

ON THE PREVALENCE AND RELATIVE IMPORTANCE OF INTERSPECIFIC COMPETITION: EVIDENCE FROM FIELD EXPERIMENTS

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Submitted December 28, 1982; Accepted April 21, 1983

How much does present-day interspecific competition affect the distribution, abundance, and resource use of species in natural communities? This is a question that continues to engender controversy among ecologists. Ideally, it might be answered by measuring the influence of interspecific competition on a population relative to that of other relevant processes affecting it, such as the weather, predation, parasitism, mutualism, intraspecific competition, disturbances, etc. If a large number of such case studies existed we might then make a general evaluation of the relative importance of each process. In the absence of such information, I decided to examine some published studies of competition in an effort to address three questions: (1) How frequently does interspecific competition occur at present in nature; (2) what mechanisms account for the variability in its occurrence; (3) when it does occur, how strong is it compared to intraspecific competition?

To address these questions, I have taken a sample of published studies that used field experiments designed to detect interspecific competition. In previous reviews of field experimental evidence (Connell 1974, 1975), I have assessed the relative importance of competition, predation, and physical factors in community structure. Here I compare only the strengths of intraspecific and interspecific competition. This would have been difficult to do before now since field studies distinguishing them have begun to be published only recently. Although laboratory and greenhouse experiments designed to do this have been done for many years (de Wit 1960; see review in Harper 1977), to my knowledge the first controlled field experiments designed specifically to distinguish the two types of competition appeared in the past decade (e.g., Harger 1970*a*, 1970*b*, 1972; Wilbur 1972).

A comparison of the relative strengths of intraspecific and interspecific competition is interesting in several contexts. The first concerns the coexistence and abundance of competitors. If species A is superior to species B in interspecific competition, one might conclude that A will eventually eliminate B, unless something interrupts the process. If, however, intraspecific competition in A is stronger than interspecific competition on B, A may be self-limited below the density

necessary to eliminate B. This was suggested as a possible mechanism promoting coexistence of grazing gastropods by Underwood (1978) and Creese and Underwood (1982). Some theoretical models also use the relative strengths to predict the possibility of stable coexistence of two competitors at equilibrium. Where competitors coexist, we might be interested in the relative roles of these processes in determining the density of both species. Another aspect concerns the partitioning of resources or habitats, in which the two types of competition act in opposing directions. In theory, increasing intraspecific competition should expand a species' niche whereas increased interspecific competition should reduce it.

Here I will confine my attention to evidence from controlled field experiments. This is not meant to imply that such experiments are always superior to nonexperimental evidence. In many circumstances experiments are neither feasible nor appropriate to test particular hypotheses. To address the questions posed in this paper, however, field experiments probably provide some of the best evidence available.

METHODS

The idea of using field experiments to study present-day competition is not new (Jackson 1981), but unless they are designed and executed so as to test relevant hypotheses (which many are not), they are of limited use. In fact, since field experiments are often regarded as the ne plus ultra of ecological research, poor ones can be worse than useless since the conclusions based on them are often accepted with little question. When field experiments were few the tendency was to use this small amount of information rather uncritically. Now there are plenty of field experiments to choose from and I feel that it is time to reexamine the evidence.

Birch (1957, p. 6) defines competition between animals as follows: "Competition occurs when a number of animals (of the same or of different species) utilize common resources, the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or another in the process." (This definition should also apply to plants and microorganisms.) In most field experiments, the degree of resource competition or interference is experimentally manipulated by changing the population densities of the competitors.

The Design of Field Experiments to Measure Competition

A common sort of field experiment involves changing the abundance of one possible competitor, species A, and comparing the response of the other, species B, to its behavior in an unmanipulated control; this design is called type 1 in the studies listed in Appendix A. The response measured is usually (1) a change in density; (2) a change in some rate that could affect density, e.g., fecundity, growth, physiological condition, mortality, etc.; or (3) a niche shift, e.g., a change in type of resource used, microhabitat occupied, etc. While this experiment will detect interspecific competition, for the first two responses it is open to the

alternative interpretation that the same or a greater response might have been seen in species B with a similar change in its own density. In other words, intraspecific competition might be equal to or stronger than interspecific.

To distinguish the two types of competition, a different design is required. The density of each species needs to be varied while either keeping the density of the other species constant or removing it entirely. The experimental design depends upon whether the species can be transplanted and/or enclosed without ill effects. If so, densities can be both increased and decreased from the ambient condition within the same experiment. This has the advantage that it reveals the density above which interspecific and intraspecific competition begin to occur. For example, Underwood (1978) caged grazing snails both in single-species and mixed-species treatments at a range of densities above and below average, all within a single experiment.

If, on the other hand, the species cannot be transplanted or enclosed without ill effects, densities can only be reduced, not increased. A possible design is to reduce one of the species to a series of lower densities while either leaving the second species unchanged or removing it entirely. Simultaneously the second species is reduced with the first unchanged or removed. While this design will also measure the strengths of both intraspecific and interspecific competition it is less powerful than the first, since it does not include densities in the upper part of the natural range, at which competition is more likely to occur. However, it is worth doing to measure both sorts of competition; I know of only one instance of the application of such a design, Fonteyn and Mahall (1981). In both designs, it is useful to include several intermediate densities to reveal possible nonlinearities in the competitive response. These designs, if properly controlled and replicated, should enable one to calculate directly both the per capita effect of one competitor on the other and, since densities are known, the competitive effect of the populations on each other. As will be seen later, few studies have as yet done such a complete analysis.

A third design is sometimes used in which total densities are kept constant. Such experiments have been referred to as "replacement series" by de Wit (1960) or a "reciprocal α " design by DeBenedictis (1974). If used alone it can only reveal the relative, not the absolute, strengths of interspecific versus intraspecific competition. This has the disadvantage that if no significant differences are found in the response to mixed versus single-species treatments at the same total density, it is impossible to decide whether any competition is occurring at all.

Some Practical Problems in Doing Field Experiments

The nature of controls is a crucial factor in doing good field experiments. Because environmental conditions vary in time and space, controls need to be done both contemporaneously with the treatments and as close as possible to them, without at the same time being so close that the process of manipulation itself affects the controls (e.g., removal of individuals may cause immigration from adjacent areas, or cages may change the immediate environment around them [Hurlberg and Oliver 1980; Underwood and Denley 1983]). The aim is to

arrange the controls so that, aside from the manipulations of the experiments, the controls and treatments will both experience the same degree of environmental variation. In principle, one can then regard them as differing only in the factor being manipulated experimentally.

Since both populations and environments vary in space and time, however, replication is absolutely essential. In a single experiment, replication of controls and treatments ensures that the results will not be strongly influenced by an extreme event. In addition to such within-experiment replication, repetition of the whole experiment at another place and/or time is also very useful. This ensures that, if competition is occurring but also varying markedly in intensity, the chances of detecting it will be improved.

The second practical problem concerns the population densities to be used in the treatments. Usually one is interested in whether competition occurs over the range of densities found in nature, so this defines the range of the experimental densities. However, it is of little relevance to arrange experimental densities far above the nature range, as some earlier studies did. It is useful to have some treatment density below the range of natural densities because the performance (e.g., fecundity, growth rate, etc.) at the lowest treatment density serves as the baseline against which that at higher densities is compared.

Another problem is that of deciding whether the experimental results can be applied to natural populations. If the treatments consist simply of reducing densities in otherwise natural conditions, there is usually little problem. If, however, mobile animals are placed in enclosures at various densities or if populations are protected from predators, or if the experiment is done in somewhat artificial conditions (e.g., in crops, orchards, artificial ponds, settlement panels placed in conditions different from natural ones, etc.), the problem exists. In such cases, additional information is needed to judge how far the results of such studies can be generalized to natural conditions. Some of the papers reviewed below included such information, indicating that the environmental conditions, individual behavior, and population densities used in the experiment matched reasonably closely those found in populations of the same species living under natural conditions. In cases in which no such information was given, it could probably be gathered by subsequent observations in the communities where the species live naturally.

Finally there is the problem of interpreting the results of a field experiment. Since natural populations interact with many other species, an experimental reduction or increase of a potential competitor population will probably have some effect on species other than the target one. These others, e.g., predators, parasites, prey, competitors, pollinators, etc., may then in turn have a different effect than before on the target species. Such indirect effects should not be considered artifacts; they probably happen commonly when populations fluctuate naturally, and may have important effects on community structure. They make it difficult, however, to be precise about the mechanism that produced the observed result of the experiment.

The best way to deal with this problem is to incorporate it into the design of the experiment. If possible, one should measure the changes in those other species most likely to be affected by the experimental manipulations, and, ideally, manip-

ulate them in turn. The more closely one can observe the changes occurring during the course of an experiment, the greater is the likelihood of discovering the actual mechanism that is operating. This subject is discussed further in the section *Positive and Indirect Interspecific Interactions*.

Measuring the Variability of Interspecies Competition

Probably the most direct way to decide how the occurrence or strength of competition varies is to repeat the field experiment on the same species at a different time or place; this has been done by a few authors. I know of only one instance in which a different person has repeated an experiment (Keough 1983). Ecologists seem reluctant to do this, possibly because they fear that if the result comes out the same it will not be publishable because it is not original enough. A second, indirect, method is to estimate the natural variability of population density or resources by long-term and/or more widespread observations, to see how general (or special) the conditions were during the original experiment. In this way the experiment is set in context, allowing one to judge the conditions under which competition might be expected to occur. If the abundances of the populations or resources can be related to physical variables, it may be possible to use other long-term records, e.g., of weather or hydrography, to estimate indirectly the variability of the populations or resources, as well as how typical the conditions were during the original experiment.

A SURVEY OF FIELD EXPERIMENTS ON COMPETITION

In earlier papers (Connell 1974, 1975) I reviewed many of the field experiments on interspecific competition published through 1973. Since then the number of such field experiments has increased enormously so that my present review can include only a sample. To obtain an objective sample I included only papers from the years 1974 through 1982 in the following six general ecological journals: *Ecology*, *Ecological Monographs*, *Journal of Ecology*, *Journal of Animal Ecology*, *The American Naturalist*, and *Oecologia*. Although I tried to examine all papers, there were several hundreds to scan, and I may have missed some relevant papers and misinterpreted some results; for any such errors I apologize to the authors. Of all these papers, I have included only those with field experiments satisfying certain criteria. In brief, the study needed to have adequate controls and presentation of data analysis, and sufficient information to judge (a) how similar the experimental setup was to natural conditions, and (b) whether or not interspecific competition was occurring. The introduction to Appendix A contains details of these criteria.

