the exclusion of others. Thus too narrow a concern for competitive interactions may lead to important predatory species' being neglected in what purports to be a community study (as stressed, for example, by Faeth and Simberloff, 1981a), and, conversely, too much emphasis on prey-predator relations can cause competing species to be overlooked (particularly if they are taxonomically different from the main species being studied). Mounting my own current hobbyhorse, I note that few indeed are the community studies that take account of the influence of pathogens and parasites on population dynamics and community structure. Yet parasites—broadly defined to include viruses, bacteria, protozoans, fungi and helminths—arguably play major roles in shaping many communities, even on a biogeographical scale (Anderson and May, 1979; May and Anderson, 1979).

CONCLUDING REMARKS

Ecology is a difficult science, partly because evolution has only given us one world, and it is not easy to perform controlled experiments. There nevertheless exist a variety of techniques whereby the evolution and ecology of communities can be elucidated in an unambiguous way; these

include systematically compiled comparative studies, manipulative experiments in the field and laboratory, and (as repeatedly evidenced in this book) the testing of putative patterns against appropriate "neutral models." The philosophical status of these investigative techniques has been lucidly discussed by several people recently (Hull, 1974; Ruse, 1977, 1979; McIntosh, 1980; Simberloff, 1980; Strong, 1980; Wimsatt, 1980), especially in relation to the more ineluctable procedures found in the physical sciences. As observed by Southwood (1980) and others, evolutionary biology and ecology are characterized by mixtures of probability and pattern (Monod's "chance and necessity"). Even when trends and patterns can be confidently identified, predictions will usually need to be cast as probabilistic statements; this characteristic is often disconcertingly at variance with the crisp determinacy of most predictions in physics.

The complications inherent in most studies of ecological communities are unfortunately such that it can be hard to keep a balanced view of all the relevant factors and contending hypotheses. Although this danger is present in all the sciences, the unconscious temptation to superimpose one's prejudices upon the data is more easily yielded to by virtue of these complexities.

If any simple lesson can be said to emerge from the examples discussed above, or more generally from the papers assembled in this volume, it is that no single method—theoretical or experimental—can be guaranteed to give useful results about community patterns. Past advances have come about in many different ways, from many different styles of investigation. Without going to Feyerabend's (1975) extreme of "anything goes," I believe that the creative tensions among different schools of researchers are a continuing source of new insights and new approaches; it is paradoxical that some of those who are most sensitively aware of the need to keep sight of alternative explanations for observed patterns in community structure seem, at the same time, occasionally to accept that there is only one True Way to do science. I believe that, both in our pursuit of an understanding of the structure of ecological communities and in the scientific methods we employ to this end, we should be guided by Whitehead's precept (as cited by Birch, 1979): "seek simplicity, and distrust it."

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Experimental Tests

Inferences and Experimental Results in Guild Structure

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"We cannot go out and describe the world in any old way we please and then sit back and demand that an explanatory and predictive theory be built on that description. The description may be dynamically insufficient. Such is the agony of community ecology. We do not really know what a sufficient description of a community is because we do not know what the laws of transformation are like. . . ." (R. C. Lewontin, 1974, p. 8)

INTRODUCTION

In this paper, I report two studies. The results show the information that may be required for both a dynamically sufficient description of these guilds and an understanding of the laws of transformation that determine their composition. In neither example is the interspecific interaction that determines the laws of transformation obvious from the original description of the community, and I cannot claim that those laws have been specified yet. I do hope to show the scope that they must eventually cover. If guilds are to be considered ecologically meaningful groups of species, some such specification must be sought.

Both studies are of guilds of salamanders in the southern Appalachians. In one case, the guild is defined as those species of salamanders that spend most of their lives on the deciduous forest floor. Studies of stomach contents (Hairston, 1949; Whitaker and Rubin, 1971; Powders and Tietjen, 1974; Burton, 1976; Sarah Stenhouse, pers. comm.) demonstrate that all of the species share the resource of food: insects and other small invertebrates. They thus conform to the usually accepted definition of a guild. The second guild consists of the coexisting species of the genus *Desmognathus*. Guild membership is based on overlapping food (Hairston, 1949; Krzysik, 1979), similarity of life histories, and the assumption of similarity of requirements implicit in the close taxonomic relationship.

SALAMANDERS OF THE DECIDUOUS FOREST FLOOR

The composition of this guild varies slightly from location to location in the southern Appalachians. In the two areas where I carried out my experiments, 10 species were found in both areas, and an 11th species was present in one of them. Four of the 10 species have life histories and/or ecological distributions that preclude them from being considered part of the guild. *Pseudotriton ruber* and *Gyrinophilus porphyriticus* spend 32 months or more as larvae, and the adults are uncommon, although both were seen some distance from the streams. *Desmognathus quadramaculatus* is mostly aquatic (Hairston, 1949, 1973, 1980b; Organ, 1961), and in this study was only seen on the plots immediately adjacent to running water. *Desmognathus monticola*, while less aquatic than *quadramaculatus*, is still a stream-bank salamander, 85.4% of the specimens seen having been on the same plots to which *quadramaculatus* was confined.

The remaining species spend all or most of their lives on the forest floor, and in no case could the abundance of any of them be related to the distance of the plots from streams or seepage areas. These species are *Plethodon jordani*, *P. glutinosus*, *P. serratus*, *Eurycea bislineata*, *Desmognathus ochrophaeus*, and *D. wrighti*. *Desmognathus imitator* was also present in the Great Smoky Mountains, but only part of the specimens are separable from *D. ochrophaeus* in the field, and it has been lumped with that species in the following account. The compositions of the guilds and the relative abundances of the species are shown in Table 2.1.

The study was carried out in two areas where the altitudinal distributions of *Plethodon jordani* and *P. glutinosus* are quite different. In the Great Smoky Mountains, *P. jordani* is confined to higher elevations and *P. glutinosus* to lower ones. Their distributions overlap in a zone that is 70–120 m wide vertically, the altitude depending on the direction in which

Table 2.1. The membership and abundances of the guild of salamanders of the deciduous forest floor in the southern Appalachians. In the Great Smoky Mountains, *Desmognathus ochrophaeus* includes *D. imitator*. Numbers are total seen on 90 searches of control plots in each area.

Species	Balsam Mountains	Great Smoky Mountains
<i>Plethodon jordani</i>	3182	2473
<i>Plethodon glutinosus</i>	392	450
<i>Plethodon serratus</i>	89	61
<i>Eurycea bislineata</i>	18	72
<i>Desmognathus ochrophaeus</i>	15	297
<i>Desmognathus wrighti</i>	25	7

the slope faces. In the Balsam Mountains, the two species are found together over an altitudinal range of 1220 m (Hairston, 1980a). This difference prompted me to carry out paired experiments in the two areas to test the hypothesis that competition was enough stronger in the Smokies to result in competitive exclusion there. The experiments involved setting up a series of marked plots in each of the two areas. *Plethodon jordani* was removed from one pair of replicates at each location; *P. glutinosus* was removed from another pair of replicate plots.

Although the original purpose of the experiments was to test for competitive release of the two species, the abundances of all salamanders were monitored throughout the study, which was continued for 5 years because of the long generation times of the two most abundant species. Thus, the experiments also tested the effects of each of those two species on the other guild members.

The methods, which involved complete searches of the plots at night, are described in detail elsewhere (Hairston, 1980a). The plots are equilateral octagons 24.384 m (80 ft) in diameter, covering approximately 0.04 ha. Each plot was searched 6 times per year, twice each in May–June, July–August, and September–October. As is shown in Table 2.1, the abundances of the different species were very unequal. A result of the inequality was that successful removal of about 56–64% of the *P. jordani* reduced the total salamander biomass by 40–50%. Similarly, removal of *P. glutinosus*, the largest member of the guild, reduced the total salamander biomass by 10%. It must be admitted that the foregoing estimates are based on the assumption that all species are, on the average, equally represented in night censuses, since all of my data are in number per plot search. The assumption may not be valid. For example, in preliminary studies I removed all *P. jordani* from two plots 7 times in 20 nights. The data conform reasonably well to a constant loss rate of 0.25 per removal, and I conclude that on an average night about one-fourth of the *P. jordani* are active and available for removal, the remainder being underground. I have no comparable data for any of the other species, but it is obvious that major deviations from the estimate based on *P. jordani* could cause deviations in the estimates of the proportion of total biomass removed. There are limits to the error, however, because *P. jordani* constitutes such a large proportion of the total number of salamanders seen (73% in the Great Smoky Mountains). If all of the other species have only one-tenth of their individuals active on one night, then only 52% of the total population are *jordani*. If half of their numbers are active at one time, *jordani* constitutes 84% of the total. These percentages are uncorrected for biomass, but they give a realistic picture of the potential error in the estimates, as *jordani* is the second largest member of the guild.

