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The Controversy over Interspecific Competition

Thomas W. Schoener

Despite spirited criticism, competition continues to occupy a major domain in ecological thought

Several years ago this journal published, only months apart, two articles seemingly in total disagreement as to the importance of interspecific competition in nature. On one side, Wiens (1977) argued that substantial competition between many species is intermittent, perhaps even rare, and that its importance as an agent of natural selection may therefore be minimal. On the other, Diamond (1978) argued that competition is often a major driving force of natural selection, that Darwin saw this, and that his forgotten wisdom was only now being rediscovered. Scientists who work on particular organisms are prone to generalize from them, and Wiens and Diamond explicitly supported—and indeed have continued to support—their opposing views with data from their own work. Yet both study birds! Here is an example of the kind of controversy about how the world works that makes contemporary ecology simultaneously so exciting and so frustrating.

A few years have now passed, and the controversy on competition has steadily simmered, occasionally coming to a boil. My purpose here is to describe the progress of the controversy to date and to attempt a resolution of certain apparent contradictions in light of some new discoveries and some new ideas. To a degree, I will offer a compromise view, though my compromise is admittedly skewed toward Diamond's position.

For a quarter of a century, and until very recently, the view that competition is the dominant ecological interaction was the prevailing one, so much so that it has been referred to as the competitionist's "paradigm" (Strong 1980). The apogeal position on interspecific competition can be presented as six main propositions. First, species "too" similar in the resources they use cannot coexist "for long"; one will competitively exclude—i.e., exterminate—the other. This is the Gause principle. Second, species that coexist in nature do so by virtue of "sufficient" differences in ecological niche, or equivalently, in use of resources. Third, interspecific competition is a powerful evolutionary force, selecting

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for adaptations that result in species differing in use of resources—for example, differences in beak size that are correlated with differences in the size of the seeds consumed. Fourth, geographic distributions of species are often determined by competitive pressures: species "too" similar ecologically have disjunct ranges. Given enough time, competitive pressures determine how many and which species coexist in a community. Fifth, species may compete by interference—for instance, by aggression or the production of toxins—as well as by depletion of resources. However, interference is unlikely to evolve if resources are not "sufficiently" scarce.

A sixth proposition is that experiments performed on species with "substantial" overlap in their use of resources should detect interspecific competition. For example, the introduction of individuals of species B into a place inhabited by species A should depress the latter's population, or should affect individuals of species A in ways—for instance, decreased growth or body size—that will ultimately depress its population. Removal of individuals of species B should have the reverse effect. Of course, species that have diverged in their genetically controlled adaptations as a result of competition to such a degree that the overlap in their use of resources is "slight" should not be affected much, if at all, over the "short term" in such experiments—a fairly obvious point that seems to have caused a lot of confusion until recently.

In preparing this list, I have placed vague qualifiers in quotation marks; as we will see below, much mathematical and some empirical effort has been invested in attempts to sharpen such terms.

Origins of the theory

The process by which the competitionist's "conventional wisdom" (Wiens 1977) became conventional occurred over a period of about thirty years, during which three streams of influence flowed together: the experiments of Gause, which motivated the formulation of his principle and which showed that species using the same food supply did not coexist in the laboratory; the mathematics of Lotka and Volterra, used extensively by Gause as a theoretical basis; and the data and methodology of the "New Systematics," a major synthesizing of various evolutionary principles by Mayr and Huxley, among others.

Much of the crucial blending seems to have taken place in Britain during the 1940s, the principals being David Lack and Julian Huxley. Lack's autobiography

(1973), written long before his death but published posthumously, is probably the most reliable record of what went on:

I became puzzled to know whether, and if so how closely, different species could resemble each other in ecology, and slowly over some six months during 1943, I came to elaborate Gause's principle of competitive exclusion. . . . In 1939 I had read, but immediately dismissed, Gause's simple statement of this principle . . . , and in 1942 I read, but did not pay attention to Huxley's idea ... that size differences between related species in the same habitat might have been evolved to reduce competition. I now painfully rediscovered both ideas for myself. In 1944 I contributed to a meeting of the British Ecological Society on Gause's principle, but was widely disbelieved, though for almost the only time in our lives, Charles Elton and I were on the same side, he through his studies of animal communities. [p. 429]

In an appended eulogy, Mayr elaborates: "The emphasis in species studies during the 1930's and 40's was strongly on the nature of isolating mechanisms . . . . It was David Lack more than anyone else who restored balance by emphasizing the importance of ecological compatibility between species. Darwin had seen this quite clearly . . . and, of course, Gause had provided the first experimental verification, but the principle of competitive exclusion was at that time largely ignored" (p. 433).

But this was only the start. Much of the later important development of these ideas occurred in the New World, primarily as a result of crucial papers by G. E. Hutchinson and his student Robert MacArthur. As their papers testify, both were keenly influenced by what was going on in Britain.

What was it about these papers—a blend of the three streams of influence described above—that resulted in the subsequent strong advocacy of competition? A number of factors seem to have been involved. First, certain patterns were given a simple, plausible explanation. For example, resource partitioning—the regular and/or marked differences in the diet, habitat, or other "niche dimensions" of coexisting species—could be accounted for (see Schoener 1974a), as could patterns in associated morphological characters such as beak size. Moreover, motivation arose for the collection of new data to test the theory further. Less loftily, detailed natural history studies of particular species, which would have been done anyway mostly for the fun of it, were given a sophisticated rationale. Beyond such ties with data, however, was the stimulating way in which Hutchinson and MacArthur, especially, presented their ideas. What biologist would not be lured to read a paper subtitled "Why Are There So Many Kinds of Animals?" (Hutchinson 1959). And finally, a quantitative theory of competition between natural populations appeared well within reach.