Among those papers included there still remains a high degree of variability in quality. Degree of replication, rigorousness of design, and thoroughness of data analysis all varied considerably. In some cases the effect of the observed competition on the abundance of the species was clearly demonstrated. In others, such an effect must be inferred from very little data. In the future, as more thorough studies accumulate, inferences from the literature should become more reliable.

For each study I used the following operational definition in deciding whether interspecific competition was affecting a species. Following an experimental change in abundance of a potential competitor, if there was a statistically significant response in the opposite direction in the species being studied, interspecific competition was judged to be occurring. The response could be a change in either breadth of resource use (e.g., food type, microhabitat type) or in abundance (including those variables that affect abundance, e.g., natality, mortality, growth, emigration, immigration, feeding activity, etc.). The response must have been in the opposite direction, e.g., an increase in abundance (or a change in fecundity, mortality, etc., that would increase it) after the competitor was reduced. The degree of statistical significance of the response was judged by comparison to the controls.

The purpose of the present literature survey was to address the questions posed in the introduction: How prevalent and variable is interspecific competition in nature, and what are the relative strengths of intraspecific versus interspecific competition? To answer these questions it was important to get a quantitative estimate of how, for a single species, competition varies in time or space, or in relation to the other species with which it might interact.

To get this information I had to go beyond the methods I had used in previous literature reviews of field experiments (Connell 1974, 1975). Schoener (1983) has recently reviewed the literature on field experiments on competition, with some of these same questions in mind. Like my former reviews, his review is both more extensive and less intensive than the present paper. He has tallied, for 164 studies, the number of species in which competition occurred always, never, or some of the time. In my present survey I have gone a step further. In each paper reviewed, I determined for each species the number of experiments that did or did not show competition. These data provide a quantitative estimate of the variability of competition within species, as well as indicating which estimates are more reliable by virtue of greater sample size. Since it takes more time to extract additional data, I decided to limit my survey to a strictly defined sample of the recent literature, namely the years 1974–1982, in six general ecological journals. This survey yielded 72 papers including 215 species with 527 field experiments that satisfied the criteria described above.

The Frequency of Occurrence of Interspecific Competition

Appendix A gives pertinent information on each of the 72 studies. In this list the frequency of occurrence of interspecific competition is expressed as the fraction: (number of experiments that showed competition)/(total number of experiments done on that species). For the different species, the number of experiments varied. In some cases, competition with several other species was measured, in others, competition with a single other species was measured at several places or in several seasons or years. In contrast, in other cases the response of only one member of a pair of potentially competing species was measured at a single time and place.

To see whether the estimate of the frequency of occurrence of competition was

affected by the number of experiments done, the fractions (expressed as percentages) from Appendix A were tallied and analyzed as shown in table 1. As can be seen, the estimate of this frequency is strongly affected by sample size. In studies in which one experiment was done on only one species at a single time and place, competition was found in all but one of the 15 studies, or 93%. In contrast, in those studies in which, as before, only one experiment was done on each species, but more than one species was studied, the frequency fell to 48%. As more experiments were done on each species the frequency dropped even lower (table 1).

This abrupt drop in incidence from 93% when only one species was studied to 48% when two or more species were studied indicates that the former figure is probably an artifact. In many pairs of species studied, one member was being affected by interspecific competition but the other was not (see below). Yet when only one species was studied at a single time and place, in almost every case the investigator apparently chose the member of the pair that was being affected by competition. The survey by Schoener (1983) provides an independent sample of field experimental studies involving only one species at a single time and place. In 29 such studies not included in my present survey, 26 of the 29 species showed competition, or 90%, almost identical to the frequency in my sample.

I suggest that the reason for this trend is to be found in the behavior of scientists, and probably of scientific editors. The original impetus for most scientific studies is the expectation of discovering something. We study competition in a particular context because we hypothesize that it might be occurring there, but if we suspect it is not, we may not even start. Thus a literature survey is already biased toward finding high frequencies of occurrence of competition (or for that matter, any subject searched for). Also, if a single experiment yields a negative result, the investigator may not bother to write it up for publication. If he or she does so, an editor may not accept it; it is probable that authors, editors, and readers are not much interested in single negative results. What this all means is that any estimate of the frequency of interspecific competition gained from a literature survey such as this is probably too high. It is difficult to decide how much of an overestimate the average of 43% for all experiments in table 1 is.

I believe, however, that we can use the results of such a survey to compare different categories of organisms or habitats, unless there is an *a priori* reason to believe that competition is easier to find with field experiments in certain kinds of organisms or habitats. (For example, wide-ranging animals, the marine plankton, and deeper benthos will probably always be underrepresented in field experiments relative to other groups.) To this end I have tallied the results in three ways: by habitat (terrestrial, freshwater, marine), by broad taxonomic group (plants, invertebrates, vertebrates), and by trophic level (plants, herbivores, carnivores).

Excluding the 15 studies of one species at a single place and time, this leaves 57 papers. In three of these (studies 32, 51, and 67 in Appendix A), no type 1 experiment was done, so that it is uncertain whether interspecific competition was occurring. Of the remaining 54 papers having type 1 experiments, some interspecific competition was found in 83%; Schoener (1983) found this percentage to be 90% in the 164 studies in his survey. This method yields an overestimate,

TABLE 1
EFFECT OF SAMPLE SIZE ON ESTIMATES OF THE FREQUENCY OF OCCURRENCE OF INTERSPECIFIC COMPETITION

No. of Experiments per Species Studied	Studies of One or More Species at a Single Time and Place			Studies of the Same Pair of Species at Different Times or Places			All Studies			
	No. of Species	Mean, Over All Sp., of % of Exp. per Sp. Showing Competition		No. of Species	Mean, Over All Sp., of % of Exp. per Sp. Showing Competition		No. of Species	No. of Exp.	% of Exp. per Sp. Showing Competition	
		Sp. Showing Competition			Sp. Showing Competition				Mean	Coeff. Var.
1 (only 1 sp. in the study) ...	15	93			15	15	93	28
1 (>1 sp. in the study)	65	48			65	65	48	106
2	14	64		49	46		63	126	50	92
3	22	27		15	49		37	111	36	112
4	10	22	{	8	{	38	18	72	38	106
5	3			1			3	15		
6	1			{			2	12		
7	3						3	21		
8	4						4	32		
11	2	{	1	{	1	3	33	9	110	
12	13		1			12				
13			1			13				
Total	124*	41.0*		76	44.8		215	527	43.0*	105*

NOTE.—For each species, the percentage of experiments showing competition for one response was used as a datum.
* These totals exclude the first line (studies of only 1 sp. at a single time and place).

however, since even in studies with positive results some of the species showed no competition. In 55% of the 200 species in the 54 papers some interspecific competition was found; Schoener (1983) found it in 76% of the species in his survey. This method also yields an overestimate since in those species where some interspecific competition was found, it often did not occur in all places or times, or against all other species in the study. To take this variation into account, I used, for each species, the percentage of experiments showing competition; these are the same percentages tallied in table 1. When these percentages were averaged (excluding the above 15 studies), competition was found 43% of the time in the 200 species (table 1). (In this and subsequent analyses, the experimental result for only one response variable per species was included. Since in some studies several variables were measured, e.g., changes in density, mortality, fecundity, growth, etc., a decision had to be made as to which to use. I decided to use the response variable most directly related to a change in abundance. This is the first response listed in each study in Appendix A.)

In tables 2 and 3, the average over all species of the fractions for each species is given for each category of habitat/organism. This weights species equally but experiments unequally because different species had different numbers of experiments. So I also give the percentage of all experiments that showed competition in each category, which weights experiments equally. Since in these analyses I was interested in comparing populations open to the influence of grazers, predators, vagaries of weather, etc., it was necessary to exclude the 13 studies done in enclosures. These were included in later analyses. The studies involving only one species done at a single time and place were also excluded on the basis of the discussion above.

The comparisons in these two tables can be used to test some a priori hypotheses that have been proposed concerning the incidence of interspecific competition. Hairston et al. (1960) (hereafter HSS) proposed that in terrestrial habitats herbivores as a trophic level are not likely to compete for common resources, being controlled by their predators, whereas the other trophic levels of producers (plants), carnivores, and decomposers should compete. If we assume that individual populations represent the behavior of their trophic level, this modification of the original hypothesis can be tested with the present data, with one constraint.

Slobodkin et al. (1967) specified that the hypothesis in HSS applies only to those terrestrial herbivores that feed on the plant itself, not on its products such as nectar, pollen, and seeds. Nine of the species in three studies (nos. 56, 57, and 61) satisfy this criterion and are listed separately, as phytophages, in table 2. Their average frequency of competition did not differ significantly from either the terrestrial plants or carnivores. Slobodkin et al. (1967) also predicted that those herbivores that eat nectar, pollen, or seeds would compete, in contrast to the phytophagous herbivores. The average frequency of competition of the 10 species in the former category were tested against that of the nine phytophagous species and found not to differ. None of these results are consistent with the HSS hypothesis. However, since the sample sizes of terrestrial phytophagous herbivores are small and all were insects living on *Heliconia* plants, it is hardly a definitive test of the hypothesis.

TABLE 2

LITERATURE SURVEY OF FIELD EXPERIMENTS ON INTERSPECIFIC COMPETITION, COMPARING THREE TROPHIC LEVEL GROUPS IN THREE HABITATS

A. Average of percentage of experiments done for each species that showed interspecific competition

	TERRESTRIAL		MARINE		FRESHWATER		TOTAL	
	No. Spp.	Ave. %	No. Spp.	Ave. %	No. Spp.	Ave. %	No. Spp.	Ave. %
Plants	50	39	22	59	2	50	74	45
Herbivores	19	21	9	78	0	...	28	39
(Phytophages)	(9)	(18)						
Carnivores	17	10	4	75	1	67	22	24
Total	86	29	35	66	3	56	124	41

B. Percentage of all experiments in each category that showed interspecific competition

	TERRESTRIAL		MARINE		FRESHWATER		TOTAL	
	No. Exp.	%	No. Exp.	%	No. Exp.	%	No. Exp.	%
Plants	205	30	31	68	2	50	238	35
Herbivores	45	20	13	69	0	...	58	31
(Phytophages)	(22)	(23)						
Carnivores	36	11	5	60	3	67	44	20
Total	286	26	49	67	5	60	340	32

NOTE.—Student's *t* tests on the percentages for each species used in Part A above to test certain a priori hypotheses (see text). Phytophagous herbivores were not significantly different ($P > .05$) from either plants or carnivores in the terrestrial habitat ($t = 1.40, .75$, respectively). This is also true for the same comparisons using all herbivores, in terrestrial ($t = 1.66, 1.04$), and marine ($t = .99, .09$), and total ($t = .54, 1.18$). Plants were different from carnivores in the terrestrial habitat ($t = 2.64, P < .02$) but not in marine or total ($t = .59, 1.90$). Between terrestrial vs. marine habitats, plants were not different ($t = 1.78$), but herbivores and carnivores were different ($t = 3.62, P < .002$; $t = 3.32, P < .01$). Within terrestrial herbivores, the 9 phytophages were not different ($t = 0.29$) from the 10 species that ate plant products such as nectar, pollen, or seeds.