Results

The most striking result of the removal experiments was the response of *P. glutinosus* to the removal of *P. jordani*. In the Great Smoky Mountains, *P. glutinosus* was significantly more abundant where *jordani* was removed than on the control plots, starting in the third year of the experiment and continuing through the fifth year. In the Balsams, the same effect was found, but only at the end of the fourth year and during the fifth year (Hairston, 1980a). When *P. glutinosus* was removed, *P. jordani* showed an increase in reproduction, reflected in a significant increase in the proportion of one- and two-year-olds, but the difference in abundance between experimental and control plots was not significant statistically. Again, the effect was greater in the Smokies.

None of the remaining members of the guild was affected by the removal of either of the two most abundant members. This pattern is well exemplified by the congeneric species *Plethodon serratus* (Figure 2.1). Sixteen statistical tests compared mean densities of each of the 4 species on control plots with their densities on *jordani*-removal plots and on *glutin-*

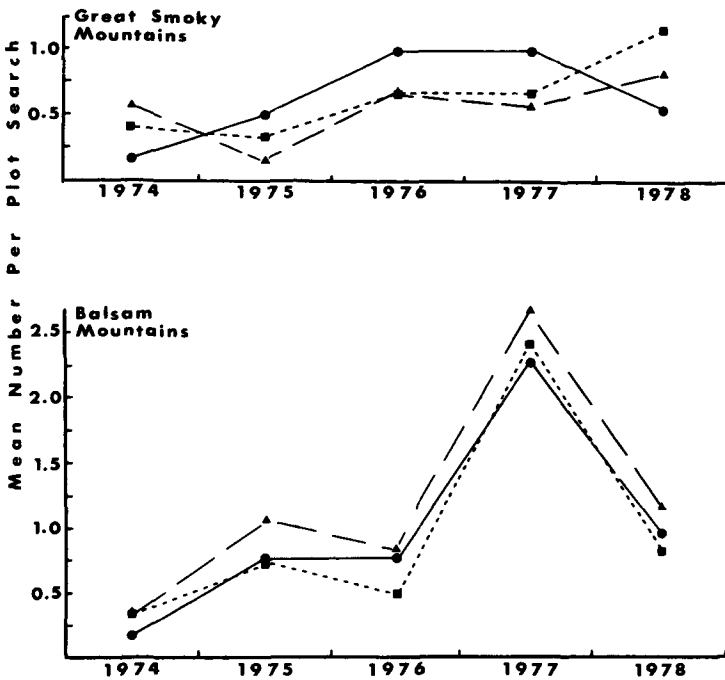


Fig. 2.1. *Plethodon serratus* populations during experimental removal of *P. jordani* (dashed lines connecting triangles) and *P. glutinosus* (dotted lines connecting squares), compared with controls (solid lines connecting circles).

osus-removal plots in both Smokies and Balsams (Hairston, 1981). In one case, that of *Desmognathus ochrophaeus* on plots in the Balsam Mountains from which *P. glutinosus* had been removed, the mean density on treatment plots was significantly greater than on controls. Inasmuch as "significance" is expected by chance once in 20 comparisons, no important meaning can be attributed to this isolated example. Furthermore, it was possible to test the same differences year by year for 71 comparisons. In two of these, there was a significant difference, but both of them were for 1974, the first year of the experiment. For any meaning to be attributed to the result, significant differences would have to be found at the end of the experiment.

We have here a guild that can only be demonstrated to contain 2 species. The remaining 5 species were not close enough ecologically to those 2 to be affected by reductions in their density, even though as much as half of the total biomass was removed, and even though the diets of all 7 species overlap broadly. There does not appear to be an acceptable *a priori* way in which to define this guild so as to include those species that interact ecologically, and so as to exclude those that do not. Restricting the guild to a single genus (*Plethodon*) would not solve the problem, because *P. serratus* is not affected by the removal of either congener. I conclude that we need to know the exact ecological relationships to a degree that is unlikely to be attained for this or for most other guilds, or that this and many other claimed examples of guilds are products of our imaginations.

SALAMANDERS OF THE GENUS *DESMOGNATHUS*

In the southern Appalachians, the members of this genus occur together in combinations of 3, 4, or 5 species. They are usually thought of as stream-bank salamanders, but individually the species vary from being mostly aquatic (*D. quadramaculatus*) through the "typical" *monticola*, *fuscus*, and *santeetlch* (see Tilley, 1981) to mostly terrestrial *ochrophaeus* and *imitator* and fully terrestrial *wrighti* and *aeneus*. All species lay their eggs in or near water, and the female remains with them until they hatch 2 or 3 months later. Except for *wrighti* and *aeneus*, all have larval stages, which vary between species in duration from a few weeks to 2 years.

For a number of years, I have had classes record the distance from surface water for each metamorphosed salamander. Data covering the years 1979 and 1980 are shown in Table 2.2. The results are typical for intermediate elevations (see Hairston, 1949, 1973, 1980b; Organ, 1961). The 4 species overlap broadly, but each has a characteristic spatial distribution that is different from all of the others. Until recently, such data were interpreted as representing the result of interspecific competition, natural

Table 2.2. Ecological distribution of four species of *Desmognathus*, elevation 686 m, Coweeta Hydrologic Laboratory, North Carolina. Class data, 1979 and 1980. The proportional distribution of each species is given.

Species	N	Distance from Stream (m)				
		0	<.3	.3-1.5	1.5-6	> 6
<i>quadramaculatus</i>	48	.812	.104	.020	.040	.020
<i>monticola</i>	179	.290	.318	.251	.133	.005
<i>ochrophaeus</i>	97	.175	.257	.340	.185	.041
<i>aeneus</i>	16			.187	.312	.500

selection favoring the adoption of a sufficiently different distribution for each species to reduce competition to the level that permitted coexistence.

It is generally agreed (Dunn, 1926; Piatt, 1935; Wake, 1966) that the evolution of the genus has proceeded from a largely aquatic ancestor to increasingly terrestrial species, and that the series we see provides a reasonably accurate model of what happened over evolutionary time. Newly acquired data (Hairston, 1980b) and new interpretations (Tilley, 1968; Huheey and Brandon, 1973; Hairston, 1980b) have raised doubts about the conventional interpretation of the evolutionary history of the *Desmognathus* species, although that interpretation continues to be used (Krzysik, 1979). The decrease in size with an increasingly terrestrial habitat is inconsistent with competition as the driving force of natural selection, because competition requires increasing efficiency, and increased evaporative water loss with increased surface-volume ratio accompanying smaller size would seem not to promote increased efficiency.

There are also considerations arising from the fact that some species are missing from certain areas. In the Black Mountains of North Carolina, for example, *D. monticola* does not occur above an elevation of about 1200 m and *D. wrighti* virtually disappears below that elevation. If competition is important in structuring the present community, I would expect different ecological distributions of *D. quadramaculatus* and *D. ochrophaeus* in the presence and absence of the other 2 species. Both should converge on the stream-bank habitat of *monticola* at high elevations and tend to avoid it at low elevations. They show no such tendencies (Hairston, 1980b), even though the absence of *wrighti* at low elevations should make the forest a favorable place for *ochrophaeus*.

If, on the other hand, the sizes of the species are the result of competition forcing them to be different, I expect *D. quadramaculatus* to be larger at the low elevations, where it occurs with *monticola*, than it is at high elevations, where *monticola* is absent. As a matter of fact, *quadramaculatus* is larger at high elevations, although not significantly so for the data in hand.

Tilley (1968) and I (Hairston, 1980b) have advanced the hypothesis that predation, rather than competition, has been the most important force of natural selection in driving the evolutionary history of the species of *Desmognathus*. It is argued that predation on salamanders is much heavier in the streams than it is in the forest, and that, at each speciation, the smaller of the two was under selective pressure to become more terrestrial, thus reducing the effect of predation by large aquatic salamanders and fish.

This hypothesis readily explains the size-habitat relationship that causes difficulty for the hypothesis that competition has been the driving force in selection in the genus. Predation in the streams is also the most plausible reason for Organ's (1961) finding that survival of juveniles is positively related to how terrestrial the habitat of the species is. Predictions from the absence of *D. monticola* and *D. wrighti* do not apply to the predation hypothesis.

I have begun experiments designed to permit a choice between these two hypotheses. On a series of streams, which are used as blocks, *D. ochrophaeus* is being removed from one series of plots. If competition is the important interspecific interaction, *D. monticola* should be favored in comparison with its performance on control plots. With predation important, no such prediction is permissible, and *monticola* and perhaps *quadramaculatus* might decline in abundance because of the loss of an important prey item. On another group of plots, *monticola* is being removed. This removal should result in a benefit to *ochrophaeus* under either hypothesis, but *quadramaculatus* should gain only if competition is important. If the predation hypothesis is correct, it might decrease.