Lotka and Volterra had much earlier done considerable modeling of the population dynamics of competition. In their formulation, a crucial parameter in determining the outcome of competition is the so-called "competition coefficient." This is a dimensionless number that gives the effect of a heterospecific individual as compared to a conspecific one on the growth rate of a given species population. But it was MacArthur and Levins (1967) who made the first attempt to link overlap in the use of resources—i.e., the data of resource-partitioning studies—to the competition coeffi-

cient and thereby to propose a quantitative answer to the question of just how similar species can be and still coexist.

They assumed that

$$\alpha_{ij} = \frac{\sum_h p_{ih} p_{jh}}{\sum_h p_{ih}^2}$$

where α_{ij} is the competition coefficient and p_{ih} is the fraction of resource use by species i that is in resource category h. For example, if the resources in question are habitat types, p_{ih} is the fraction of time spent by all individuals of a population of species i in habitat h; if the resources are food types, p_{ih} is the fraction of the population's diet obtained from food h. The crucial property to note about this coefficient is that it varies directly with overlap in use of resources: the more similarly species use resources, the more similar are the p_{ih}'s, and the larger is α.

In the same optimistic spirit, May and MacArthur (1972) computed from a variety of approaches a relatively invariant "limiting similarity," which expresses in terms of the ecological niche (defined as the p_{ih}'s) how similar species can be and still coexist. If the p_{ih}'s of a given species along a particular niche dimension such as prey size can be represented as normal distributions identically spaced and shaped, similarity can be measured as d/w, where d is the distance between the peaks of the distributions and w is their common standard deviation. Conveniently, limiting similarity worked out to be about 1.0 for a stochastic model embodying various amounts of environmental fluctuation; a treatment appropriate for a nonfluctuating environment—that is, a "deterministic" one—gives a somewhat larger and less restricted d/w (May 1974).

Initially, a great variety of data were interpreted as confirming what by then deserved to be called the theory of competition. Many observations of resource partitioning and geographic distribution seemed to be in accord (see Pianka 1981). In addition, certain observations testing the quantitative predictions of the theory in its pure, early 1970s form were remarkably supportive. Pulliam (1975) showed that the theory could predict the identities and relative abundances of species of seed-eating sparrows in several desert communities. Werner (1977) found that species of sunfish coexisting over broad areas had diets and foraging abilities that closely matched the predicted limiting similarity.

Perhaps the most impressive correspondence of all was discovered by Fenchel (1975), who studied two species of estuarine snails nourished by organic "scuz" adhering to small inorganic particles that they ingest. Wherever the species occurred together, the difference in their body sizes was such that the predicted ecological limiting similarity in the size of the particles ingested held true. Moreover, the species showed character displacement: where they did not occur together, they were about the same size. Apparently through genetic change, the species diverged to the limiting similarity whenever their ranges merged, which happened independently a number of times during the last 150 years.

Experimental tests of the theory were rare, though some laboratory work with beetles and flies supplemented the early experiments of Gause with micro-

organisms (see Pianka 1981). These early studies helped to enrich the theory, especially as they illuminated the role of interference competition, showing that it was sometimes more important than competition in use of resources and often the sole kind of competition detectable. Through the early 1970s, however, field experiments had very little influence on the theory. For one thing, few had been performed, and fewer still were remembered (Jackson 1981). Those that became prominent were viewed as consistent with the theory of competition though not really directed toward its major propositions. Connell (1961), for example, showed that when one species of intertidal barnacle was removed another expanded into its habitat; inasmuch as the resource in question is space, and therefore relatively uniform, the experiment seemed to confirm Gause's principle. The competitive mechanism, however, was interference—one species overgrew and shoved aside the other—and the sort of competition in use of resources envisaged in MacArthur and Levins's equation did not occur.

The optimism surrounding the competitionist view peaked in the mid-1970s and began to erode during the second half of the decade. As a sure sign of the uncertain times, papers written by newly emerged Ph.D.s became apologetic or admonitory. What was the nature of the case that was building against the original theory? Attacks were methodologically varied, coming from new mathematical formulations, from fresh statistical analyses of old observations, from new observations, and from a burgeoning number of field experiments. Some of the criticism was clearly "friendly," modifying or extending various aspects of the original theory. Other criticism was potentially revolutionary, challenging the underlying world view. Five kinds of issues, summarized below, have been especially influential.

Mathematical modifications

More than any other critics, mathematical theorists were sympathetic; those who had an opinion believed in the importance of competition in nature.