This table does not include studies of one species at a single place and time (study nos. 1, 2, 3, 6, 13, 29, 30, 38, 41, 43, 44, 48, 49, 50, 53), nor studies done in enclosures (study nos. 7, 9, 11, 35, 36, 37, 39, 45, 46, 59, 66, 72), nor studies of omnivores (study nos. 5, 8, 12, 28, 42, 57 (3 spp.), 58 (2 spp.), 62, 71).

Schoener (1983) used the numbers of studies or of species showing some competition to test the HSS hypothesis. For terrestrial populations the sample size of unenclosed populations of phytophagous herbivores was, like mine, very small (5 studies, 8 species). One study with three species of insects overlapped with my sample; the others in Schoener's sample were four rodent species and one insect. Comparisons with other trophic categories showed a lower frequency of competition in the eight phytophagous species as compared to producers and carnivores, in two out of three statistical tests on unenclosed populations. Although Schoener (1983) considers that the results support HSS, the small sample size of unenclosed terrestrial studies in Schoener's (1983) survey, as in my own, makes any judgment quite tentative at this stage.

TABLE 3

LITERATURE SURVEY OF FIELD EXPERIMENTS ON INTERSPECIFIC COMPETITION, COMPARING THREE TAXONOMIC GROUPS IN THREE HABITATS

A. Average of fraction of experiments done for each species that showed interspecific competition

	TERRESTRIAL		MARINE		FRESHWATER		TOTAL	
	No. Spp.	Ave. %	No. Spp.	Ave. %	No. Spp.	Ave. %	No. Spp.	Ave. %
Plants	50	39	22	59	2	50	74	45
Invertebrates	23	17	24	31	0	...	47	24
Vertebrates	25	23	9	89	1	67	35	41
Total	98	30	55	52	3	56	156	38

B. Percentage of all experiments in each category that showed interspecific competition

	TERRESTRIAL		MARINE		FRESHWATER		TOTAL	
	No. Exp.	%	No. Exp.	%	No. Exp.	%	No. Exp.	%
Plants	205	30	31	68	2	50	238	35
Invertebrates	57	16	37	32	0	...	94	22
Vertebrates	47	23	10	90	3	67	60	37
Total	309	26	78	54	5	60	392	32

NOTE.—Student's *t*-tests as in table 2. Invertebrates had a lower percentage than plants in terrestrial ($t = 2.18$, $P < .05$), marine ($t = 2.09$, $P < .05$), and total ($t = 2.58$, $P < .02$). Invertebrates were also lower than vertebrates in marine ($t = 3.65$, $P < .001$), but not in terrestrial or total ($t = 0.49$, 1.72). The studies done in enclosures and those done with only one species at a single place and time were excluded, but omnivores were included in this table (see table 2).

Although the original HSS hypothesis was limited strictly to terrestrial phytophagous herbivores, it is interesting to see whether the general concept might apply more broadly. Since the comparisons of herbivores as a group to either plants or carnivores in all habitats in table 2 show no significant differences, they do not support such an extension of the hypothesis.

Schoener (1983) also compared trophic levels in other habitats; the sample sizes of herbivores in unenclosed experiments in marine and freshwater habitats (19 and 12 species, respectively) were somewhat larger than in the terrestrial comparison discussed above. The tests with marine herbivores were never consistent with HSS, while the freshwater ones were so in two thirds of the tests. When number of studies showing some competition was used by Schoener (1983), rather than number of species, marine and freshwater studies showed no significant differences between trophic levels. Terrestrial studies are consistent with HSS but the sample size of unenclosed herbivores is small, only five studies. Thus his evidence is not consistently supportive, and does not take into account the variation within species, as this paper does. When both his and the present survey are taken together the evidence is still insufficient and too inconsistent either to support or reject HSS.

A second hypothesis concerning trends in competition across trophic levels is that of Menge and Sutherland (1976). They predict that, in the organization of guilds within trophic levels, interspecific competition will be more prevalent at higher levels. This hypothesis predicts the same trend as HSS for the upper two trophic levels: Predators will compete more than herbivores. For the lower two levels it predicts the opposite of HSS: Herbivores will compete more than plants. The data in table 2 support neither of these predictions; only one of the comparisons between trophic levels within habitats showed a significant difference, and it was in the direction opposite to that predicted. This analysis is perhaps not a strong test, since this hypothesis also implies that populations at a lower trophic level should compete if they have somehow escaped from control by their predators.

A third *a priori* hypothesis which could be tested with these data is the prediction that interspecific competition is less likely to occur in habitats or groups of organisms that are more vulnerable either to harsh physical conditions or to natural enemies (Connell 1975). Smaller-bodied individuals are often more vulnerable than larger ones to both these hazards. In my paper (Connell 1975, figs. 2–5) I suggested a model of how body size might interact with gradients in the physical environment and predation to affect the degree of mortality from these agents and so the degree of interspecific competition experienced by an organism.

The invertebrates in table 3 all have smaller body sizes than either the plants or the vertebrates. (There were no small or microscopic plants in the studies reviewed here.) As a consequence, my hypothesis would predict that the invertebrates would be less likely to compete than would plants or vertebrates. The analyses in table 3 are consistent with this prediction for marine but not for terrestrial species. Also, since the terrestrial herbivores (insects and small mammals) are probably more vulnerable to predation than the marine herbivores in these studies (sea urchins), the same predictions apply. The analysis in table 2 confirms this prediction. Schoener (1974) had also suggested that smaller animals would compete less than larger ones, and analysis of the data from his recent survey (Schoener 1983) is consistent with this prediction.

One other clear trend shown in tables 2 and 3 is that, without exception, terrestrial organisms showed a lower frequency of interspecific competition than marine ones. With regard to the plants, I suspect that the lower frequency of terrestrial than marine competition may be a consequence of the fact that most of the terrestrial studies were made of herbs on grazed pastures, mown turfs, or on sites of recently abandoned agriculture. Grazing and mowing act in the same fashion as predation in reducing competition (Harper 1969; Connell 1975); also, on recently abandoned fields the abundance may not have reached levels high enough to result in strong interference between the plants. In contrast, the marine plant examples all come from natural stands of larger algae which may not have been greatly affected by grazing. This is not always the case; other grazing studies have indicated that sea urchins are capable of greatly reducing the abundance of larger algae (Paine and Vadas 1969).

The terrestrial invertebrates (insects and spiders) were about the same size as the marine invertebrates (except for sea urchins), so that vulnerability to preda-

tion probably cannot account for the differences. The same applies to the vertebrates; in any case the studies of marine vertebrates were too few to permit useful comparisons. Probably there is no single explanation for the contrast in competition between terrestrial and marine organisms.

The results to this point all refer to responses that were either changes in abundance or in a variable that could affect abundance. A few studies measured changes in resource use, i.e., competitive niche release. These 14 papers indicate that competitive release occurred in about three quarters of these species (see table 4). Five studies involved only one experiment at a single time and place, and as indicated in table 1, a tally of such estimates tends greatly to overestimate the frequency of occurrence of interspecific competition. One paper (Holbrook 1979; study no. 28) studied competitive release of a species paired with more than one other species; none was done with the same pair at different times or places.

Variation in Occurrence of Interspecific Competition

A species may vary in at least two ways in the degree to which it competes. It may compete with some species in the community but not others, and it may compete with a particular other species at some times or places but not at others. The mechanisms producing the former sort of variation are difficult to investigate, since they are in part a reflection of the evolution of the species. The mechanisms producing variation in space and time are more amenable to investigation, since they may sometimes be correlated with contemporary environmental variations.

Thirty-six of the 72 studies gave data on interspecific competition between the same species at different places or times. The results are shown in table 5. In about half of the species in these studies no interspecific competition was found, so no conclusions can be drawn concerning variation. In those species that showed some competition, however, 59% showed annual variation and 31% showed spatial variation. Where data on annual variation are available, competition occurred in 35% of the years; the corresponding figure for spatial variation was 46% of the sites studied.

Schoener (1983) also discusses temporal variability in interspecific competition. Eleven of the studies in his review showed annual variability, three others possibly did so, and 12 showed none. Within-year variability occurred in one case and not in two others. Thus in the studies that had evidence for it, competition was variable in about half of the studies in his review. This is about the same degree of variation that emerges from my analysis of variability within species. Apparently it is not rare for competition to vary in either time or space, although Schoener (1983) and I differ in this judgment.

Reasons for these variations have been suggested in some cases. Wiens (1977) has proposed that competition might occur only when resources are scarce. I will discuss three studies of lizards in detail since they provide very interesting evidence concerning this hypothesis. Dunham (1980, study 15) studied *Urosaurus ornatus* and *Sceloporus merriami* in 1974–1977 in Texas, and Smith (1981, study 58) studied the same *Urosaurus* sp. and *Sceloporus virgatus* in 1973–1976 in Arizona. Insect prey became scarce in dry years; two of the four years (1975 and

TABLE 4
FIELD EXPERIMENTS ON COMPETITIVE RELEASE IN NICHE BREADTH (Response measured was a change in horizontal or vertical distribution toward that of a competitor, following an experimental reduction in the abundance of that competitor.)

Study No.	Habitat	Organism	No. of Taxa	Change Measured	No. of Exp. per Taxon (no. comp. found/total no.)
38	freshwater	plant	1	horizontal zonation from pond edge	1/1
34	marine	algae	2	intertidal ht., 2 sites	2/2, 2/2
70	terrestrial	spiders	2	ht. of web	0/1, 0/1
6	marine	snails	1	intertidal ht.	1/1
50	marine	snails	1	intertidal ht.	1/1
5	marine	crabs	2	intertidal ht.	1/1, 0/1
27	marine	fish	2	subtidal depth (2 yr for 1 sp)	0/1, 2/2
33	marine	fish	2	subtidal depth	1/1, 1/1
54	marine	fish	5	horizontal distribution	5@ 1/1
64	terrestrial	lizard	1	aboreal vs. ground	0/1
8	terrestrial	mammal	2	altitude on mt.	0/1, 1/1
28	terrestrial	mammal	3	aboreal vs. ground	0/1, 1/1, 2/2
28	terrestrial	mammal	3 (same)	horizontal, veg. type	0/1, 1/1, 1/2
42	terrestrial	mammal	2	horizontal, veg. cover	1/1, 1/1
49	terrestrial	mammal	1	horizontal, veg. type	1/1
55	terrestrial	mammal	2	horizontal, veg. type	0/1, 0/1

SUMMARY: 11 of the 15 studies (73%) showed some interspecific competition; 22 of the 29 species (76%) showed some interspecific competition; 26 of the 37 experiments (70%) found interspecific competition.