Tilley (1980) attempted the removal of *D. monticola* from a rockface habitat. He removed 128 specimens on 7 visits over a $3\frac{1}{4}$ -year period. He observed no effect on the *ochrophaeus* population, but did observe an increase in the proportion of young *monticola*. The absolute number of adults was not affected by the removal, and although the lack of control areas makes complete interpretation hazardous, 2 removals per year do not appear to have been enough to have an effect on those *monticola* most likely to prey on *ochrophaeus*. Tilley does not report any impact on *quadramaculatus*, although that species was present. His study shows that, in order to reduce the population of a species of *Desmognathus*, a much more intense effort will be required.

DISCUSSION

The 2 guilds that I have described demonstrate that intuitively reasonable and frequently used descriptions of nature may be dynamically insufficient for community ecology, to continue borrowing Lewontin's term. The insufficiency seems to be related to the implicit assumptions that are

the basis for the forms of the descriptions. The choice of the salamanders of the forest floor involves the assumption that consuming overlapping resources (food species) is sufficient to bind them together in an ecologically important way. If food is not limiting the populations of these salamanders, the assumption is false, and the basis used for the delimitation of the guild is nonexistent. But food is so important generally that the assumption seems intuitively reasonable, and it is fair to ask what better basis could be found for delimiting the guild. It can be maintained that the nature of the species' life histories would form a better basis for describing the community, thus separating the 4 species that return to the streams to breed. It has already been noted, however, that most of their feeding time is spent on the forest floor, and to abandon food *a priori* would require knowledge that the populations of the 4 species are regulated during the time when they are at the streams. Even if this knowledge were available, there would remain the problem posed by *Plethodon serratus*, a completely terrestrial congener of the 2 competing species. It is true that it is most active in spring and fall, while the larger species have summer as their period of activity, and it seems likely that the eggs of *serratus* are laid in a more superficial situation. To make use of all such facts in delimiting a guild would, if it is necessary, make the delimitation pointless. After all, the simultaneous consideration of ecologically related species is the heart of community ecology, and to admit a completely reductionist requirement would remove any hope that we have a scientifically valid field.

To consider the co-occurring species of *Desmognathus* to be a guild involves a different set of assumptions from the ones already discussed. It has been assumed that taxonomic affinity implies ecological impact, and furthermore that the impact is interspecific competition. The nature of the resource for which competition is assumed does not yet need to be specified. It is further assumed that the ways in which the species differ are the result of natural selection operating through the impact of the competitive relationships. I believe that I have shown that these assumptions are neither necessary nor sufficient to explain the observations (Hairston, 1980b), even though I advocated their acceptance in the past (Hairston, 1949, 1973). The experiments may or may not demonstrate ecologically important interactions, but given two plausible explanations, some means of choosing between them is necessary, and experiments are to be preferred to *a posteriori* arguments.

There are three kinds of direct ecological interaction between species: competition, predation, and mutualism. Up to now, theoretical ecologists have been principally concerned with how communities can be constructed from these interactions, principally competition. It has been common to cite data confirming the proposed mechanisms, and to conclude

that the correct inferences have been drawn about the way in which nature works. This approach is always subject to the weakness that the explanation is sufficient but not necessary. It is my contention that community ecology will never escape from its agony until we begin the self-conscious application of a rigorous scientific method. Its success in rocky intertidal communities is encouraging, but in many areas, great ingenuity will be required to identify the implicit assumptions and to devise adequate experimental or other truly *a priori* tests of the explanations that are offered for what we see in nature. The task will be particularly difficult because we have only unfounded ideas about what to look for. The greatest need is for legitimate means of identification of interacting groups of species. The identification should be based on characteristics that are determined by the nature and strength of the interactions, and we need characteristics that discriminate between the effects of different interactions as well as those that separate interacting from non-interacting groups. Three characteristics that I have shown to be insufficient alone or in combination are co-occurrence, taxonomic affinity, and utilization of a common resource. Until we can discover the necessary characteristics, I believe that separate experiments testing hypotheses applicable to individual "communities" provide our only assurance of progress.

Exorcising the Ghost of Competition Past: Phytophagous Insects

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SUMMARY

Orthodox community theory is dominated by the assumptions of density-dependence and interspecific competition. Population growth inexorably depletes resources and shortages govern interactions both within and between species in this theory. Here, I summarize research with phytophagous insects of the tropical monocot *Heliconia*, which coexist in a manner quite opposite to this orthodox theory. Resources are not depleted by these insects. They do not feed from or occupy host plants in a density-dependent manner, and species do not compete among themselves. Although analyses of the forces that do affect these populations are not complete, preliminary observations indicate that natural enemies such as parasitoids greatly affect populations of these insects and may hold them at their very low densities. Other factors, such as host phenology, seasonality, and environmental stochasticity may also substantially affect these communities.

Insects on *Heliconia* are not unique among phytophagous insects. Many insects apparently coexist normally without the neo-Malthusian forces of interspecific competition. Non-competitive coexistence may be the usual situation for insects on plants, which comprise over 25% of the diversity of macroscopic organisms now in existence. Even for some organisms other than insects, several authors indicate that, upon scrutiny, the assumption of inevitable interspecific competition is also often untenable. Without inevitable interspecific competition the ghost of competition past need not be conjured up to explain species differences, niches, and "resource partitioning" in present communities.

Mainstream community theory is based upon Gause's extrapolation of Malthusian population theory to interspecific relations (Hutchinson, 1978). The centerpiece of this neo-Malthusian theory is deterministic

density-dependence based upon resources. Population growth rate changes primarily as a function of density; populations inexorably grow until density is so high that food or accommodations limit more growth. Gause extended Malthusian theory to the interspecific realm with the notion of ecological niche. "It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor" (Gause, 1934, p. 19). The definition and implications of niche were modified and amended from Elton (1927, p. 63). Elton used niche at that time only to denote where an animal lived and what is fed upon. Inferences about competition and displacement were Gause's.

After Gause, much community theory continued on the neo-Malthusian track. Lack (1947) and Hutchinson (1959) interpreted the structure of natural communities in terms of competition. Orthodox interpretation of niche theory is based upon Gause's "admission" and infers that interspecific competition in the past caused niches to diverge, with the differences between species that we see today in communities as the result (Schoener, 1947b). The assumption that former competition is the general cause of species differences in communities has been satirically termed "the ghost of competition past" (Connell, 1980).

My purpose is to focus critical attention upon the major assumptions of neo-Malthusian community ecology for phytophagous insects in nature. Phytophages have had relatively little influence upon this theory, even though they make up over 25% of extant animal species (Southwood, 1978). One of my main points is that interspecific competition is not common in communities of phytophagous insects, probably because other natural factors frequently intervene to hold densities so low that populations do not usually deplete crucial resources. Natural communities of insects might be contrasted with those in mathematical theories or in very simple laboratory environments, where one has eliminated the normal influences of seasons, host plant phenology, spatial patchiness, predation, parasitism, and the effects of the larger composite community that interacts intermittently and relatively diffusely with the species in question, and where disturbances from the weather and other natural forces that cause environmental stochasticity have been eliminated. In these simplified models, populations can be forced to behave in a density-dependent manner, and communities may be forced into neo-Malthusian behavior. It is just this complex of additional factors listed above that are frequently quite important in real communities and that are ignored by neo-Malthusian theory in favor of competition. Suites of the above factors tend to reduce both density-dependence and the importance of competition in natural communities. How the complex of real factors actually

affects communities in nature can only be discovered by careful description and experiment. Thus, the ultimate community questions are empirical. How do communities really behave?

ROLLED-LEAF HISPINES ON *HELICONIA*

Hispine beetles that live in the scrolls formed by young *Heliconia* leaves are good material for community studies. Adults of as many as eight species can intermingle in the scrolls at a single site, and as many as five species can simultaneously occupy one scroll (Strong, 1977a, b). The scroll is the food as well as the shelter. Adults spend their entire long lives in or moving among scrolls, feeding and mating. Scrolls unfurl within a few days, so associations are repeatedly reshuffled during the life of a beetle.

I have studied interactions, associations, and the use of resources by these hispines in Central America (Strong, 1982a, b). Interspecific and intraspecific relations of adults are distinctly harmonious. Beetles have no aggressive tendencies toward their own or other species, and live in intimate contact. No evidence for interference competition could be found in patterns of species association in scrolls, in comparisons from many sites from Trinidad through Costa Rica. The presence and abundance of a species in a scroll has no discernible influence upon other species, and density has no influence upon interspecific association in scrolls. My experiments produced patterns of neutral interspecific association quite similar to those found in nature, and reinforce the idea that hispine species mix independently of one another in scrolls. Finally, the number of *Heliconia* species that a hispine species uses at a site is apparently not affected by other hispine species.