MacArthur and Levins's initial justification for their competition-coefficient formula was moderately vague; the formula was presented as reflecting simultaneous spatial overlap in attempts to gain resources. Later, seemingly by coincidence, the same formula, festooned with additional terms, fell out of a system of equations devised by MacArthur that dealt explicitly with consumers and their resources. The principal difference was that in the case of dietary data, electivities—measures of preference in which p_{ih} is divided by the relative frequency of resource type h in the environment—took the place of the p_{ih}'s (Schoener 1974b). Terms incorporating how much food is consumed per individual also appeared; hence larger competitors, which eat more, could be competitively superior (e.g., Wilson 1975). Other competition-coefficient formulae can be justified in other ways, and Abrams (1975) has shown that the particular value of limiting similarity is substantially affected by the particular formula used. Moreover, even if MacArthur and Levins's equation is used, very different values of limiting similarity result when the p_{ih}'s are not normally distributed (see Roughgarden 1979).

In another vein, it became apparent that a class of models different from that formulated by Lotka and Volterra more strongly favored coexistence, all other things being equal (Ayala et al. 1973; Schoener 1974c and 1978). A major property of these new "concave zero-isocline" models is that the rarer a given species is, the more individuals of a second species must be introduced for the equilibrium population of the rare species to decrease by a fixed amount. In other words, sufficiently rare species should be little affected by the amount of competition that might be produced by, say, an experimental introduction. In Lotka and Volterra's model, by contrast, introduction of a given number of individuals of a second species always reduces the equilibrium population of the first species by a fixed amount, no matter how rare it is. The new models have received considerable support from certain laboratory experiments (e.g., Ayala et al. 1973), though not all (Vandermeer 1969).

Turning to stochastic models, Turelli (1981) greatly modified the original mathematics of May and MacArthur, concluding that environmental fluctuations may or may not promote competitive exclusion, depending on relatively minor variations in the structure of the model. More optimistically, he found that small amounts of environmental fluctuation have small effects, so that the simpler deterministic approach is often adequate.

Finally, a number of researchers focused on the evolution of niche properties, making different assumptions about what features of the niche are subject to evolutionary change and calculating the differences species should show once niches stabilize in evolutionary time (see Roughgarden 1979, and Case 1982). Such differences are sometimes substantially greater than the ecological limiting similarity.

The gist of all these mathematical findings is that ecological and morphological differences between species should not necessarily be constant from one system to another, although under certain circumstances they may be. Moreover, an array of qualitative predictions about how similarity should vary with varying biological characteristics now exists. Simberloff and Boecklen (1981) have disparaged the more complicated theory as a "panchreston," something that "by explaining everything, explains nothing" (p. 1224). Rather than deploring its diversity, however, I view the new mathematical theory as better reflecting nature's own diversity. Unfortunately, few of its aspects have yet been tested in any kind of detail.

Statistical reevaluation

Recently the sort of observational evidence originally used to support the competitionist view has been vigorously scrutinized. For example, many scientists, following the lead of Huxley, Lack, and Hutchinson, have claimed that regular or large size differences or both characterize otherwise similar coexisting species. Such data, including those from the archetypal example of the Galápagos finches (Abbott et al. 1977), have been critically reexamined by a group centered at Florida State University. This group has also reanalyzed data on geographical distributions used to support the claim that fewer similar species coexisted on given islands than would be expected were the distributions random (see Strong et al., in press).

With some exceptions, the critics could not distinguish the allegedly patterned data from random expectation. To generate the latter, elaborate null models were sometimes constructed; these took various forms such as randomizations and Monte Carlo simulations. For example, Strong, Szyska, and Simberloff (1979) shuffled together the sizes of existing species of finches in the Galápagos archipelago and repopulated the islands by random draws from this pool.

Despite the recentness of these challenges, extensive rebuttals have already appeared. The rebuttals vary the technique of arriving at a null hypothesis—there are many ways of generating a "random" expectation. The defenders invariably found more pattern than did the critics, and Simberloff has now agreed that the Galápagos finches in any event do sometimes show differences in size greater than would be expected were the differences random. Nonetheless, to be fair to the critics, they have had their effect. Not as much observational evidence in support of competition appears to exist as some once hoped, and that which does exist is now being more carefully presented and is therefore less vulnerable to criticism.

Out of all this furor came another, more basic kind of rebuttal to the critics of the competitionist view: the technique of using null models was itself questioned. Certain analyses do indeed point out biases in particular null models. For example, Colwell and Winkler (in press) showed by simulation that the technique used by Strong and his co-workers to determine whether size differences are patterned, as well as similar methods, underestimate the role of competition. Species especially vulnerable to competition—say, because of morphological similarity to other species—may go extinct everywhere. Hence they would be unavailable to form the pool from which species are sampled to determine if existing combinations show greater differences than would be expected if species populated islands randomly.

Nonetheless, the fact that particular null models are biased seems insufficient reason to abandon the technique altogether; any statistical model embodies assumptions that must usually fail to match the specific situation to which it is applied. To forego such analyses is to forego hope of ever rigorously evaluating the evolutionary effects of competition; observational evidence is all we are ever going to have in most cases, contrary opinion notwithstanding. Given that we often do not know which assumptions are false, or that we sometimes know all of them are false but also know how they are false, the use of several null models to bracket the possibilities seems the best we can do.