TABLE 5

VARIATION IN TIME AND SPACE IN THE OCCURRENCE OF INTERSPECIFIC COMPETITION (Entries are the number of species that were observed for the number of years, seasons or sites shown, and that competed in the given % of those times or places.)

	NO. OF SPP. WITH FOLLOWING % OF YR OR SITES THAT SHOWED COMPETITION					SPECIES SHOWING SOME COMPETITION	ALL SPECIES	
	0	1-33	34-66	67-99	100	No.	% Spp. with Some Variation	Ave. % Yr or Sites with Comp.
A. ANNUAL VARIATION (seasonal in parentheses)								
No. Yr. Obs.								
2	12 (5)		7 (3)		6 (6)	13 (9)	54 (33)	25 (14)
3	7			3	1 (1)	4 (1)	75 (0)	11 (1)
Total ...	19 (5)		7 (3)	3	7 (7)	17 (10)	59 (30)	36 (15)
								35 (57)
B. SPATIAL VARIATION								
No. Sites Obs.								
2	18		2		15	17	12	35
3	5	1			3	4		9
4	1	1	3	1	2	7	58	8
13		1				1		1
Total ...	24	3	5	1	20	29	31	53
								46

NOTE.—A. Study nos. with data on annual var.: 11, 12, 15, 16, 22, 27, 29, 45, 46, 52, 58, 62, 64, 68, 71; seasonal var.: 9, 17, 35, 46, 47, 59, 66. B. Study nos. with data on spatial var.: 4, 7, 9, 10, 12, 19, 20, 23, 24, 25, 34, 39, 40, 46, 56, 68, 72.

1977) were exceptionally dry in Texas, one of the four years (1974) was exceptionally dry in Arizona. Wiens' (1977) hypothesis predicts that competition would be more likely to occur in the drier years when food resources are scarcer. Evidence consistent with this hypothesis was found as follows. In *Urosaurus* in Texas, competitive effects were found on growth in two dry years but not in two wet years, and on foraging success in early summer when food was scarce but not in late summer when food was abundant. For *Urosaurus* in Arizona, competitive effects on survival of young females were found in one dry year, not in two wet years. In *Sceloporus virgatus* in Arizona, competitive effects on growth and survival of young females were found in the dry year but not in the next wet year. However, some evidence in the Texas study is inconsistent with the hypothesis. Competitive effects on yearling survival of *Urosaurus* occurred in one wet year but not in a dry year. Also, competitive responses in density of *Urosaurus* were found in both a wet and a dry year, but not in the other dry year. In a third study of effects on *Sceloporus undulatus* of removal of two other lizard species in another location in Arizona, Tinkle (1982, study 64) found no competitive effects in four different responses in two years. Overall, as shown in Appendix A, interspecific competition occurred rarely in all three studies; when it was found, some re-

sponses were consistent with Wiens' (1977) hypothesis, others were not. *Urosaurus ornatus* showed more competitive effects in the drier Texas site than in the more mesic Arizona site, which is consistent with Wiens' hypothesis. These excellent studies demonstrate the value of measuring different responses over long periods.

Another study showing annual variation is that of Ericksson (1979, study no. 16) of carnivorous ducks competing with fish in Swedish lakes. In two years there were significantly more ducks on lakes without fish than on those with fish added; in the third year the difference was not statistically significant. In the year when the numbers of ducks were most different between treatments the insect prey were also the most different. However, in the other two years the competitive effects were not correlated with abundance of food. Overall these results are consistent with Wiens' (1977) hypothesis.

One study of marine invertebrates gave evidence of annual variation. Sutherland (1978, study no. 62) removed two sessile colonial species from fouling panels in each of two years. The effects of these treatments differed in the two years, because all species, both those that were experimentally manipulated and those being affected, varied greatly in abundance between the two years. These differences may have been the result of temporal variations in the rates of recruitment from the plankton of many of these species.

Spatial variation was observed in several instances. Miles (1974, study no. 40) studied the effects of removing the canopy and litter on eight species of plants on four forest sites with different soils. In one species no competition was found on any site; in two species competitive effects were found on all four sites, while competition varied between sites in the other five species. The strongest effect was caused by interference with germination by the litter from the canopy plants. Differences in competition between sites may have resulted from variations in the soils, or in the type and amount of litter present. One other terrestrial study had data on spatial variation. Seifert and Seifert (1976, study no. 56) found competition between a pair of insects in the flower bracts of one species of host plant but not in a congener. As shown in Appendix A, interspecific competition was rare in this ephemeral community and this variation between hosts may be simply a chance occurrence.

Spatial variations in competition in marine algae were found by Dayton (1975, study no. 10). Two species showed no spatial variation; the third, a group of "fugitive" species, showed no variation in competition with *Lessoniopsis* but did show variation in competition with *Hedophyllum*. The reason for the latter variation was simply that *Hedophyllum* was relatively rare in one of the sites so that its removal there did not open up much of the free space which the fugitive species require. Menge (1976, study no. 39) found that barnacles were outcompeted by mussels in only four of the 13 sites in which both species were capable of covering all the space. Three of the four were in places where predatory snails could not feed, either because of heavy waves or a high shore refuge. The fourth was classified as a temporary escape from predation. In the other nine sites, heavy predation prevented the mussels from outcompeting the barnacles.

In summary, interspecific competition may not occur for several reasons. In the

cases of the sessile marine animals studied by Sutherland (1978), recruitment may sometimes fail to occur. In others, e.g., Dayton (1975), the species being experimentally reduced may be so rare that effects on other species are too slight to be detectable against the background of normal variation. Third, in some years or sites resources may not be limiting (Wiens 1977); some evidence of this comes from the studies of lizards and ducks described earlier. Fourth, predation may reduce the populations to such low levels that they are not pressing on their resources. Some examples from this survey are: predation by snails on mussels (Menge 1976); by sea urchins on algae (Dayton 1975; Duggins 1980); and by various predators on tadpoles (DeBenedictis 1974). Lastly, the process of competition may be interrupted by physical disturbances, as seen in marine intertidal plants and sessile animals (Sousa 1979; Taylor and Littler 1982).

The Relative Strengths of Interspecific Versus Intraspecific Competition

If we are interested in the coexistence of competing species, it is not sufficient to measure only interspecific interactions. As discussed earlier, it is necessary to do experiments designed particularly to distinguish the two sorts of competition. Of the 72 papers, 14 did this, studying 42 species with 123 experiments. As shown in table 6, for 31% of the species and 17% of the experiments interspecific competition was stronger than intraspecific competition. Eleven of the 14 studies also performed type 1 experiments on the same species and found interspecific competition for 71% of the species and 40% of the experiments. Thus a comparison of the results of the two types of experiments shows that when interspecific competition was found by a type 1 experiment, a type 2 experiment showed it was stronger than intraspecific in less than one-quarter of those cases.

It is important to evaluate how representative this sample is. As shown in table 6, all three habitats are represented, as well as the three taxonomic and trophic groups used earlier. The terrestrial habitat and invertebrate herbivores are over-represented, however. Also, the percentage of species showing interspecific competition with type 1 experiments in table 6 (71%) is higher than the average of 55% for all species; however, the 40% of experiments showing competition is only slightly higher than that in tables 2 and 3.

Asymmetry and the Rank Order of Competitive Ability

Competition is the term used when each species of a pair has a negative effect on the other. If only one species of a pair is affected negatively, this has been termed "amensalism" (Burkholder [1952] used the signs $(-, -)$ for competition, $(0, -)$ for amensalism). In the present survey, both members of a pair of species were studied with type 1 experiments in 98 cases. Of these, 44 pairs showed no interaction, 33 pairs showed apparent amensalism with only one species affected, and 21 pairs showed competition with a reciprocal negative effect (table 7).

If one member of a pair of species that are competing for the same resources is strongly affected by the second, it seems reasonable to expect that there could be some reciprocal effect, however slight, but with the weaker one being undetect-

TABLE 6

RESULTS OF ALL STUDIES WITH TYPE 2 EXPERIMENTS MEASURING BOTH INTRASPECIFIC AND INTERSPECIFIC COMPETITION, COMPARED TO THE RESULTS OF TYPE 1 EXPERIMENTS FROM THE SAME PAPERS (Entries are number of experiments and, in parentheses, number of species.)

STUDY No.	HABITAT/ ORGANISM & TROPHIC LEVEL	No. OF TAXA	RESPONSE	No. OF EXPERIMENTS (no. spp.)							
				TYPE 1 EXPERIMENT		TYPE 2 EXPERIMENT					
				INTERSP. COMP.		INTER =		INTER >			
				Found	Not Found	INTRA	INTRA	INTRA	INTER		
17	ter./plant	2	physiol.	4 (2)		3 (2)	1				
32	ter./plant	4	wt.	4 (2)	4		4 (2)		
51	ter./plant	2	growth	2 (1)	3 (1)		1		
37	ter./inv./herb.	7	repr.	16 (7)			7 (3)		9 (4)		
56	ter./inv./herb.	6	dens.	5 (4)	19 (2)	4 (3)			12 (3)		8
57	ter./inv./herb.	4	dens.	1 (1)	11 (3)				3 (1)		9 (3)
70	ter./inv./herb.	2	surv., repr.		2 (2)				2 (2)		
7	fw./inv./herb.	2	repr.	6 (2)		3 (1)	1		2 (1)		
59	fw./inv./herb.	2	pop. gr.	8 (2)	8	1 (1)			1 (1)		
67	fw./vert./carn.	2	surv.		2 (2)				
9	mar./inv./herb.	3	mort.	3 (2)	5 (1)	3 (2)	2		3 (1)		
46	mar./inv./herb.	2	growth	1 (1)	22 (1)				8 (2)		15
66	mar./inv./herb.	3	mort.	3 (2)	5 (1)	1 (1)	2		2 (2)		
54	mar./vert./herb.	1	feeding	1 (1)					1 (1)		
Total no. species				24	10	13	6	20		3	
% of total				70.6		31.0	14.3	47.6		7.1	
Total no. experiments				48	72	21	22	48		32	
% of total				40.0		17.1	17.9	39.0		26.0	
% of exp. that found competition					23.1	76.9				

NOTE.—ter. = terrestrial, inv. = invertebrate, herb. = herbivore, fw. = freshwater, carn. = carnivore, mar. = marine, vert. = vertebrate, physiol. = physiological, wt. = weight, repr. = reproduction, dens. = density, surv. = survival, pop. gr. = population growth, mort. = mortality.