These earlier studies concentrated mainly upon potential interference competition in hispine communities. Here I will concentrate upon potential exploitation competition. For hispines, interference might result from aggression that led to beetles' leaving scrolls or beetles' avoiding scrolls as a function of their occupants. Fouling or marking of scrolls could cause interference, just as could aggression. The most straightforward form of exploitation for these insects would be depletion of the food in scrolls by feeding beetles. Of course, resource depletion might precipitate interference. If accommodations inside scrolls were effectively used up by occupants, exploitation competition might cause interference competition. My experimental studies with potential exploitation among hispines have been done mainly at Finca La Selva in Costa Rica, with the insects of *Heliconia imbricata*. The two most abundant species of rolled-leaf hispines on *H. imbricata* at La Selva are *Chelobasis perplexa* and *Cephaloleia consanguinea*.

The most striking fact germane to the question of exploitation competition is that densities of hispines are usually very low relative to the amount

of accommodation and food in scrolls. Leaves can be as large as a square meter, and the interiors of scrolls grow to many times the volume of beetles ever found inside, and as the studies described above indicate, beetles do not stay in or leave scrolls in a density-dependent manner. Food in scrolls is abundant relative to that eaten by hispines and other phytophagous insects. Figure 3.1 shows the fractions of leaf area eaten by the 13 most abundant phytophage species of *Heliconia imbricata* during the first

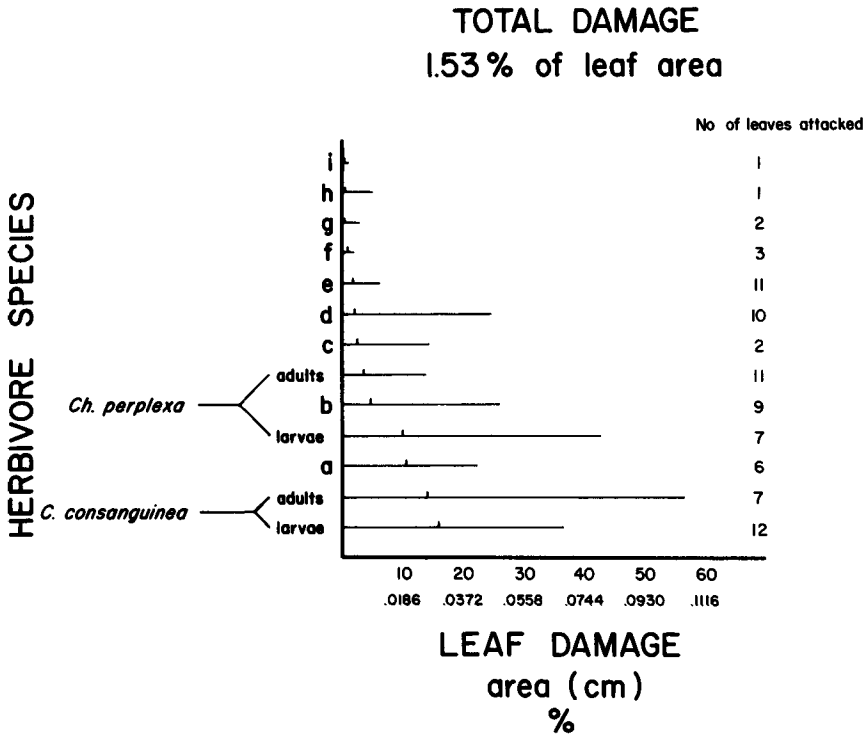


Fig.3.1. Insect feeding from *Heliconia imbricata* over the first 60 days of life of 12 leaves, at Finca La Selva, Costa Rica, during June, July, and August 1976. Leaves were randomly chosen along the River Road Trail. All leaves were within an abandoned cacao plantation and shaded by canopy trees. Length of each horizontal line indicates the maximum feeding by that insect on any one of the 12 leaves. Vertical marks on the lines indicate the average feeding for the 12 leaves. Numbers to the right of lines indicate the number of leaves that each species fed upon. "a" = larvae of leaf miner sp. *a* (Coleoptera, Buprestidae), "b" = Orthoptera, "c" = larvae of leaf miner sp. *c* (Coleoptera, Buprestidae), "d" = larvae of Lepidoptera, "e" = adults of *Hemispherota* sp. (Coleoptera, Cassidinae), "f" = larvae of unidentified leaf miner, "g" = larvae of *Cheirisa dorsata* (Coleoptera, Hispinae), "h" = larvae of leaf miner sp. *h* (Coleoptera, Buprestidae), "i" = adults of *Cheirisa dorsata*.

60 days of life of 12 leaves. Each day the leaves were inspected, and the amount of new feeding by each insect was recorded. In this way an accurate cumulative tally of each species' feeding was built up. Larvae and adults of *Cephaloleia consanguinea*, a monophagous rolled-leaf hispine, caused most feeding damage to the leaves. Another species of rolled-leaf hispine that was abundant during the study was *Chelobasis perplexa*. Its larvae ranked fourth, and its adults ranked sixth, in damage caused to the leaves.

The fractions of *H. imbricata* leaf eaten by these herbivores are very small. In total, all insects ate only 1.53% of the leaf area. Even though leaves normally last between 12 and 18 months, most feeding is done within the first 30 days of a leaf's life. Most leaf damage, on the average, was done by the larvae of *C. consanguinea*, which took approximately 0.03% of the leaf area. The maximum feeding damage on any single leaf was caused by *C. consanguinea* adults, which ate between 0.09 and 0.11% of one of the leaves. *Cephaloleia consanguinea* larvae found their way onto all 12 rolled leaves in this study; adults of this insect fed upon only 7. Note that other insect species attacked fewer than the total 12 leaves. I paralleled this study of feeding upon *H. imbricata* with studies of *H. latispatha*, *H. tortuosa*, *H. pogonantha*, and the related plant *Ishnosiphon* sp. (Marantaceae). All of these plants are attacked by rolled-leaf hispines and other insects, which include both host-specific and more polyphagous species. The amounts eaten from *H. imbricata* were greater than those from any of these other species. No insect species came close to depleting the area of leaf that it fed upon. These results are typical of the very low rates of herbivory on *Heliconia* in nature.

One possibility is that, although phytophages use only a very small fraction of *Heliconia* leaf, less than the total amount of a leaf or fewer than all leaves are desirable to the insects. In a previous study, I had found that 20% to 40% of scrolls were unoccupied by hispine adults (Strong, 1982a). Are the unoccupied leaves chemically or physically less desirable than occupied leaves? One indication that leaves do not vary in inherent desirability comes from feeding experiments comparing the desirability of scrolls of *H. imbricata* that contained no hispines with that of scrolls that contained relatively high densities of hispines. For these two classes of scrolls I compared feeding by hispines in experiments done in Petri plates. Scrolls of the two classes were brought back to the field station. From each scroll, a circle of tissue 10 cm in diameter was cut from the area on which the beetles feed. The circles were cut from the section of the leaf that had most recently been exposed by the natural unfurling of the scroll. Each circle was cut in half, and each half placed in a separate Petri plate. I recorded all previous damage, then placed two *C. consanguinea* adults in one of the Petri plates and two *Ch. perplexa* in the other. Twenty-four

hours later the beetles were removed and released, and the area that had been eaten was measured. The results showed that neither beetle species ate discernibly different amounts from the two classes of scrolls (empty and occupied) (Figure 3.2). My suspicion of inherent heterogeneity among leaves was not confirmed.

Thus, empty and occupied scrolls are apparently not differentially desirable to hispines on the basis of inherent physiological or phytochemical

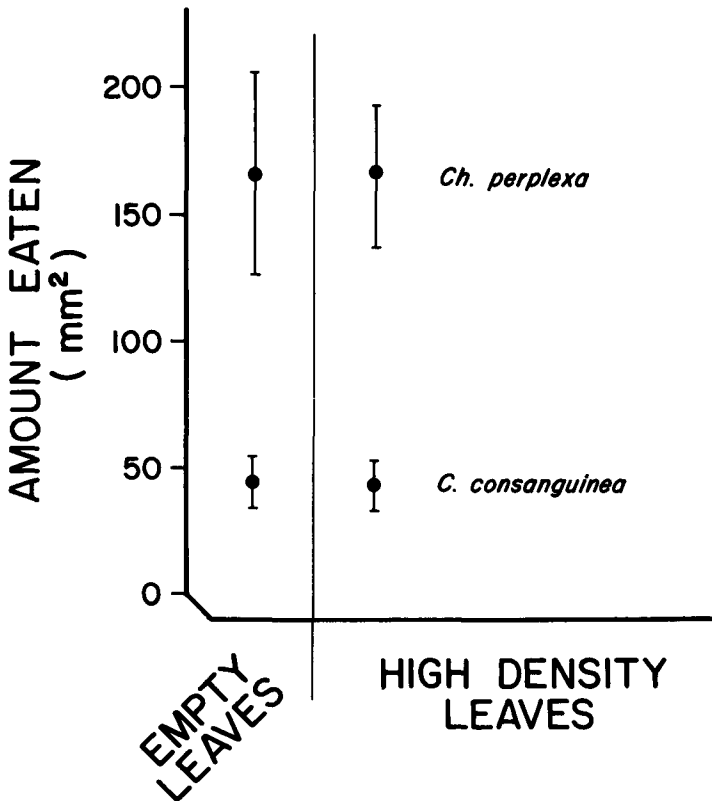


Fig. 3.2. Amounts eaten in laboratory experiments from *H. imbricata* scrolls found to be empty and scrolls found to contain relatively high densities of hispines in nature. Experiments were performed in Petri plates on leaf tissue that had been cut from fresh leaves, at the Finca La Selva field station. Dots indicate means, and bars extend one standard deviation above and below each mean. Each of the four treatments consists of 12 replicated observations. Each observation is the amount of feeding done in 24 hours by one pair of adults of the same species in a Petri plate. For *Ch. perplexa* the t statistic = 0.004, for *C. consanguinea* t = 0.155, when the amounts eaten from tissue excised from empty scrolls are compared to the amounts eaten from high-density scrolls.

properties. Of course, other sources of heterogeneity could reduce desirable scrolls to fewer than the total number. But, in my 9 years of experience with these insects and plants, I have found no pattern that indicates fewer than all *Heliconia* scrolls to be physiologically desirable and available to rolled-leaf hispines.