Variable environments

Unlike the category of objections based on statistical considerations, the variable-environment view is an opinion about the prevalence of competition in the real world. This view is most well developed as an antithesis to the competitionist position and is roughly as follows. For reasons having little to do with biological interactions of any kind, environments fluctuate markedly over time. Populations are frequently well below the carrying capacity of their environments, in a state of plenty as far as resources are concerned. During such times, compe-

tition—and therefore selection for characteristics reducing interspecific competition—is much less intense or does not occur at all. Occasionally this state of plenty is punctuated by a "crunch"—a period of scarcity during which competition does occur. However, the effects of any directional selection that might have occurred during the lean period could easily be quickly obscured by an increase in phenotypic variability once the crunch ends. The twofold implication is, first, that competition will normally not be detectable by any means, and second, that genetically controlled characteristics will often not be understandable on the basis of selection driven by competition.

This simplified summary of the variable-environment view approximates its most prevalent version, that launched by Wiens in his 1977 article. However, related ideas had been advocated in ecology well before 1977, most notably by Andrewartha and Birch (1954), who believed that climatic factors rather than biological interactions such as competition were primary. It is perhaps inaccurate to call this idea an antecedent; the tree of ecological thought is ramiform, with numerous terminal branches and a great deal of noncontemporaneous parallel evolution. Rather, Wiens's ideas about variable environments were based primarily on his own studies of birds in the shrubsteppe of continental, cold-temperate North America. He and his colleague Rotenberry were unable to find much constancy in the densities of species coexisting at local sites from year to year, nor much pattern in their size differences, nor much year-to-year variation in population size explainable as a precise tracking of fluctuations in the availability of resources (Wiens and Rotenberry 1980; Rotenberry 1980). Thus their results suggested that shrubsteppe birds are very different from birds in certain other ecosystems, especially those of tropical islands such as the Galápagos and the sites studied by Diamond in the southwest Pacific.

Wiens and Rotenberry's data, like the tropical island data, were of necessity largely based on observation. However, recent experimental studies of other kinds of organisms have provided some support for the presence of variation in the intensity of competition from year to year. For example, two field experiments with lizards in areas just to the south of the North American shrubsteppe found that competition was detectable only during drought years, when arthropod prey were relatively scarce (Dunham 1980; Smith 1981); but in contrast to the hypothetical examples illustrated in Wiens's graphs (1977), in these studies crunches in resources were quite frequent, occurring in approximately one year out of two.

Indeed, a considerable literature has now developed on the experimental investigation of interspecific competition in nature (Schoener, in prep.). Even with a very strict definition of a field experiment, about 140 such studies had been carried out by the end of 1981—a veritable explosion! What do the field experiments tell us about year-to-year variability in the intensity of competition? Two points can be made. First, most studies do not run long enough, relative to the generation time of their subjects, to be able adequately to detect variation if it occurred. Even so, the great majority of studies find competition in all years during which it is sought. Thus, averaging over all studies, little suggestion of inter-

mittency exists. Second, of those studies that do span several generations, three—the lizard studies cited above and a study of rodents by Morris and Grant (1972)— show variability in the existence of competition, and ten others show variability in the intensity of competition. Many long-term studies show no obvious variability, and in one case—a four-year study of competition between rodents and ants (Brown et al. 1979)—the investigators point out that competition is continuously intense, despite the fact that the study took place in a continental desert—again, a relatively variable environment. Thus little experimental support exists for the idea of intermittent crunches in resources correlated with strong competition, and what does exist suggests that crunches are not infrequent. But of course so far few experiments have been directed toward testing this idea, and those that are performed in the future are going to require a major effort.

Primacy of predation

The fourth issue deals with the relative importance of predation. Like the variable-environment view, the view that stresses predation represents an opinion about the natural world; unlike the former, however, the predation view developed largely as a result of field experimentation. In its most extreme form, as espoused by Connell (1975), it holds that predation, not competition, is the predominant interspecific interaction, and that it should therefore be given conceptual "priority." Connell's position derives mainly from experiments performed in the marine intertidal region, and secondarily in ponds and terrestrial plant communities.

In a variety of experiments, the most famous of which is Paine's work with intertidal predatory starfish (1966), investigators found that removal of one or more predator species causes a decline in the number of prey species, essentially because of competitive exclusion that is normally prevented by predation. The effect is strong under two conditions: when predators prefer the competitively stronger species (Paine, pers. comm.; Harper 1969; Lubchenco 1978), and when the intensity of predation on a given prey type increases in proportion to the relative abundance of that type (Roughgarden and Feldman 1975). In theory the effect can work without either condition, however (see Hassell 1978).

Recent reviews of field experiments are somewhat less supportive of the prevalence of predation. Surveying the intertidal experiments known to them at the time, Menge and Sutherland (1976) concluded that strong competition occurs at the top of the food web. In relatively complex communities, large predators such as starfish occupy this position. In communities where severe disturbance by waves exists, such predators are unable to feed and organisms of the underlying level—primarily barnacles and mussels—compete furiously. Further examples of competition among intertidal organisms other than large predators, including the algal producers, have since appeared. Moreover, numerous field experiments with terrestrial plants, many absent from Connell's review (1975), provide evidence for the presence of ongoing competition not necessarily unaffected by, but certainly unsuppressed by, the action of herbivores.