TABLE 7

ASYMMETRY IN INTERSPECIFIC COMPETITION; EVIDENCE FROM ALL STUDIES IN WHICH TYPE 1 EXPERIMENTS WERE PERFORMED ON BOTH MEMBERS OF A PAIR OF SPECIES (If more than one pair was studied or more than one response variable per pair, this information is indicated in parentheses after the study code number.)

-
1. SYMMETRICAL COMPETITION (both members of the pair responded)
Study nos: 7 (fecundity only), 9 (growth 1 pr), 15 (first yr survival), 17, 29, 33, 35, 36, 37 (8 pr), 42 (4 variables), 58 (survival only), 59 (2 pr), 69. Total 21 pr.
 2. ASYMMETRICAL COMPETITION (only one member responded)
Study nos: 4 (5 pr), 5, 7 (growth only), 8, 9 (2 pr), 10 (2 pr), 15 (6 var.), 18 (4 pr), 21, 24, 27, 28 (2 variables), 35 (2 pr), 42 (2 variables), 46, 56 (5 pr), 57, 58 (growth young females), 59, 62, 66 (3 pr). Total 33 pr exclusive of those in symmetrical category.
 3. NO COMPETITION (shown by either member of the pair)
Study nos: 4 (17 pr), 9 (mortality, 1 pr), 10, 11, 18 (9 pr), 28 (1 variable), 42 (1 variable), 45, 55, 56, (6 pr), 57 (5 pr), 58 (several variables), 60, 61, 70. Total 44 pr, exclusive of the above two categories.
 4. REVERSALS OF RANK ORDER: evidence for reversals in the order of competitive superiority in a pair is presented only in the following studies: (a) reversals occurred in study nos. 15, 35, 46 (see text); (b) no reversals occurred in study nos. 4, 7, 9, 24, 56, 58, 59, 66.
-

able against the background environmental variation. Therefore I suggest that the term asymmetrical competition be used, as Lawton and Hassell (1981) have done, in place of amensalism. The latter term has never taken hold in ecology; all the authors in the present survey used competition, never amensalism.

Of the 54 pairs in table 7 that showed some competition, 61% were strongly asymmetrical. Lawton and Hassell (1981), in a survey of insect species, found 66% of 35 pairs to be strongly asymmetrical; 15 of these pairs are included in the present survey. In Schoener's (1983) survey, 61 studies contained experiments on both members of one or more pairs (32 of these studies are included in the present survey). Eighty-four percent of these 61 studies had some pairs showing strong asymmetry. Clearly it is the rule rather than the exception.

With strong asymmetry one can easily rank the species in competitive ability. In an asymmetrical pair, the species unaffected in a field experiment should be superior in competition to the one affected. Even in symmetrical pairs, exact equivalence is seldom expected, although it may be more difficult to rank the species than when strong asymmetry exists. If the rank order remains the same, and if interspecific competition is stronger than intraspecific in the superior species, in theory the inferior one should eventually be eliminated, all other things being equal (which they seldom are).

However if the rank order of competitive superiority were sometimes reversed, competitive elimination is less likely. Few studies are sufficiently comprehensive to provide evidence concerning such reversals. To obtain such evidence requires at least two experiments on both members of a pair, which is rarely done. In the present survey, 11 studies contained sufficient data to judge this (see table 7); in eight of these no reversals were found. In the other three the order of competitive superiority changed as follows. Lynch (1978, study 35) found that *Ceriodaphnia* was superior in a summer experiment whereas *Daphnia* was superior in an

autumn experiment. Dunham (1980, study 15) found that when using first-year survival as the measured response, only *Urosaurus* was affected in 1974, whereas only *Sceloporus* was affected in 1975. Using other responses, only *Sceloporus* was affected for adult survival, whereas only *Urosaurus* was affected for all other responses. Peterson (1982, study 46) found that, when using either growth or gonad mass as a response variable, *Protothaca* was affected but not *Chione*, but when recruitment was measured, only *Chione* was affected. Thus the rank order of competitive superiority within a pair of species changed in these three studies, either in different seasons or years or among the different response variables measured.

Field experimental evidence on reversals in the rank order of competitive superiority between members of a single pair of species is sparse, as shown by the present survey. However, another source of evidence exists in the studies of interactions between sessile marine organisms on hard substrates. Direct observations of contacts between neighbors can yield evidence as to whether one is killing its neighbor by overgrowth, allelopathy, or other means of aggressive interference. If enough observations are made of contacts between individuals or colonies it is possible to test the null hypothesis of equivalence in wins between two species (Kay and Keough 1981). A recent review (Connell and Keough 1983) indicates that there is now sufficient evidence to test this hypothesis in a few studies (Jackson 1979; Buss 1980; Kay and Keough 1981; Russ 1982; Rubin 1982; Connell and Keough 1983). In some pairs of species, competition was asymmetrical and consistent, one species always winning. In other pairs there were frequent reversals, each species winning some of the contests. In other contests, neither species won; some of these standoffs lasted many years (Connell 1976).

What determines competitive superiority? Among many possibilities, size has been suggested as being important by several authors, the larger species usually (but not always) being superior (see review in Schoener 1983). With organisms that compete for space, and in particular the clonal ones such as plants and attached colonial animals, competition occurs mainly between neighbors. Here, individual size varies enormously and usually the larger neighbor is superior, regardless of species; taller forest trees suppress smaller ones, larger colonial animals win over smaller ones (Buss 1980; Russ 1982). Thus competitive ability, rather than being species specific becomes size specific or age specific. In such cases, reversals of competitive rank between species should be common, reducing the degree of asymmetry.

Positive and Indirect Interspecific Interactions

Some responses to the interspecific experimental manipulations in the present survey were positive. These occurred in four studies of plants (nos. 4, 10, 18, 63 in Appendix A), seven studies of herbivores (nos. 14, 35, 37, 46, 56, 57, 61), and three studies of omnivores or carnivores (nos. 15, 28, 62). Most of these positive responses involved only one member of a pair; mutually positive responses occurred only in studies 37 and 56. In some studies (nos. 4, 15, 18, 46) a large

number of experiments were done, so that some of the results in these studies may be attributable to chance.

What mechanisms might account for these positive interactions between species on the same trophic level? Direct positive interactions between species are clearly possible. For example, in study no. 10 (Dayton 1975) the larger overstory algae probably protected the smaller understory species from desiccation or radiation damage. The larger species of sea urchin in study no. 14 (Duggins 1981) apparently protected the smaller species from predatory starfish. Alternatively, negative effects acting indirectly through other species may produce positive outcomes. For example, let us assume that species B competes with both species A and C, but the latter two do not compete. If A were experimentally increased, this could cause B to decrease, which would allow C, being released from competition, to rise. A reasonable but incorrect interpretation is that A and C interact positively. This possibility was suggested by Fowler (1981) to account for the positive responses in study no. 18; other examples of such complex competitive interactions have been studied and discussed by several other authors (Neill 1974; Wilbur 1972; Smith-Gill and Gill 1978).

A second type of indirect interaction involves predators that are specialized on particular prey species. For example, if the prey compete but the predators do not, an experimental increase in one predator might cause a decrease in its prey A, a consequent increase in prey B because it was released from competition, and so an increase in its predator. A reasonable but incorrect interpretation of this experimental result is that the predators were interacting positively. This idea was called "complementary feeding niches" by Dodson (1970) and has been discussed theoretically by Levine (1976) and Vandermeer (1980). A mechanism similar to this was suggested by Lynch (1978) to explain the positive responses in his study.

The converse is also possible. If prey A and B were interacting positively instead of competing in the above experiment, both would decrease, causing a reduction in the second predator. An investigator ignorant of the prey interactions might incorrectly conclude that the predators were competing.

Quinn and Dunham (1983) point out the problem posed by such multiple causes acting simultaneously, and warn against testing "univariate hypotheses" that postulate, for example, that only competition or only predation is responsible for a given pattern. This problem has bothered ecologists for many years and to overcome it several approaches have been tried. First and foremost is the necessity of studying the system from all angles so as not to miss the important interactions; there are no quick and dirty ways to do ecology. Second is the testing of several hypotheses; Jackson (1981) has pointed out that plant ecologists have been doing field experiments on the effect of grazers on plant competition since at least 1917. Although it has not often been done, the technique of simultaneously varying the densities of both competitors and predators in a nested experimental design is to be recommended. For example, by doing this I was able to indicate the effect of predation on interspecific competition in intertidal animals (Connell 1961), a situation very similar to the example given by Quinn and Dunham (1983). Two studies from the present survey performed simultaneous manipulations of

competitors and predators (DeBenedictis 1974; Peterson 1982), while Dayton (1975) and Sousa (1979) studied both grazing and competition in separate experiments. As Simberloff (1983) suggests, the fact of multiple causality in ecology only demands more ingenuity in framing hypotheses and choosing tests whose outcomes are unambiguous.

SUMMARY

In a strictly defined sample of competition studies using controlled field experiments, covering 215 species and 527 experiments, competition was found in most of the studies, in somewhat more than half of the species, and in about two-fifths of the experiments. In most of these experiments interspecific competition was not distinguished from intraspecific competition. In the few studies in which the two were separated, interspecific competition was the stronger form in about one-sixth of all experiments done. When competition was demonstrated, intraspecific competition was as strong or stronger than interspecific in three-quarters of the experiments.

Some evidence from this literature survey suggests that negative results may be underrepresented, so that the absolute values of these figures may be too high. Since this bias should apply also to studies of all taxa, habitats, or other interactions it should not greatly affect estimates of the relative prevalence of competition. Since these estimates come from field experiments open to other influences such as predators, grazers, weather, disturbances, etc., they should provide a fair approximation of the relative prevalence of interspecific and intraspecific competition in natural ecological communities.

The prevalence of competition in these studies varied. Marine organisms showed consistently higher frequencies of competition than terrestrial ones as did large-sized organisms as compared to smaller ones. Plants, herbivores, and carnivores showed similar frequencies of competition in all habitats compared. The incidence of competition varied considerably from year to year and place to place.

In some categories, evidence concerning competition is sparse. More studies are needed of all freshwater species, marine vertebrates, parasites, effects on resource partitioning, and particularly the relative strengths of interspecific versus intraspecific competition. When both members of a pair were studied and some competition found, only one member was affected in well over half the experiments. Such strong asymmetrical competition is not always consistent in direction; reversals in the rank order of competitive superiority have been demonstrated by field experiments and direct observations.