It is possible that food is depleted within desirable sections of leaves without depletion of a large fraction of the total leaf area. This possibility is extremely unlikely because only small fractions of leaf area are eaten even within parts of the scroll. The above tests (Figure 3.2) indicate that the leaf adjacent to eaten portions was desirable as food; this was the tissue fed to beetles from the high-density scrolls. Among scrolls, even the most isolated leaves in an area frequently contain hispines, so spatial patchiness does not effectively reduce densities of leaves. Leaves in both the sun and shade normally contain adults of these beetles, so this factor of microhabitat does not reduce usable leaves either. As I have speculated before (Strong 1982a), weak intraspecific attraction, and perhaps weak attraction among species of rolled-leaf hispines, may cause the slight pattern of clumping of beetles within leaves. Twice in my sampling experience, I have found scrolls so close together that they were touching, with one scroll containing relatively high densities of hispines and the other scroll empty. It is difficult to calculate the null probability of finding this sort of occurrence, but contiguous leaves with high and low densities are consistent with the idea that microhabitat differences in the forest do not cause observed density differences among leaves.

Is hispine feeding density-dependent? Do beetles of a species crowd one another or preempt available parts of the scroll so that less is eaten per beetle at high densities? To answer this question, I measured the influences of density upon the amounts of leaf eaten from scrolls of *H. imbricata* growing naturally in the forest. Plastic bags placed over very young scrolls created virgin rolled leaves that no beetles had occupied. Experimental beetles were placed inside when the tips of virgin scrolls had opened to 2 cm in diameter. Plastic bags were replaced loosely over experimental leaves, allowing beetles to exit via the base of the bag, but preventing new beetles from entering.

I have included only the data for scrolls that retained all of their allotment of experimental beetles for the full 24-hour duration of the experiment. Because beetles tend to move frequently among scrolls independently of density or previous occupants (Strong, 1982a), and many beetles left scrolls before the experiment was over, more trials were run at each density than produced usable data. If I had not allowed beetles to leave the bagged leaves, the feeding data would have been much more variable, because tying the bases of the plastic bags tightly would have produced data composed of at least two types of scrolls, those contain-

ing only beetles that fed without attempting to exit and those containing would-be emigrants, which were less interested in feeding. I found no obvious qualitative difference between scrolls that retained all of their experimental beetles and others. Both were healthy, and tissue from abandoned virgin scrolls was eaten normally by beetles in the lab.

The results of the intraspecific experiments are shown in Figure 3.3. *Cephaloleia consanguinea* is the smaller of the two hispine species in

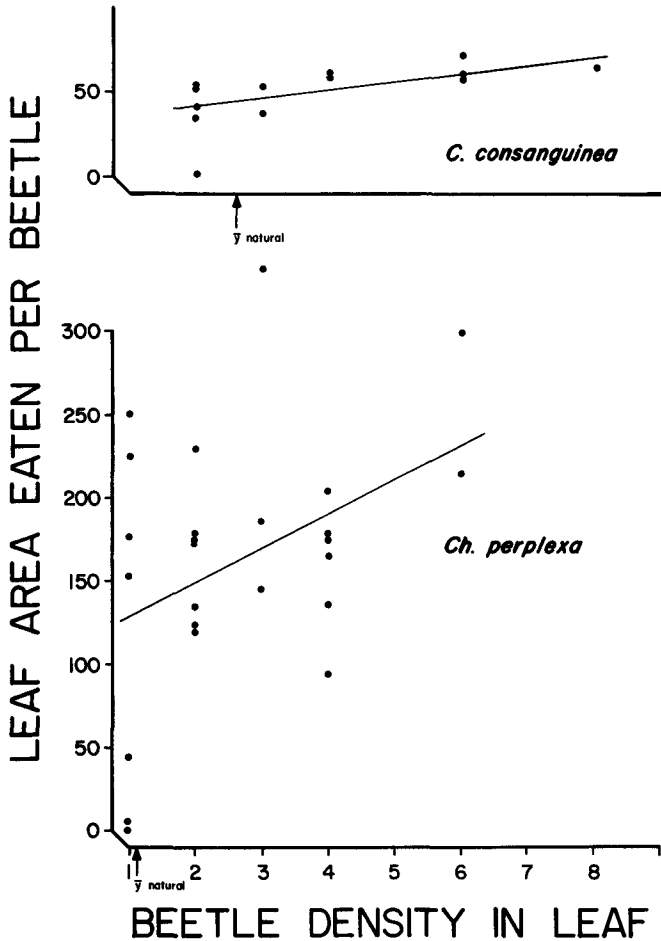


Fig. 3.3. Feeding rates as a function of density within species of hispines on *H. imbricata*. Data are from scrolls in nature. The average natural density of the two experimental beetle species in *H. imbricata* scrolls during July 1976, when the experiments were done, is indicated by arrows on the abscissa. Lines indicate linear regressions through the points. For *Ch. perplexa*, area eaten = $20.77 \text{ density} + 109.11$. For *C. consanguinea*, area = $5.89 \text{ density} + 28.39$.

these experiments and ate less than *Ch. perplexa*. Both hispine species responded to density in an inversely density-dependent fashion; both species ate more from scrolls at high than at low density, per individual. This result is indicated by correlation coefficients that were significantly positive (*C. consanguinea*, $r = 0.65$, $n = 13$, $p < 0.05$; *Ch. perplexa*, $r = 0.41$, $n = 25$, $p < 0.05$). The inverse density-dependence appears even though the feeding response was highly variable within densities. Most variability appears at low densities, as would be expected, where fewer beetles were responsible for a datum than at higher densities. At higher densities the fraction of feeding done by single individuals is a small part of the datum, so extreme individuals affect the datum less. Suggestions of non-linearity can be found in the relationships for both species in Figure 3.3. However, with the relatively few points and great scatter in the data, complex curve fitting is unsatisfactory.

The data show no evidence of crowding, interference, or resource depletion that would be manifested through density-dependence. Most scrolls in nature have densities much lower than the highest densities in these experiments. The average density of beetles in leaves during the time of experiments is shown on the abscissa of Figure 3.3. Average densities at other times were never as high as the median densities in these experiments (Strong, 1982a). The reason for inverse density-dependence, and not just a lack of any relationship to density, is still a mystery similar to the unknown reason for the slight clumping of these beetles among leaves that has been found in previous studies (Strong, 1982a). My current idea is that social interactions cause beetles to remain longer in high- than low-density scrolls and that remaining beetles feed intermittently.