In fact, the field experiments carried out thus far are largely supportive of a frequently forgotten but extraordinarily prescient paper by Hairston, Smith, and Slobodkin (1960). They argued that competition should prevail among top predators, whereas predation should prevail among organisms of intermediate trophic status, mainly herbivores. Because the herbivores are held down by competing top carnivores, competition should prevail again among the herbivore's food species, green plants. As is obvious, this scheme fits many of the experiments just discussed, and certain others as well. Many exceptions do exist, but most are explainable within the original logic of the paper or as a natural extension. In particular, noxious or large organisms, whatever their trophic status, are relatively free of predators and so should compete, all other things being equal. It may well be that in terms of sheer numbers more populations are dominated by predation—herbivorous insects, for example, comprise about a quarter of the earth's known species (Strong, pers. comm.). However, we already know too much to assume indiscriminately the primacy of predation. Were conceptual priority desirable for any ecological interaction, the scheme just outlined would seem the wisest one.

Overlap in resources

The fifth issue deals with a basic tenet of the simple theory of competition: the greater the overlap in use of resources, the greater the competition coefficient, and—all other things being equal—the greater the intensity of competition. This seemingly plausible proposition has created something of a brouhaha, with many ecologists excitedly arguing that overlap and competition need not be related.

In theory, their argument is as follows. Species having a high degree of overlap in their use of resources yet coexisting may be doing so by virtue of their lack of competition, for example because their populations are held down by predators (Colwell and Futuyama 1971; Vandermeer 1972). Indeed, if they were competing, selection should have caused evolutionary divergence in their use of resources. A small amount of spatial overlap, on the other hand, may indicate a high degree of competition between species ecologically similar in other respects. Species may occur in different macrohabitats because of interspecific aggression, or they may avoid one another, sometimes to feed in habitats not depleted by the other species (see, for example, Pyke et al. 1977; Schoener 1974d; Werner and Hall 1979). Habitats may thus be the arenas rather than the objects of competition (Schoener 1974c). Finally, overlap in habitat may simply indicate a patchy environment in which individuals travel through, but do not use resources from, inappropriate places (Schroder and Rosenzweig 1975).

In practice, the following observations, which seem to be inconsistent with the way simple competition theory treats overlap, have been made. Overlap varies both seasonally (Smith et al. 1978) and from year to year (Dunham, in press; Lister 1980) (see Table 1). In nearly all cases, overlap is *smaller* during the lean season, potentially the time of *greater* competition; in fact, Dunham could demonstrate competition between two species of desert lizards only during lean years. Additionally, Schroder and Rosenzweig (1975) showed experimentally that a high degree of overlap in habitat between two

rodent species in the field is associated with no competitive response, while Koplin and Hoffman (1968), also experimenting with rodents in the field, demonstrated that a low degree of overlap is associated with a high competitive response.

Taken together, these conceptual and empirical considerations would seem to be quite damaging to the original theory. But are they really? Nearly all ecologists would agree that overlap need not be related to competition; where they would disagree is in the extent to which it is legitimate to make the assumption that overlap measures competition. Some undoubtedly feel that the relation between overlap and competition must be demonstrated experimentally for every kind of system, perhaps for every set of study populations. Others, myself included, are willing to use formulae like MacArthur and Levins's equation in a practical spirit where the underlying assumptions seem biologically likely. For the reasons just given, among others, overlap in macrohabitat may be the least useful measure in this regard.

But what about the observations on seasonal and year-to-year variation in overlap? Certainly they serve to check the indiscriminate use of data on overlap to test the theory of competition. Minimal rather than average overlap values should be used, and in a variable environment long-term studies are necessary to ascertain those minimal values. But the data on temporal variation in overlap do not contradict the logic of the simple theory. One must realize that these data refer to the *same* set of species at different times, under *different* resource regimes. The competition-coefficient equation, on the other hand, is typically used in the theory to compare competition intensities for *different* sets of species at the *same* time, under the same resource regime. Viewed this way, the original overlap concept can be shown to be consistent rather than inconsistent with the findings of field experiments. An excellent demonstration of this sort was recently performed by Pacala and Roughgarden (1982) in a study of lizards on two West Indian islands; they showed that lizard species more similar to one another in morphological characters and associated resource use competed more strongly than less similar species.

Other experimentally demonstrated relationships between degree of overlap in use of resources and degree of competition also exist. A partial exception is Hairston's experiments with salamanders (1981); however, his failure to detect competition among rare species is consistent with the concave zero-isocline competition models discussed above, although Hairston concludes that the rare species are not in fact affected by competition. Finally, where the object of competition is space, a relatively uniform resource, competition is particularly intense, as has been shown in experiments with numerous intertidal organisms as well as with some terrestrial plants.

Methodological and logical issues aside, the data on seasonal and year-to-year variability in ecological overlap are extremely significant because of what they suggest about how competition operates in nature. In 1978 Smith and his colleagues tabulated examples of such variability. Table 1, an expansion of their compilation, lists 30 cases of variable overlap, 2.5 times the number available to them. With few exceptions (Ro-

tenberry 1980), it shows that similar species overlap less during the lean season, a finding that can be interpreted as supporting the idea of Lack and Svardson that there would be less overlap during times when resources are scarce. Although Lack and Svardson did not specify a detailed mechanism, presumably part of the notion is that if the competition occurring during lean times is too severe, extinction of one or more species will take place—the Gause principle. This is all fine, but then why should overlap increase, often markedly, during good times rather than remaining constantly low?

I would like to present my resolution of this question as a hypothesis; it embodies parts of other discussions (Smith et al. 1978; Baker and Baker 1973; Lister 1980; Grant and Grant 1980) but forms a unique whole.