Some positive interactions were found. These may have been a consequence of actual positive influences or of negative ones acting indirectly through other species. The latter may also apply to some of the negative interactions interpreted as competition in these studies. If only the input and output of an experiment are known, it is difficult to decide what mechanism produced the observed effect. While many of the experiments probably have been correctly interpreted, the present survey illustrates how difficult it is to produce a clear and unambiguous demonstration of interspecific competition.

ACKNOWLEDGMENTS

I would like to thank the following for their discussions and criticisms of this paper: J. Bence, R. Black, A. Blaustein, J. Choat, S. Cooper, P. Dayton, R. Dean, E. Denley, J. Dixon, B. Downes, R. Doyle, M. Dungan, A. Dunham, P. Fairweather, M. Fawcett, N. Hairston, S. Holbrook, K. Hopper, J. Jackson, M. Keough, B. Mahall, M. Marsh, W. Murdoch, C. Osenberg, R. Paine, D. Peart, C. Peterson, M. Price, J. Quinn, P. Raimondi, M. Saunders, R. Schmitt, S. Schroeter, B. Sheehan, D. Shiel, D. Smith, A. Smythe, W. Sousa, D. Spiller, A. Stewart-Oaten, S. Swarbrick, A. Underwood, J. Wild, B. Menge, and T. Schoener.

APPENDIX A

SUMMARY OF EXPERIMENTAL RESULTS

Entries for each study are: study code no., author, year, habitat, trophic level, phylum or other broad classification of organism studied, variables measured and other relevant details, if necessary. If the study was done in other than natural conditions, these are indicated. Experimental results are given under two experimental types: type 1, occurrence of interspecific competition, and type 2, relative strength of intraspecific competition vs. interspecific. Type 1: For each response studied (e.g., growth, mortality, etc.), the fraction listed for each species (or group of species as indicated) is the number of experiments in which interspecific competition was found/the total number of experiments performed. If data on temporal or spatial variation exist, the fraction indicates the number of experiments in different years (yr), seasons (t), or sites (s). If in a pair of species density was manipulated for both, the results for the pair are given as follows: If one responded and the other did not, this asymmetrical result is indicated by "asym."; if both responded, it is so indicated; if neither responded, it is so indicated. These responses refer only to ones indicating competition; a response indicating a positive interaction was scored as no competitive response, and these are indicated separately. Type 2: For each taxon studied, the strength of intraspecific competition relative to interspecific with every other taxon is given for each variable studied. The meanings of the abbreviations used are, e.g., "Sp. X, intra > with Y" indicates that for sp. X, intraspecific competition is stronger than interspecific competition with sp. Y; "inter > from Y" indicates that interspecific competition from sp. Y is stronger than intraspecific; "intra = with Y" indicates that the two types of competition are equivalent. If neither type is detectable, no entry is given. If there are only two species, the species abbreviations are omitted as being unnecessary. Exp. = experiment(s).

Some papers with field experiments on competition in the journals and years examined were not included for the following reasons: (1) The setup of the experiment bore little apparent resemblance to any existing natural situation, and no data were provided to indicate whether such a resemblance exists. (Such arrangements are properly designed to test certain hypotheses, but it is very difficult to know whether the results can be extended to nature.) (2) In some cases it was impossible to decide whether the effect could be caused by interspecific competition. A group of species was manipulated together and the subsequent response of the same group observed. Thus the responses seen may have resulted from either intraspecific or interspecific interactions. (3) Instead of providing the analyzed or summarized data, only the probability level of the significance test was given so that it is not possible for the reader to evaluate the results. (4) If the species potentially could compete, but the interaction was a predator-prey one, some workers regard this as an extreme form of interference. However, I did not include any papers in this category. (5) If controls were absent, or were not done at the same time as the treatments, or if the control sites had different environmental conditions from the treatments, these were excluded.

1. Abramsky et al. 1979. Terrestrial mammal omnivore density on irrigated and fertilized field. Type 1: 1 sp. 1/1.
2. Abramsky and Sellah 1982. Terrestrial mammal granivore density. Type 1: 1 sp. 0/1. No positive response.
3. Adams and Traniello 1981. Terrestrial insect (omnivore), effect on immigration of one sp. to food (bait) guarded by another sp. Type 1: 1/1, short-term behavioral response.
4. Allen and Forman 1976. Terrestrial plants, herbs on three 6-yr old fields, density. Type 1: all exp.: *Potentilla* 3/4, *Convolvulus* 2/11, *Aster* 0/11, *Hieracium* 0/8; 3 other spp., each 0/4; 2 other spp., each 0/3. Of these, the following had data on spatial variation: 2 pairs of spp. on each of 2 different sites, 4 @ 0/2 s; 1 pair of spp. on 3 sites, 2 @ 0/3 s. Pairs: 17 neither, 5 asym.: *Aster* > *Potentilla*, *Fragaria* > *Convolvulus*, *Solidago* > *Convolvulus*, *Hieracium* > *Potentilla*, *Plantago* > *Potentilla*; no reversals within pairs. Positive response: *Aster* 1/11.
5. Bertness 1981. Marine omnivorous crustacea, crabs transplanted to pools, short-term behavior (emigration), 2 spp. Type 1: 1/1, 0/1. Pair: asym. No positive response.
6. Black 1979. Marine molluscan herbivore density, intertidal shore height, 1 sp. Type 1: 1/1.
7. Brown 1982. Freshwater herbivorous snail fecundity and growth, 2 spp. in 1-liter containers in 3 ponds. Type 1: *Physa* fecundity 3/3 s, growth 0/3 s; *Lymnaea* fecundity 3/3 s, growth 1/3 s. No positive responses. Pairs: fecundity both; growth asym., no reversals. Type 2: *Physa* fecundity inter >, 3 ponds; growth intra >, 3 ponds; *Lymnaea* fecundity intra >, 1 pond, intra =, 2 ponds; growth intra >, 1 pond, intra =, 2 ponds.
8. Chappell 1978. Terrestrial omnivorous mammals, shift in altitudinal distribution on mountain, 2 spp. Type 1: 0/1, 1/1. Pair: asym. No positive response.
9. Creese and Underwood 1982. Marine herbivorous snails in cages, mortality (mort.), growth, and weight (wt.). *C.* = *Cellana*, *S. v.* = *Siphonaria virgulata*, *S. d.* = *S. denticulata*. For mort., exp. were done in the following 2 periods: May–Aug. 1977 with all 3 spp., July 1979–Jan. 1980 with *C.* and *S. d.* only. For growth, exp. were done in either 2 or 3 separate areas for the above 2 periods, respectively, giving a total of 5 exp. for *C.* and *S. d.* and 2 exp. for *S. v.* For weight, 3 exp. in the second period for *C.* and *S. d.* For mixed spp. densities of 20, treatments with 15 *C.* were not included since treatments could not be maintained because of high mort. Type 1: After each fraction is shown the other sp. in the pair. *C.*: mort. 0/1*S. v.*, 0/2*S. d.*; growth 0/2*S. v.*, 0/5*S. d.*; wt. 0/3*S. d. S. v.*: mort. 1/1*C.*, 0/1*S. d.*; growth 2/2*C.*, 2/2*S. d. S. d.*: mort. 2/2*C.*, 0/1*S. v.*; growth 5/5*C.*, 2/2*S. v.*; wt. 3/3*C.* No positive responses. Temporal (seasonal) variation (same for both mort. and growth): 2 @ 0/2 t, 2 @ 2/2 t; spatial variation (growth only): 2 @ 0/2 s, 4 @ 2/2 s, 0/3 s, 3/3 s. Type 2: All comparisons are between single sp. vs. 2 spp. treatments at the same total density. *C.*: mort., intra > with *S. v.*, 1 exp., intra > with *S. d.*, 2 exp.; growth, intra = with *S. v.*, 2 exp., intra = with *S. d.*, 5 exp.; wt. intra > with *S. d.*, 3 exp. *S. v.*: mort., inter > from *C.*, 1 exp., intra = with *S. d.*, 1 exp.; growth intra = with *C.*, 2 exp., intra = *S. d.*, 2 exp.; *S. d.*: mort., inter > from *C.*, 2 exp., intra = with *S. v.*, 1 exp.; growth, intra = with *C.*, 5 exp., intra = with *S. v.*, 2 exp.; wt. intra = with *C.*, 3 exp. Pairs: mort.: *C.* > *S. v.* asym., *C.* > *S. d.* asym.; *S. v./S. d.* neither; growth *C.* > *S. v.* asym., *C.* > *S. d.* asym. *S. v./S. d.* both; wt. *C.* > *S. d.* asym. No reversals within pairs.
10. Dayton 1975. Marine algal cover (figs. 3, 4 only, since in other exp. [figs. 1, 2] algal removal was confounded with herbivore departure). Type 1: Spatial variation, 2 sites: fugitive spp. when *Hedophyllum* (*H.*) removed 1/2 s; with *Lessoniopsis* (*Le.*) removed 2/2 s; *H.* when *Le.* removed 2/2 s. With no data on variation: fugitive spp. when *Laminaria* (*La.*) removed 0/1, *H.* with *La.* removed 0/1, *La.* when *H.* removed 0/1, *La.* when *Le.* removed 1/1; other ephemeral spp. when *Le.* removed 1/1; obligate understory spp. when *H.* removed 0/1. Total by sp.: fugitive 1/2 s, 2/2 s, 0/1; *H.* 2/2 s, 0/1; *La.* 0/1, 1/1; other ephemeral spp. 1/1, obligate understory 0/1. Pairs: (fig. 4) *Le.* > *H.* and *Le.* > *La.* both asym.; *H./La.*, neither. Positive response: obligate understory to *H.* 1/1.
11. DeBenedictis 1974. Freshwater omnivorous larval amphibians of 2 spp. in pens; 4 responses measured were: survival, duration of larval period, body length, and biomass at metamorphosis. Type 1: Competition found when predators excluded but no competitive effects in open pens with predators; 2 yr, 2 spp. @ 0/2 yr for each of the 4 responses. Pairs: neither for all responses. No positive responses.
12. Dhondt and Eyckerman 1980. Terrestrial omnivorous bird density: 1 sp. Type 1: no variation in 2 yr or between 2 sites in 1 yr: 3/3.