Interspecific effects upon feeding rates were tested by placing beetles of different species together in the same virgin scrolls (Figure 3.4). Loose plastic bags over the scrolls excluded other beetles and allowed emigrants to leave. As in the intraspecific comparisons, I include only data from scrolls that retained all experimental beetles for the full 24 hours of the experiment. In Figure 3.4, I compare the amount eaten when the species were alone at the particular densities (from Figure 3.3) with the amount eaten when the species were physically together in the same leaf. Means for the species grown alone are the sums of the means for each species at the appropriate density from the data of Figure 3.3. The estimated sample variance for the species alone is calculated as by Steele and Torre (1960, eq. 5.13, p. 81). By the test of Cochran and Cox, I did an approximate t test of feeding, comparing beetle species along with those together in scrolls (Steele and Torre, 1960, p. 81). The approximate t value for the low species-density (1 *Ch. perplexa*, 2 *C. consanguinea*) = 0.11 (ns); that for the high species-density combination (2 *Ch. perplexa*, 4 *C. consanguinea*) = 0.59 (ns). Thus, just as with the intraspecific comparisons, there

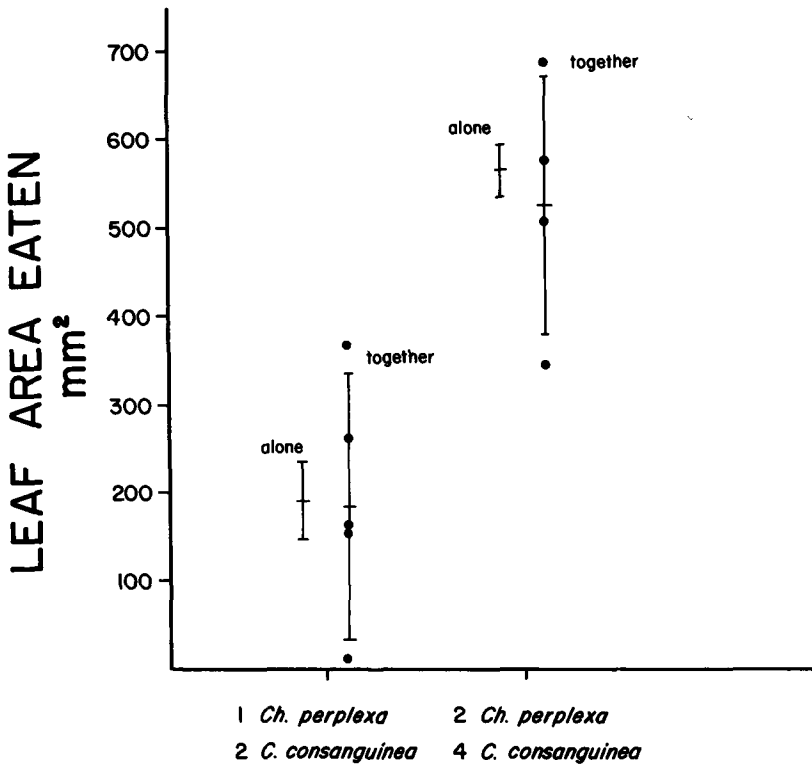


Fig. 3.4. Feeding rates of hispines for species alone in scrolls compared to rates for two species together. Means and standard deviations for species alone are shown as the center and ends, respectively, of the bar. For species alone, means and standard deviations were calculated by pooling data for the two species at the particular density. See text.

is no indication that densities of hispines roughly equal to those that occur in nature deplete resources sufficiently to cause competition. These experiments indicate little or no interspecific competition for food and corroborate the earlier finding of no interspecific competition for occupancy of scrolls (Strong, 1982a). Seifert (this volume) reaches a similar conclusion about hispine interactions with other arthropod species on *Heliconia*.

PARASITIDS AND HOST PLANT CHEMISTRY

Parasitoids and predators are likely very important in keeping the densities of *Heliconia* phytophages so low (Figure 3.5) (Morrison and Strong, 1980; Strong, 1982a). Of course, critical tests will come only from

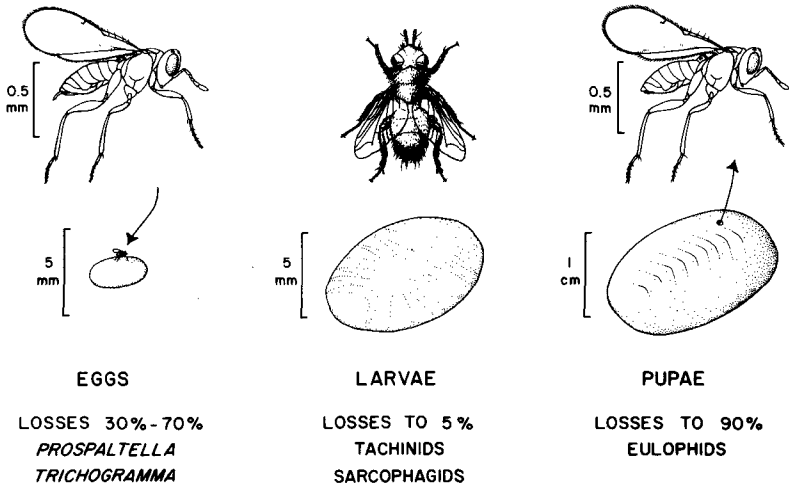


Fig. 3.5. Rolled-leaf hispines suffer high parasitism rates in the egg and pupal stages mainly from parasitic hymenoptera. Larvae are parasitized at much lower rates, and mainly by tachinid flies.

experiments that elevate and reduce mortality from natural enemies. An inadvertent experiment of this sort has been done on a large scale with bananas in Costa Rica. Banana is a close relative of *Heliconia*, and many *Heliconia* phytophages have become pests of bananas (Auerbach and Strong, 1981). During the 1950's and 60's, agriculturalists sprayed bananas heavily with organo-synthetic insecticides, often with a result opposite to that expected. Parasitoids disappeared, phytophage populations grew to very high densities, and defoliation followed. Parasitoids and other natural enemies of banana pests recolonized plantations when wholesale aerial application of insecticides was stopped about 1970, and then populations of phytophages fell to quite tolerable levels. Now, most banana growers no longer apply large amounts of insecticide (Ostmark, 1974; Clyde Stevens, pers. comm.). I have found most of the known leaf-eating species of banana pests, as well as very high rates of parasitism upon these insects, in unsprayed Costa Rican plantations since aerial spraying was stopped. The few outbreaks of phytophages that my colleagues and I have been able to find on bananas since spraying was stopped were on plantations with new owners, who were ignorant of the history of insecticide use on bananas. Every banana outbreak that I have seen followed heavy application of insecticides from aircraft. I have never found higher than 5% parasitism rates of any life history stage of any insect in sprayed banana plantations during an outbreak. Phytophage eggs and pupae in

unsprayed plantations normally have parasitism rates in excess of 50% (Strong, unpublished).

The idea that parasitoids prevent high densities of folivorous insects, and thus prevent defoliation, is not new (Howard and Fiske, 1911). Parasitoid control of phytophages has had great application in agriculture (DeBach, 1974). In recent ecological theory, parasitoids have been advocated as a major cause of low phytophage populations by Hairston, Smith, and Slobodkin (1960, = HSS). This part of the HSS theory has been distinctly unpopular. The major enduring objection to the HSS hypothesis has been that the empirical evidence adduced by its authors, that green vegetation is commonly abundant and thus not in shortage to folivores, is misleading. The objection can be paraphrased thus: foliage contains noxious phytochemicals, so what is green is not necessarily edible; folivores may be in shortage of food even with an abundance of vegetation (Janzen, 1975a; Murdoch, 1966). However, vegetation does not have to be generally edible to many species of herbivores for the HSS hypothesis to be valid (Slobodkin *et al.*, 1967). Even if phytochemistry and other factors restrict the number of potential defoliators to a small fraction of the local herbivore species, a few species always remain that are adapted to the particular chemistry and can defoliate the plant. Parasitoids can certainly prevent adapted phytophages from defoliating plant species that they specialize on. I agree with HSS, and do not argue that phytochemistry has no effect on any insect, but that it usually does not regulate phytophages adapted to a particular plant species.

The serendipitous "experiment" by banana growers with pesticides provides ample evidence that phytochemistry does not prevent defoliation by specialist phytophages in the absence of parasitoids. The potential complication of insecticides' "fertilizing" the plants, or changing their chemistry in some odd way to increase vulnerability to herbivores, is not a factor in this system. Bananas grow quite rapidly, and the outbreaks last many months after a single spraying. Rolled-leaf hispines do not occur on bananas, but many lepidopteran pest species have come to this crop from *Heliconia*. The lepidopterans are very sparse on *Heliconia*, just as they normally are on unsprayed bananas, and they suffer high rates of parasitism on *Heliconia* just as on bananas.

The lack of herbivore outbreaks and the chronically low densities of both hispines and Lepidoptera on *Heliconia* probably do not result from phytochemical protection, because *Heliconia* lacks many of the potentially noxious phytochemicals that protect other plants (Gage and Strong, 1981). An intense effort has uncovered none of the alkaloids, saponins, cardenolides or bufadienolides, cyanogenic glycosides, tannins (condensed or hydrolysable), or insect gut enzyme inhibitors that have been

found in other host plants. Moreover, extracts of *Heliconia* leaf do not inhibit feeding or growth in laboratory feeding experiments.

NEED THE GHOST OF COMPETITION PAST BE EXORCISED?

I have emphasized the influence of natural enemies in maintaining populations of insects on *Heliconia* far below densities that would cause neo-Malthusian forces to operate among species. For phytophagous insects in general, other factors are known to complement the influences of natural enemies (Lawton and Strong, 1981), and I would argue that hispine communities are, *a priori*, no exception. Host plant phenology, seasons, and environmental stochasticity in the form of weather variations may also contribute to population dynamics and densities of these insects.