During lean times, strong directional selection resulting from interspecific competition produces in each species adaptations most suited for resources used relatively exclusively by the species. For example, Baker and Baker (1973) have argued that migratory sandpiper species are optimally adapted to their winter, rather than summer, feeding niches—that is, to their lean season. More recently Boag and Grant (1981) have shown extraordinarily strong directional selection upon the beak of a Galápagos finch during a lean year in contrast to a fat year. Large-beaked birds survived the lean year because they were able to crack the large seeds then predominating (e.g., Grant and Grant 1980).

During times of plenty, different types of resources increase differentially in abundance, and it then becomes more profitable to use types other than those for which the trophic phenotype has specifically been selected. Moreover, the newly profitable resource types are the same for a number of species, and the species converge upon them. We can use foraging theory (Schoener 1974d; Pyke et al. 1977) to predict the circumstances under which such a convergence should take place. First, and perhaps most likely, if a resource type occurs in patches, either because it is a habitat to begin with or because it is a food that occurs in clumps rather than being randomly dispersed, an increased abundance could reduce the locomotory cost of feeding to the point at which an individual should feed where such items occur, no matter what the other costs and benefits. Second, certain food types that are intrinsically profitable in terms of the net energy required per unit of handling time could increase in abundance, and those types might be profitable for a number of species simultaneously. During lean times these especially profitable foods selectively decrease in abundance, either because they are mostly consumed by then (Grant and Grant 1980) or because of extrinsic environmental changes. Then each species would pull back to its own more or less exclusive set of resource types—those to which it was at that time best adapted.

My hypothesis has several implications. First, certain resource types should increase disproportionately rather than proportionately during the fat season. Where information is available, this appears to be nearly always true, and often it is strikingly so. This kind of increase could imply a greater overlap during the fat season purely as a statistical artifact; however, overlap formulae that incorporate the relative abundance of resources minimize this possibility. Second, species should con-

verge on abundant resources if those resources are sufficiently restricted in area. This appears to occur in a large number of cases in Table 1. For example, British songbirds forage mainly in leaves during the summer; large mammalian herbivores congregate on ephemeral grasses and herbs during the African rainy season; and all lake fishes in Sweden eat the superabundant bottom food available after the ice breaks.

Species should also converge on food types if those types are especially profitable in terms of net calories per unit of handling time. Though examples of this are less common than instances of convergence on spatially restricted superabundant resources, a few do exist: during the rainy season Galápagos finches concentrate on the then abundant "easy-to-handle" seeds and fruits; Peruvian litter frogs converge on the large prey that abound in this season; and lizards concentrate on swarms of alate termites.

According to foraging theory, exceptions to the tendency for overlap to decrease during the lean season should occur in two situations: when some very profitable food increases in abundance then, as has indeed been shown to be the case both for two species of

Table 1. Temporal variability in overlap in use of resources among trophically similar species

Species and habitat	Nature of overlap[a]	Period of least overlap	Reference
insects streams UK	kind of food	lean (winter/ spring)	Townsend and Hildrew, 1979, *J. Anim. Ecol.* 48:909–20
frogs rain forest Peru	kind and size of food (large prey)	lean (dry)	Toft, 1980, *Oecologia* 45:131–41
frogs rain forest Panama	kind and size of food	lean (wet)	Toft, 1980, *Oecologia* 47:34–38
fishes streams Panama	kind of food (caddis flies); habitat (more stream surface available)	lean (dry)	Zaret and Rand, 1971, *Ecology* 52:336–42
catfish streams Panama	habitat (protected substrates)	fat (wet)	Power, 1981 diss., Univ. of Washington
fishes lakes Sweden	kind of food (superabundant bottom prey)	lean (late summer)	Nilsson, 1960, *Report of the Inst. of Freshwater Res., Drottingham* 41:185–205
lizards desert Texas	kind of food; microhabitat	lean (dry yrs.)	Dunham, 1982, in *Lizard Ecology: Studies of a Model Organism*, Harvard Univ. Press
lizards desert N. America, Australia	kind of food (alate termite swarms)	lean (dry)	Pianka, pers. comm.
lizards forest (2 sites) Puerto Rico	habitat (2 sites); kind and size of food (1 site)	lean (dry)[b]	Lister, 1981, *Ecology* 62:1548–60
shorebirds intertidal, tundra, taiga Florida, Canada	method of foraging; habitat	lean (winter)	Baker and Baker, 1975, *Ecol. Mono.* 43:193–212
hawks forest, farmland Netherlands	size of food (highly vulnerable young birds)	lean (winter)	Opdam, 1975, *Ardea* 63:30–54
doves thorn scrub Senegal	kind of food (seeds available in patches)	lean (dry)	Morel and Morel, 1972, in *Productivity, Population Dynamics and Systematics of Granivorous Birds*, Polish Sci. Publ.
bark-feeding birds pine forest Colorado	foraging zone	lean (winter)	Stallcup, 1968, *Ecology* 49:831–42
hummingbirds disturbed habitats Costa Rica	kind of food (superabundant nectar)	lean (summer/ winter)	Feinsinger, 1976, *Ecol. Mono.* 46:257–91
thrashers riparian woodland, chaparral Texas	kind and size of food; habitat	fat (spring/ summer/fall)[c]	Fischer, 1981, *Condor* 83:340–46
titmice pine woods Netherlands	part of tree (caterpillars abundant in crown)	lean (winter/ summer, certain yrs.)	Tinbergen, 1960, *Arch. Neerl. Zool.* 13:265–343

Galápagos finches that feed on *Opuntia* flowers (Grant and Grant 1980) and for certain British songbirds (Lister 1980); or when all food types decrease in abundance by the same proportion—then all species should, if anything, use a wider range of resources and thus overlap more. Exceptions may also occur, of course, if competition is not a significant interaction. For example, Power (1981 diss.) suggests that the relatively high overlap among tropical stream catfish and similar species during the dry season results from the fact that all species converge on the habitat that is safest from predators.