13. Duggins 1980. Marine algal cover, taxon is a group of annuals. Type 1: 1/1.
14. Duggins 1981. Marine herbivorous echinoderms, effect of removal or addition of 1 sp. on density of 2 other spp. Type 1: density 0/2, 0/2; gonad index 0/2, 0/2. No pairs. Positive responses: density 1/2; gonad index 1/2, 0/2.
15. Dunham 1980. Terrestrial carnivorous lizards, *Urosaurus* (U.) and *Sceloporus* (S.), for up to 4 yr. Type 1: Data on annual variation: density: U. 2/3, S. 0/3; first yr survival U. 1/3, S. 1/3; adult survival U. 0/3, S. 2/6; growth U. 2/4, S. 0/4. Seasonal variation: foraging rate U. 1/2, S. 0/2; no data on variation: body lipids U. 2/2, S. 0/2; body mass U. 2/2, S. 0/2. Pairs: 5 variables asym. S. > U., 1 variable asym. U. > S., first yr survival both. Positive responses: first yr survival U. 1/3, adult survival U. 2/3.
16. Eriksson 1979. Aquatic predaceous bird density, competition with fish. Type 1: annual variation, (bird) 2/3 yr. No positive responses.
17. Fonteyn and Mahall 1981. Terrestrial plants in desert, effect of removal of each sp. on xylem pressure potential of other sp. Type 1: Seasonal variation, *Larrea* 2/2, *Ambrosia* 2/2. Pairs: 2 seasons, both. Type 2: *Larrea* autumn 1977 inter >, spring 1978, intra =; *Ambrosia* autumn 1977 and spring 1978, both inter >. Note: table 3 in Fonteyn et al. (1981) contains typographical errors; the above correct results were given me by the authors.
18. Fowler 1981. Terrestrial plant percentage cover on field regularly mown for 30 yr; 8 spp. removed one at a time; no data used for removals of groups of spp. Type 1: *Plantago* (Pl.) 1/6, *Poa* 2/7, *Rumex* 0/7, *Anthoxanthum* 1/3, *Trifolium* 0/3, *Allium* 0/3, *Cynodon* (Cyn.) 1/7, *Salvia* 1/8, *Carex* 0/4, *Setaria* 1/5, *Paspalum* sp. 1/3, *Paspalum dilatatum* (Pa. d.) 2/4, *Paspalum laeve* (Pa. l.) 0/4, *Paspalum ciliatifolium* 0/5, winter annuals 1/3. Total 72 exp. Pairs: April: 3 pairs: *Rumex* > *Pl.* asym.; *Pl./Poa* neither, *Rumex/Poa* neither. Sept.: 3 pairs asym.: *Pl.* > *Pa. d.*, *Pl.* > *Cyn.*, *Cyn.* > *Pa. d.* (a transitive hierarchy of these 3 spp.). 7 pairs neither: *Pl./Pa. l.*, *Pl./Carex*, *Pa. d./Pa. l.*, *Pa. d./Carex*, *Pa. l./Cyn.*, *Pa. l./Carex*, *Cyn./Carex*. Total asym. 4; neither 9. Positive responses, 1 each: *Allium* to *Poa*, *Carex* to *Pa. l.*, *Rumex* to *Pa. d.*
19. Friedman and Orshan 1974. Terrestrial plants in desert, effect of removal of other spp. on fecundity of 2 varieties of a different sp., 2 sites. Type 1: spatial variation: no irrigation 0/2 s, 0/2 s; with experimental irrigation, 1/2 s, 1/2 s. Pairs: neither on both sites. No positive responses.
20. Friedman et al. 1977. Terrestrial plants in desert, taxon is one group of annual spp. on 2 sites, response to removal of bushes of 2 spp. Type 1: density 2/2 s, weight 1/2 s. No pairing. No positive responses.
21. Grace and Wetzel 1981. Freshwater plant (cattails) productivity, 2 spp. Type 1: 1/1, 0/1. Pair: asym. No positive response.
22. Gross 1980. Terrestrial plants on third-yr old field, effect of removal of 3 spp. groups, singly or in combination, on the density and survival of another species, 3 cohorts of which emerged in 3 different seasons. Diffuse competition effects as follows. Type 1: survival to reproduction, 3 separate cohorts 2/3 t; seedling emergence, cohorts combined 1/1; juvenile survival 3 separate cohorts 3/3 t. No pairing. No positive responses.
23. Gross and Werner 1982. Terrestrial plants, 2 sites, herbs on old field; effect of presence of existing vegetation on establishment and survival of 4 spp. Although *Daucus* and *Tragopogon* are among the dominant sp. in 15-yr old field, they were rare in the area of the study plots, so that competition was mainly interspecific (K. Gross, personal communication). Type 1: seedling emergence: *Verbascum* 2/2 s, *Daucus* 2/2 s, *Tragopogon* 2/2 s. Seedling emergence: *Oenothera* 1/1 (table 4). Rosette survival: *Verbascum* 1/2, *Oenothera* 1/2, *Daucus* 1/2 s, *Tragopogon* 1/2 s (tables 5, 8). No pairing. No positive responses.
24. Hairston 1980b. Terrestrial salamanders (predators), 2 spp., 2 sites. Type 1: density, *Plethodon glutinosus* 2/2 s, *P. jordani* 0/2 s; age structure, *jordani* 2/2 s. Spatial variations in the rate of response, faster where altitudinal overlap of 2 spp. is least. Pair: density asym. No positive response.
25. Hairston 1981. Terrestrial salamander (predators) density. Type 1: response of 4 spp. to removal of 2 other spp. separately, all at 2 sites: 4 spp. @ 0/2 s, 0/2 s. No pairs. No positive responses.
26. Hills and Vankat 1982. Terrestrial plant biomass, herbs on first-yr old field; effects of 6 types of spp. removals on 3 taxa (annuals, biennials, perennials). Type 1: 0/2, 0/5, 0/4, respectively. No pairing. No positive responses.
27. Hixon 1980. Marine fish (predators), shift in depth distribution; exp. when fish alone removed.

- Type 1: No data on variation: *Embiotoca lateralis* 0/1; data on annual variation *E. jacksoni* 2/2 y. Pair: asym. No positive response.
28. Holbrook 1979. Terrestrial omnivorous mammal activity level and resource use. *P. b.* = *Peromyscus boylii*, *N.* = *Neotoma*, *P. m.* = *Peromyscus maniculatus*. Type 1: Activity level: *P. b.* 0/1, *N.* 0/1, *P. m.* 2/2; vegetation use: *P. b.* 0/1, *N.* 1/1, *P. m.* 1/2; arboreal activity: *P. b.* 0/1, *N.* 1/1, *P. m.* 2/2. Pairing of *P. b.* and *N.*: activity neither, vegetation use asym., arboreal use asym. Positive response, vegetation use *P. b.* 1/1.
 29. Inouye, D. 1978. Terrestrial insects (nectivores), 2 spp., 2 yr for 1 sp. Type 1: density, short-term interference 1/1, 2/2 yr. 1 pair, both.
 30. Inouye, R. 1981. Terrestrial herbivorous fungal parasite of plants (attacks leaves, flowers, fruits); effect of removal of granivorous rodent competitor, 1 sp. Type 1: 1/1.
 31. Kastendiek 1982. Marine coelenterate (predator). Type 1: nos. 1 sp. 1/1.
 32. Kroh and Stephenson 1980. Terrestrial plant weight, on first-yr fallow old field. Estimated only the relative strength of intraspecific competition vs. interspecific. *A.* = *Amaranthus*, *C.* = *Chenopodium*, *P.* = *Panicum*, *S.* = *Setaria*. Results: *A.*: intra = with *C.*, intra > with *P.* and *S.*; *C.*: intra = with *A.*, intra > with *P.* and *S.*; *P.*: intra = with *S.*, inter > from *A.* and *C.*; *S.*: intra = with *P.*, inter > from *A.* and *C.*
 33. Larson 1980. Marine fish (predators), shifts in depth distribution. Type 1: 2 spp., 1/1, 1/1. Pair: both.
 34. Lubchenco 1980. Marine algal distribution, effect of removal of 1 sp. on 2 other spp.; % cover, 2 sites. Type 1: 2/2 s, 2/2 s. No pairing.
 35. Lynch 1978. Freshwater suspension-feeding herbivorous crustaceans in containers in pond; summer exp., nos. of *Daphnia* (*D.*) and *Ceriodaphnia* (*C.*), autumn exp. nos. and clutch size of *D.*, *C.*, and *Bosmina* (*B.*). Type 1: nos.: *D.* with *C.* 1/2 t, *D.* with *B.* 0/1; *C.* with *D.* 1/2 t, *C.* with *B.* 1/1; *B.* with *D.* 1/1, *B.* with *C.* 1/1; clutch size all 3 spp. 0/2. Pairs: *D./C.*: summer *C.* > *D.* asym., autumn *D.* > *C.* asym., *D.* > *B.* asym., *C./B.* both. Total 2 asym., 1 both. Positive responses: exp. 2 autumn, *D.*: nos. 2/2, clutch 2/2. Intransitive network of the 3 spp.
 36. Mackie et al. 1978. Freshwater suspension-feeding herbivorous molluscs in containers in pond; reproductive rate. *M. t.* = *Musculium transversum*, *M. s.* = *M. securis*. Type 1: 1/1, 1/1. Pair: both. Type 2: *M. t.*: inter > 1 exp.; *M. s.* inter > 1 exp.
 37. McClure and Price 1975. Terrestrial (herbivorous) insects, no. of young produced per female at different densities of adults (equal nos. of both sexes) in cages on tree leaves; abbreviations as in paper. Type 1: *Erythroneura ingrata* (*I*) and *E. bella* (*B*) 1/1; *E. morgani* (*M*) and *E. torella* (*T*): 2/2; *E. arta* (*A*) and *E. usitata* (*U*): 3/3; *E. lawsoni* (*L*): 4/4. 8 pairs, all both. Positive responses at lowest densities: *B* to *A*, *L* to *T*, *T* to *L*, *M* to *T*, *T* to *M*, *M* to *U*. Type 2: *A*: intra = with *L*, intra > with *U*, intra > with *B*; *U*: intra = with *L*, intra > with *A*, intra > with *M*; *B* intra > with *A*; *L* intra = with *A*, *I* and *U*, intra > with *T*; *M* intra > with *T* and *U*; *I* intra = with *L*; *T*: intra > with *M*, intra = with *L*.
 38. McLay 1974. Freshwater plant density, 1 sp. Type 1: 1/1.
 39. Menge 1976. Marine invertebrate (suspension-feeding omnivore) abundance, 1 sp. in cages at 13 sites where both competitors alone can reach 100% cover. Type 1: 4/13 s. No pairing. No positive responses.
 40. Miles 1974. Terrestrial plant seedling establishment, 8 spp.; with soil bared and unfertilized, results on 4 sites for each sp.; one site modified by grazing. Type 1: *Agrostis* 2/4 s, *Deschampsia* 4/4 s, *Holcus* 4/4 s, *Hypochoeris* 2/4 s, *Luzula* 3/4 s, *Rumex* 2/4 s, *Sarothamnus* 1/4 s, *Ulex* 0/4 s. No pairing.
 41. Minot 1981. Terrestrial bird (omnivore) density, 1 sp. Type 1: 1/1.
 42. Montgomery 1981. Terrestrial omnivorous mammals, 2 spp.; first fraction *Apodemus sylvaticus*, second *A. flavicollis*. Type 1: density 0/1, 1/1; survival 0/1, 0/1; immigration 0/1, 1/1; breeding season 1/1, 1/1; body weight (sexes separate) 1/2, 1/2; microhabitat use 1/1, 1/1. Pairs: 2 responses asym., 1 neither, 4 responses both.
 43. Morse 1981. Terrestrial nectivorous insect numbers. Type 1: short-term interference 1/1.
 44. Peterson 1979. Marine crustacean (suspension-feeding omnivore) abundance, 1 sp. Type 1: 1/1.
 45. Peterson and Andre 1980. Marine suspension-feeding herbivorous mollusc growth in enclosures, 2 yr, results indicate which competitor was removed. *S.* = *Sanguinolaria*, *P.* = *Protothaca*, *T* = 2 other spp. Type 1: *S.* 2/2 yr (*T*), 0/2 yr (*P.*); *P.* 0/2 yr (*T*), 0/2 yr (*S.*). Pair: *S./P.* neither both yr.