The orthodox neo-Malthusian explanation of any absence of competition in communities is well described by Connell's (1980) wonderful rubric "the ghost of competition past"; species differences that reduce competition are assumed to be fossils of competition that selected for species differences. Advocates of this theory infer that "overdispersed niches," "niche compensation," and "resource partitioning" are evidence of ancient competition, but that such mechanisms can never be investigated experimentally because the molding forces of competition have been obviated by the evolutionary changes that were caused by the competition (Schoener, 1974b, p. 24). Like Connell (1980) and Krebs (1978), I feel that this theory is most unsatisfying because it is virtually impossible to falsify. What sort of communities would have occurred in the absence of the postulated competition? Species differences occur for a plethora of reasons other than competition. Certainly, only peculiar circular logic underlies interpreting the absence of competition as proof that it once existed.

Communities of phytophagous insects in general offer a model alternative to the assumptions of theory that invokes the ghost of competition past. Neo-Malthusian forces do not often come into play among insects eating plants, and there is little reason to conjure spirits from the past because we can see today good reasons for community structure. Actually, the lack of significant interspecific competition is not restricted to phytophagous insects. Birch (1979) has argued that the non-competitive coexistence of organisms sharing resources occurs fairly widely in ecological nature, especially among marine invertebrates. A similar conclusion is reached by Connell (1975): "the evidence . . . from controlled field experiments on invertebrates and plants, suggests that many species seldom reach population densities great enough to compete for resources, because either physical extremes or predation eliminates or suppresses them in their young stages." On another tack, introduced species would be quite prone to overt interspecific competition according to orthodox competi-

tion theory, because they would not have had time to evolve differences to reduce competition. However, this implication of the theory is not borne out by evidence. Simberloff (1981) analyzed many case histories of diverse species introduced by man into new geographical regions and concluded that interspecific competition is usually absent or so weak that no effect can be detected upon other species. This result militates against invoking competition as a general evolutionary antecedent to longstanding communities. Den Boer (1980) finds a similar lack of support for inexorable neo-Malthusian forces in communities of carabid beetles, as do Wise (this volume) for spiders and Lawton (this volume) for insects of bracken fern. Andrews and Petney (1981) have cleverly worked through the implications of the competition's-ghost theory for the niches of reptile ticks, to find that "there is no evidence to suggest that such competition in the past, or competition at present, maintains the parapatric boundaries found in these species. . . ." Thus, the ghost need not be exorcised for many organisms because there is little reason to suspect haunting in the first place.

The Role of Competition in Spider Communities: Insights from Field Experiments with a Model Organism

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Considerable ecological theory postulates a central role for interspecific competition as a cause of patterns in resource utilization, distribution, and relative abundance of animal species. Tests for competition frequently have been indirect, relying upon inferences from patterns that are consistent with competition theory but that may have alternative explanations. Continuing calls for more direct tests (*e.g.* Reynoldson and Bellamy, 1971; Connell, 1975; Colwell and Fuentes, 1975; Pianka, 1976; Wiens, 1977a) reflect an increasing awareness of the value of carefully controlled field experiments. However, field experiments have not been widely used to test for competition in animal communities, probably for two major reasons. First, most species and their resources are not amenable to straightforward manipulation. Second, many community ecologists have avoided detailed studies of a few species in preference to a holistic approach that attempts to explain broad patterns by comparing different communities.

Reliance upon field experiments requires substantial acceptance of a reductionist approach to community ecology. The question of whether we can understand multispecies interactions from studies of one or a few species fuels the controversy between "population-reductionist" and "community-holistic" practitioners of ecology (*cf.* Simberloff, 1980; Levins and Lewontin, 1980). Generality of the reductionist-empiricist approach can be increased by selecting appropriate model systems for experimentation. Ecologists justifiably envy the reductionist successes of molecular biology and physiology, and often regret that the inherent variability of ecological systems precludes finding an ecological white rat or an *E. coli* of evolutionary ecology. Although nearly everyone finds joy in the indeterminacy of natural variation, this noise that is sometimes "music to the ecologist" (Simberloff, 1980) also often grates on the ecological ear. The need to generalize requires identification of appropriate model systems with more flesh than sets of differential equations. Such an ecological

model will never be a single, or even a few, species, but rather must be a type of organism represented by many similar, yet different, species. A powerful model will be amenable to field experiments, will be widely distributed, and will have life-history characteristics that permit numerous associated behavioral, physiological, and non-experimental ecological studies. Also, the most useful ecological models will incorporate a diversity of adaptive lines, so that inferences can be generated about how biotic interactions and physical factors shape the evolution of communities.

I will examine the evidence, indirect and direct, for interspecific competition among individuals of a model terrestrial predator, the spider. My goals are (1) to address the question of competition using an ecological model that is well suited for field experiments and (2) to launch a general discussion of field experimentation as a means of testing and building ecological theory.

COMPETITION AMONG SPIDERS

Although occasionally afflicted with an irrational fascination with vertebrates, most ecologists, after detached deliberation, would name the spider as a typical terrestrial carnivore. Spiders are ubiquitous in terrestrial ecosystems and capture a major fraction of the energy in consumer species that escapes the decomposers (Menhinick, 1967; Van Hook, 1971; Moulder and Reichle, 1972; Turnbull, 1973). Species diversity is high, as is the variety of spider guilds, which range from wanderers to sit-and-wait ambushers to kleptoparasites, which steal the prey of others. Spider abundance and diversity facilitate comparative evolutionary studies (*e.g.* Enders, 1975, 1976; Anderson, 1978; Olive, 1980). The accessibility of most life-history stages makes spiders suitable for detailed behavioral and physiological studies, and for holistic investigations of community organization. Apart from these substantial virtues, many spiders, particularly web-spinners, are well suited for manipulations of resources and densities of conspecifics and heterospecifics under relatively unaltered natural conditions.

Reynoldson and Bellamy (1971) proposed five criteria that, when satisfied together, establish interspecific competition beyond "reasonable doubt": (1) indirect evidence for resource limitation, (2) indirect evidence for intraspecific competition, (3) evidence for interspecific competition from the comparative distribution and/or relative abundances of the possibly competing species, (4) direct evidence of resource limitation and intraspecific competition from controlled manipulations of resources and population density, and (5) appropriate responses by a species to the experimental addition or removal of potentially competing species. Satisfaction of the first three criteria does not confirm the existence of competition, nor does the absence of patterns that meet these criteria prove

that competition is absent. Nevertheless, indirect evidence makes field experiments more interpretable and helps unite reductionist and holistic approaches. I will summarize the current indirect and direct evidence concerning interspecific competition in spider communities.

Several ecologists have attributed differences in distribution or abundance of spiders to interspecific competition. Luczak (1963, 1966) hypothesized that differential shifts in the dominance relationships of both web-builders and wandering spiders may have resulted from changing intensities of competitive interactions in the communities she studied. Vollrath (1976) found that a kleptoparasitic species apparently shifts its diurnal activity pattern in response to decreased abundance of a congeneric species. Different phenologies have been interpreted as adaptations evolved to reduce interspecific competition (*e.g.* Luczak, 1959; Breymeyer, 1966). Uetz (1977) and Turner and Polis (1979) hypothesized that closely related wandering and raptorial spider species of similar size avoid competition by spatial and temporal niche separation. The contiguously allo-topic distribution of two wolf spider species (Greenstone, 1980) supports this interpretation of the organization of wandering spider communities. Enders (1974) suggested that two closely related orb-weavers, *Argiope aurantia* and *A. trifasciata*, respond to competition by placing webs at different heights in old-field vegetation. Uetz *et al.* (1978) have suggested that differences in both mesh size and placement of the web facilitate coexistence of these two species. Taub (1977) and Brown (1981) have also interpreted niche differences between these *Argiope* species in the context of interspecific competition. Uetz *et al.* (1978) also argue that reduced overlap in habitat utilization between congeneric forest orb-weavers, and between non-congeners with similar web characteristics, permits coexistence by reducing or eliminating interspecific competition.

Not all ecologists have concluded from their holistic studies of spider communities that competition is a major interaction among these predators. Gertsch and Riechert (1976), Post and Riechert (1977), Turner and Polis (1979), and Maelfait *et al.* (1980) conclude from their niche analyses that interspecific competition is unimportant for most spiders. High or low niche overlap can be evidence for or against competition, depending upon assumptions made about the relative importance of exploitation and interference competition and the relevance of the evidence to evolutionary versus ecological time scales. Such indirect evidence cannot be decisive, but several observed patterns in abundance, local distribution, and niche overlap are at least consistent with the theory that interspecific competition exerts a significant influence on the organization of spider communities.