If the preceding scenario is correct, several consequences follow. First, the data on seasonal and year-to-year variations in overlap belie an extreme variable-environment view, which sees especially lean times as often too infrequent, or selection during those times as often too weak, to influence adaptations significantly. Instead, the data indirectly support the notion of evolutionarily significant competition during crunches.

Variation in morphological characters may increase during fat times, as Wiens (1977) argues and as Grant and Price (1981) demonstrate for a species of Galápagos finch, and indeed this should result in small d/w's. However, averages of such characters should be much less affected, thereby preserving average differences between species over time.

Second, data on morphological differences between species, traditionally considered inferior to data on resource use itself, could in fact be superior for estimating the degree of competition between species. Ecological data may be taken at the wrong time of year, or during the wrong year, as far as competition is concerned; if morphological adaptations constitute a genetic memory of such competition, they will more accurately reflect its ecological importance.

Third, the competition and foraging theory schemes can be entirely consistent with one another. Indeed, they are complementary; competition theory accounts for the

Species and habitat	Nature of overlap[a]	Period of least overlap	Reference
titmice woodland Norway	part of tree (places where food is abundant)	lean (winter)	Haftorn, 1956, *Det. Kgl. Norske Vidensk. Selsk. Skr.* 4:1–53
songbirds pine forest UK	habitat	lean (winter/spring, certain yrs.)	Gibb, 1960, *Ibis* 102:163–208; Lister, 1980, *PNAS* 77:4185–87
insectivorous birds pine forest Finland	habitat (places with abundant insect eggs)	lean (winter)	Alatalo, 1980, *Oecologia* 45:190–96
songbirds woodland UK	habitat (leaves)	lean (spring)	Gibb, 1954, *Ibis* 96:514–43
titmice woodland UK	kind of food (superabundant caterpillars)	lean (winter)	Betts, 1955, *J. Anim. Ecol.* 24:282–323
insectivorous birds oak woodland California	habitat	lean (fall/winter)[d]	Wagner, 1981, *Ecology* 62:973–81
songbirds pine woodlands Sweden	habitat	fat (spring/fall/winter)[e]	Ulfstrand, 1977, *Oecologia* 27:23–45
titmice woodland, farmland UK	habitat (places with superabundant caterpillars, mast)	lean (winter/spring)	Hartley, 1953, *J. Anim. Ecol.* 22:261–88
honeyeaters rain forest New Zealand	habitat (places with blossoms)	lean (winter)	Gravatt, 1971, *Emu* 71:65–72
finches woodland, farmland UK	kind of food (superabundant seeds, fruits, insects)	lean (other than summer, certain yrs.)	Newton, 1967, *Ibis* 109:33–98
finches islands Galápagos	kind of food (easily handled seeds, fruits)	lean (dry)	Smith et al., 1978, *Ecology* 59:1137–50
vertebrate carnivores tundra Greenland	kind of food (lemmings during their population peaks)	lean (certain yrs.)	Lack, 1946, *J. Anim. Ecol.* 15:123–29
herbivorous mammals woodland, savanna Africa	kind of food (ephemeral grasses, herbs)	lean (dry)	Jarman, 1971, *Oecologia* 8:157–78
bats tropical dry forest Costa Rica	kind of food (superabundant flowers)	lean (wet)	Heithaus et al., 1975, *Ecology* 56:841–54

[a] Resources in parentheses are those upon which species especially converge.
[b] For habitat; in the case of kind and size of food, overlap was constant.
[c] For kind and size of food; in the case of habitat, overlap was constant.
[d] Differences in overlap were not statistically significant.
[e] Lean season ambiguous; arthropods were more abundant in summer, seeds during other seasons.

second position deemphasizes strong biological interactions of any kind.

A variety of views based on this second position can be discerned. I have stressed the variable-environment view, one of the most coherent, and I have pointed out some similarity between this view and the earlier ideas of Andrewartha and Birch. A related view emphasizes stochastic or random factors as opposed to deterministic or regular ones. Presumably the stochasticity derives from factors extrinsic to and unaffected by the biological system of interest—for example, sunspots and their effect on weather—though it might also be thought of as the net of many small factors of unknown etiology. Those who advocate a stochastic position are not necessarily those who have used null models to examine patterns purportedly resulting from competition, though there may be some overlap.

Virtually every ecologist would agree that the three main points of view outlined in this paper — those stressing competition, predation, and variable environments—all have finite domains, but they would certainly disagree as to the size of each hegemony and the degree to which they overlap with one another. The clearest

etiology of the constraints that must be specified in a foraging model. Far from being unsuitable for predicting behavior in variable environments, as has been claimed (Wiens 1977), foraging theory may be necessary. In fact, the highly opportunistic behavior that animals often show in tests of such theory is prima facie evidence for environmental variation in the availability of food.

The domain of competition

As I have shown, substantial disagreement exists as to the importance of interspecific competition in nature. Two extreme positions opposing an extreme competitionist view can be distinguished. One advocates strong biological interactions, but asserts that predation is far and away the most prevalent of these. (A similar strong advocacy for the other biological interaction, mutualism—a relationship between two species in which both benefit—has never really gotten off the ground.) A

evidence for separate domains for competition and predation, as we have seen, comes from the fact that species from different parts of the food web appear to be controlled by one interaction or the other, especially in the case of intertidal systems. From the variable-environment viewpoint, one might argue that competition is more important in climatically stable places such as the tropics; from the predation viewpoint, one might claim the opposite, because tropical areas have large, complex food webs (Paine 1966; Connell 1975). From the predation viewpoint, and to a lesser extent the variable-environment viewpoint, one might argue that competition should be more important on the relatively predator-free, climatically constant islands than on mainlands. From both the predation and the variable-environment viewpoints, one might argue that competition is more important for large organisms: they have escaped many or all predators by virtue of size and can better maintain internal homeostasis in climatic vicissitudes.

Data from field experiments support certain of these generalizations. However, although much theory is available for the population dynamics of predation and environmental variability, surprisingly little quantitative theory is available at the level of individual adaptation for these viewpoints as compared to competition. Thus critics evaluate the predictions of a competition model against those of a null model, but do not similarly evaluate the predictions of a predation model or a variable-environment model. An interesting endeavor would be to arrange a set of expectations from each of the three viewpoints side by side, and to evaluate their validity for different systems along the environmental or biological continua just discussed. Much basic information exists on both predation avoidance and dispersal abilities, so the task should not be an impossible one.

Is the competitionist view a failed paradigm? I think not. If the results of recent observational and particularly experimental studies can be taken at face value, competition must still be considered of major ecological importance. Though some have become pessimistic in light of recent criticism of competition, my own feeling is one of optimism. Certainly we were never justified in thinking that the ecological world was so simple as to be largely explainable on the basis of a single interaction. New discoveries are continually refining our understanding of the domain of competition, and we are well on the way to developing a multifaceted theory to match what is clearly a highly diverse natural world.

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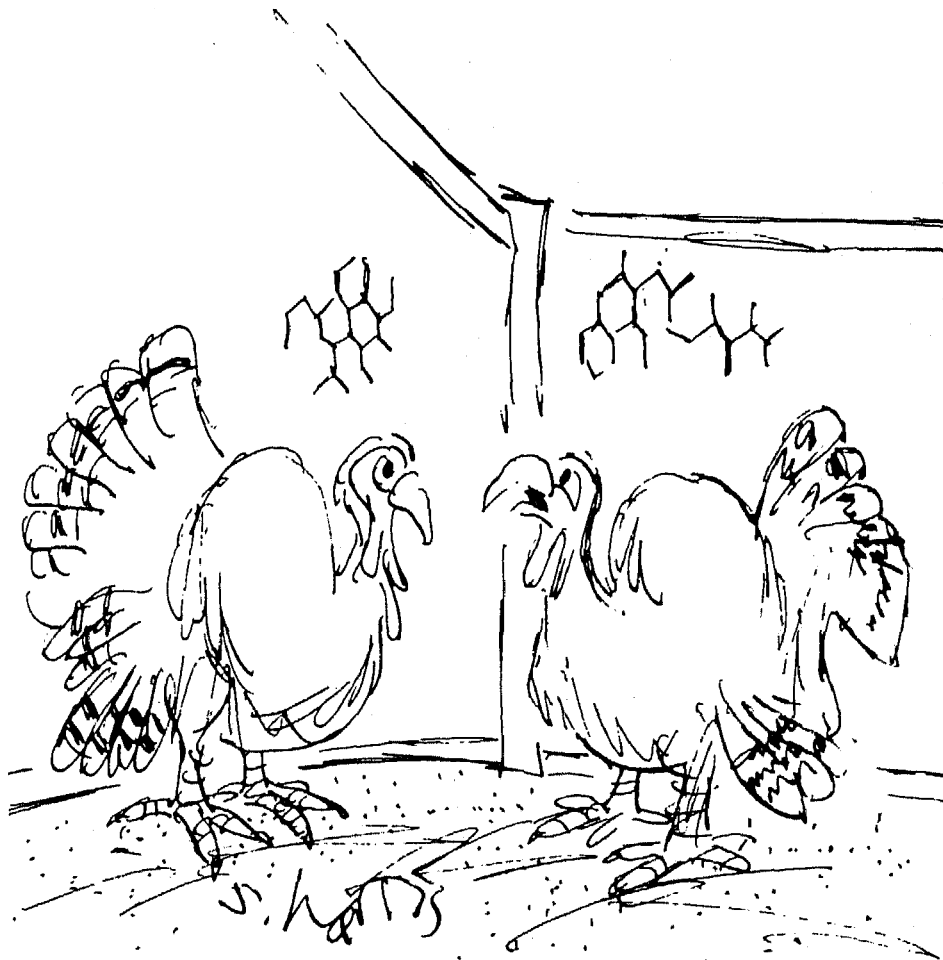
"The environment people only worry about endangered species, not endangered individuals."