Indirect evidence indicates that spider populations are resource limited, which satisfies another of Reynoldson and Bellamy's criteria. The rela-

tively low metabolic rates of spiders, particularly under food deprivation, suggest they have evolved under situations of frequent prey scarcity (Miyashita, 1968a; Anderson, 1970). Extensive yearly variation in size at maturity and fecundity also suggests that natural variation in prey availability can significantly limit spider growth and reproduction (Kajak, 1967; Wise, 1983). Temporal changes in population density and fecundity of the linyphiid *Erigone arctica* correlate with changes in abundance and activity of a collembolan, its major prey (Wingerden, 1975, 1978). Comparing the growth and reproduction of spiders in the laboratory with their performance in nature also indicates that prey often is a limited resource for spiders (Miyashita, 1968b; Kessler, 1973; Anderson, 1974; Kajak, 1978). However, this evidence suffers not only from being indirect but also from failing to indicate whether spiders compete for food. Since resource scarcity could limit growth and reproduction without behaving as a density-dependent factor, Reynoldson and Bellamy proposed experimental studies of competition within a species as their fourth criterion for establishing interspecific competition. Fortunately, both resources and spider densities, especially those of web-building species, can be manipulated under field conditions to test directly for resource limitation and intraspecific competition.

Field experiments have proven that web sites and prey levels may be limiting for web-building spiders. Colebourn (1974) modified the natural vegetation and also introduced artificial web substrate to establish that a shortage of suitable web sites limits the abundance of an orb-weaver in heather habitat. In a series of elegant studies, Riechert (1977, 1979, 1981) has proven the importance of intraspecific agonistic interactions between female funnel-web spiders as the mechanism of interference competition for a limited number of high-quality web sites. Schaefer (1978) demonstrated that a limited number of suitable sites is a major component of density-dependent population regulation of a sheet-web weaver. By manipulating both spider densities and prey levels of another sheet-web weaver, the filmy dome spider, I uncovered exploitation competition for prey among adult females (Wise, 1975).

Four of the five criteria of Reynoldson and Bellamy for establishing interspecific competition have been satisfied for the ecological model, *i.e.* spiders in general. However, clear experimental evidence of major competitive interactions between closely related spider species is lacking. Removal and density-manipulation experiments have not established interspecific competition to be a significant interaction in spider communities. Schaefer (1975) found no competitive release among wolf spiders after reducing one species on open plots and adding different combinations of species to enclosed areas. Schaefer (1978) also found that increasing the density of a sheet-web weaver in its natural habitat had no

effect upon the population of a related species in which he had experimentally demonstrated intraspecific competition for web sites. Results of a field experiment, in which I supplemented the prey of adult females, showed that natural prey levels can limit the egg production of two syntopic species of forest orb-weavers, the basilica spider and the labyrinth spider (Wise, 1979). The following year I manipulated spider densities and uncovered no evidence of interspecific competition (Wise, 1981a). Neither species affected the web placement, web-site tenacity, or egg production of the other.

Other recent or ongoing experimental studies of interspecific competition among web-building spiders have also uncovered no evidence for major interactions between species. Indirect evidence from patterns of vertical stratification, habitat utilization, and prey differences has suggested the importance of interspecific competition between the orb-weavers *Argiope trifasciata* and *A. aurantia* (Enders, 1974; Taub, 1977; Uetz *et al.*, 1978; Brown, 1981). However, two years of field experiments did not produce evidence of significant competitive interactions between these species (Horton and Wise, 1983). Two replicates of mixed and single-species populations at two densities were established in open, 12 m $\times$ 12 m plots by removal and addition of juvenile spiders early in the summers of 1979 and 1980. The manipulations uncovered intraspecific competition, which was weak and not consistently present from one season to the other. Clear evidence of interspecific competition was lacking. Much of the variation in habitat utilization and dietary overlap resulted from changes in the weather and the vegetation, not from competition with the other species. Riechert and Cady (1983) conducted a removal experiment with a community of web-builders inhabiting rock outcrops in the mountains of Tennessee. Four species were studied, each from a different family. Although the species build quite different webs, they showed high overlap along several major niche parameters. Eggs and spiders of three species, in different combinations, were removed from different cliff areas. There was no evidence of competitive release of the remaining species as measured by niche expansions or increases in demographic parameters such as survival or egg production.

The only clearly documented example of significant interspecific competition among spiders is prey-stealing by kleptoparasites such as *Argyrodes*, which are adapted for living in the webs of larger spiders (Vollrath, 1979; Rypstra, 1981). However, the competitive interaction is almost entirely one-way and represents highly specialized foraging behavior. In fact, apparently many *Argyrodes* species rarely spin their own webs.

Interspecific competition may not be a major interaction among spiders, our model terrestrial carnivore. Of course interspecific competition between non-araneid predators may be important over ecological time; the

spider has been proposed as one, not the sole, ecological model of a terrestrial predator. Of what value is the spider as a model if it does not represent a broader class of organisms? Two points are relevant: (1) non-mathematical models in ecology, *i.e.* representative species systems, will never play roles identical to those of models in the more reductionist biological sciences; (2) spiders by themselves constitute a rich ecological model that encompasses a broad range of organisms. But can a diverse assemblage function as a useful model? Returning to the question of interspecific competition in spider communities will illustrate how such a broadly defined model can function. Despite indirect evidence of interspecific competition, and despite direct experimental evidence of resource limitation and intraspecific competition in some species, experimental proof of interspecific competition among spiders is lacking. Failure to find direct evidence brings into question the relevance of competition theory to understanding spider communities. However, one might argue that the theory is weakened only when experimental evidence of interspecific competition is absent among particular species for which all four of Reynoldson and Bellamy's other criteria are satisfied. Such a view is too extreme because it defines the model organism too narrowly. To be useful, a body of general theory should work for organisms as different, yet as similar, as spiders in general.

Testing the relevance of competition theory with a particular, broadly viewed model system is valuable because additional studies with that model will yield explanations of the absence or presence of competition in terms of other interactions. Such meshing of diverse theories and concepts is necessary if ecology is to develop useful general principles. Future field experiments may uncover widespread competitive interactions between closely related spiders, but the immediate problem is to explain the absence of experimental evidence for significant interspecific competition in light of evidence, both indirect and direct, of resource limitation among spiders.

Traditional theory leads to the conclusion that similar spider species have evolved niche differences to avoid competition. Schaefer (1978) presents convincing evidence that the two species he studied do not compete because they have different web-site requirements. Niche theory, however, does not provide the best explanation for the absence of competition between the basilica and labyrinth spiders. The prey captured by the two species is remarkably similar, especially in view of their dissimilar webs (Wise and Barata, 1983). The absence of competition between these species in the field experiment discussed previously (Wise, 1981a) is most directly explained by the fact that intraspecific competition was weak or absent.

Variation in prey abundance might alleviate competition in some years. Evidence for food limitation of basilica and labyrinth spider fecundity

comes from a 1977 prey supplementation experiment (Wise, 1979). The experiment that uncovered only minor intraspecific competition was done in the same habitat but during the following year. During this study, in which food was not experimentally supplemented, the rate of egg production by each species was equal to that of females that had received extra prey the preceding year. Thus, I concluded that spiders were not competing in 1978 because prey levels were not limiting fecundity that year (Wise, 1981a). However, in 1978 food limitation was not directly tested, nor was an adequate experimental test of competition conducted the previous year. Results of two 1980 experiments (Wise, 1983) with the labyrinth spider indicate that exploitation competition is absent even in years when a shortage of prey limits growth and fecundity. In one study I tested for intraspecific competition by establishing populations of adult female labyrinth spiders at two densities on open experimental units. Initial densities varied 10-fold between the two density treatments, representing a major portion of the crowding spectrum of non-experimental populations. Although no direct information on food limitation of mature females was collected in 1980, prey probably were relatively scarce, since fecundity was lower than in the year (1977) when the field experiment demonstrated food limitation. Despite evidence of agonistic interactions over webs, and despite indirect evidence of food limitation, survival was not lower in the high-density treatment, nor was exploitation competition affecting fecundity at the high density. A similar experiment in 1980 with immature labyrinth spiders, but which incorporated prey supplementation, also uncovered no negative effects of density upon survival or growth, despite experimental evidence that scarcity of prey was limiting growth rate. Previous field experiments also showed food supply to be a density-independent factor limiting the growth of juvenile filmy dome spiders (Wise, 1975).

Exploitation competition is possibly weak or absent in these situations because spiders may capture a small fraction of the prey that enters the air space surrounding their webs; if so, one or a few additional webs in a portion of this volume might not noticeably decrease rates of prey capture. The presence of additional webs might actually facilitate prey capture (Rypstra, 1979; Uetz, in press), thereby counteracting opposing negative effects of exploitation competition. Such a positive "knockdown" effect has been documented for tropical colonial spiders, but without actual proof of its occurring among non-social temperate species, it must remain a highly speculative explanation for species such as the labyrinth spider. Some spiders may space themselves at distances that minimize competition for prey in environments where exploitation competition would occur at high spider densities. Riechert (1974, 1978) has proposed that behaviorally based spacing is widespread among spiders, and she predicts