46. Peterson 1982. Marine suspension-feeding herbivorous molluscs in enclosures; 2 spp., 3 sites, 2 yr, 2 seasons. *P.* = *Protothaca*, *C.* = *Chione*. Type 1: Growth: *P.* 1/12, *C.* 0/11; recruitment *P.* (3 seasons, 3 sites) 0/9; *C.* (1 season and site) 1/1; proportion of body mass as gonad (1 site, 1 season) *P.* 1/1, *C.* 0/1. Pairs: for 2 variables asym. *C.* > *P.*; 1 variable asym. *P.* > *C.* Positive responses: growth, *P.* 1/12, *C.* 1/11. Type 2: Small *P.* growth intra > 6 exp.; *C.* growth intra > 2 exp. No competition in other 15 exp. *P.* recruitment intra > 1 exp. no competition 8 exp. *C.* recruit inter > 1 exp. Gonad proportion, *P.* intra =, *C.* intra >.
47. Petranks and McPherson 1979. Terrestrial plant, seedling germination in forest-prairie ecotone. Taxon is group of winter annuals; effects of adding shading, toxins, and litter. Type 1: seasonal variation shading exp. 3/3 t; no data on variation; toxins exp. 1/1. No pairing.
48. Pinder 1975. Terrestrial plant productivity in 18th-yr old field; taxon a group of forb spp. Type 1: 1/1.
49. Price 1978. Terrestrial granivorous mammals in pens, microhabitat use; results included here only where there was a contemporaneous control. 3 spp. of *Perognathus* combined, table 4. Type 1: 1/1.
50. Race 1982. Marine mollusc (deposit-feeding omnivore) distribution, 1 sp. Type 1: numbers, 1/1.
51. Rahman 1976. Terrestrial plant growth, 2 spp., 3 sites; estimated only the relative strength of intraspecific competition vs. interspecific; 1969 exp. in planted plots in grassland. Results: *Dactylis* intra >, 1 exp.; intra =, 2 exp.; *Deschampsia* inter >, 2 exp.; intra =, 1 exp.
52. Raynal and Bazzaz 1975. Terrestrial plant seed production in first-yr old field, height, weight, 1 sp., 3 yr. Type 1: 3/3 yr for each response; no temporal variation. No pairing.
53. Redfield et al. 1977. Terrestrial omnivorous mammal density and date of onset of breeding season, 1 sp. Type 1: 1/1 for each response.
54. Robertson et al. 1976. Marine herbivorous fish, feeding activity. Type 1: interspecific competition: effect of removal of pomacentrid on: parrotfish 1/1; nonparrotfish 4 spp. @ 1/1. Type 2: parrotfish intra > inter with pomacentrid. No pairing.
55. Schroeder and Rosenzweig 1975. Terrestrial granivorous mammal habitat use, 2 spp. Type 1: numbers, 0/1, 0/1. Pair: neither.
56. Seifert and Seifert 1976. Terrestrial herbivore and detritivore insect density; 4 spp. insects matched in pairs in each of 2 spp. *Heliconia* plants; abbreviations use first initials of each insect genus name. *Cephaloleia* (*Ce.*), *Gillissius* (*G.*), *Beebeomyia* (*B.*) are herbivores; *Quichuana* (*Q.*), *Copestylum* (*Co.*), *Merosargus* (*M.*) feed on detritus and nectar. (Although some of these insects live underwater in the flower bracts, they are classed as terrestrial because they live on a land plant.) Type 1: *Heliconia wagneriana* (*H. w.*): *Q.* 1/3, *G.* 0/3, *Co.* 0/3, *B.* 1/3; *Heliconia imbricata* (*H. i.*): *Q.* 0/3, *G.* 2/3, *Ce.* 1/3, *M.* 0/3. Same insect sp. (*Q.* and *G.*) in both plants: in *H. w.* no competition, in *H. i.* *Q.* responded positively; *G.* responded negatively. Positive responses: *Q.* to *B.*, *Q.* to *G.*, *Ce.* to *M.*, *Ce.* to *Q.*, *M.* to *Ce.* Type 2: *H. w.*: *Q.* inter > from *Co.*; *G.* intra > with *Q.*, *B.*, *Co.*: *Co.* intra > with *Q.*, *G.*, *B.*; *B* intra > with *Q.*, *G.*, *Ce.* *H. i.*: *G.* inter > from *Q.*, *M.*; *Ce.* inter > from *G.*; *M.* intra > with *Q.*, *G.*, *Ce.* Same insect pair in different plants: *H. w.*: *G.* intra > with *Q.*; *H. i.*: *G.* inter > from *Q.* No competition of either type, 8 other exp. Pairs: 5 asym.: *Co.* > *Q.*, *G.* > *B.*, *Q.* > *G.*, *M.* > *G.*, *G.* > *Ce.*; 6 neither: *Q./B.*, *G./Co.*, *Co./B.*, *Q./M.*, *Q./Ce.*, *M./Ce.*
57. Seifert and Seifert 1979. Terrestrial herbivore and detritivore insect density; 4 spp. insects matched in pairs in one sp. *Heliconia* plant. *Cephaloleia* (*Ce.*) and *Gillissius* (*G.*) are herbivores; *Quichuana* (*Q.*) and *Copestylum* (*Co.*) eat detritus and nectar. (Although some of these insects live underwater in the flower bracts they are classed as terrestrial because they live on a land plant.) Type 1: *Q.* 0/3, *G.* 0/3, *Co.* 0/3, *Ce.* 1/3. Positive response, *G.* to *Ce.* Type 2: *Ce.* intra > with *Q.*, *G.*, *Co.*, no competition, 9 other exp. Pairs: 1 asym., *Co./Ce.* 5 neither: *Q./G.*, *Q./Co.*, *Q./Ce.*, *G./Co.*, *G./Ce.*
58. Smith 1981. Terrestrial carnivorous lizards; each fraction is the no. yr for each sp. (age or sex sometimes separated): *S.* = *Sceloporus*, *U.* = *Urosaurus*. Type 1: Nos. all ages *S.* 0/3, *U.* 0/3; survival young females *S.* 1/2, *U.* 1/2; young males *S.* 0/2, *U.* 0/2; older males and females *S.* 0/2, 0/2; *U.* 0/2, 0/2; growth (only 3 groups that grew) *S.* young females 1/2, young males 0/2, *U.* young females 0/2. Pairs: neither for all variables except asym. for growth of young females and both for survival of young females; no reversals within pairs.
59. Smith and Cooper 1982. Freshwater suspension-feeding herbivorous crustaceans in containers in a

- pond, population growth. Type 1: exp. 2, July (3 spp.): *Daphnia* (D.) 2/2, *Moina* (M.) 1/2, *Ceriodaphnia* (C.) 2/2; exp. 3, Aug. (2 spp.): D. 1/8, C. 7/8. No positive responses. Pairs: exp. 2 D./M. both, D./C. both, M. > C. asym. (Intransitive network of 3 spp., no reversals within pairs). Exp. 3 D./C. asym. Temporal variation D. 1/2 t, C. 2/2 t. Type 2: exp. 3, D., intra >, C. inter >.
60. Sousa 1979. Marine algal cover. Type 1: *Ulva* removal: *Gigartina* (Gi.) sp. 1/1; *Gi. leptorhynchus* (Gi. l.) removal: *Ulva* 1/1, *Gi. canaliculata* (Gi. c.) 1/1, *Laurencia* (L.) 1/1, *Gelidium* (Ge.) 0/1; *Ge.* removal: *Ulva* 1/1, *Gi. c.* 1/1, *Gi. l.* 0/1, *L.* 0/1. *Gi. c.* removal: *Ulva* 1/1. Totals: *Ulva* 3/3, *Gi. c.* 2/2, *Gi. l.* 0/1, *Gi. sp.* 1/1, *L.* 1/2, *Ge.* 0/1. Pairs: *Gi. l./Ge.*, neither. No positive responses.
 61. Strong 1982. Terrestrial herbivorous insect density, effect on 3 invading sp. of varying the densities of either *consanguinea* or *perplexa* in *Heliconia* host plant. Type 1: invaders: *vicina* 0/2, *consanguinea* 0/1, *perplexa* 0/1. Pairs: *consanguinea/perplexa* neither. Positive response of *perplexa* to *consanguinea*.
 62. Sutherland 1978. Marine sessile omnivorous suspension-feeding invertebrates on undersides of fouling panels hung below a dock; removed *Schizoporella* (Sc.) or *Styela* (St.) one at a time in each of 2 yr. Type 1: Data on annual variation in % cover: 5 spp. (*Balanus*, *Halichondria*, *Haliclona*, *Sc.*, *St.*) @ 1/2 yr; 4 spp. (*Bugula neritina*, *Ascidea*, *Botryllus*, *Tubularia*) @ 0/2 yr. No data on annual variation, 7 spp. @ 0/1. Pairs: *Sc.* and *St.* asym. 1 yr. Positive responses: *St.* to *Sc.* 1/2 yr, *Hydroides* to *Sc.* 1/2 yr.
 63. Taylor and Littler 1982. Marine algae, herbivorous grazers and sessile suspension-feeding omnivorous animal abundance; effect of removal of sea anemone on % cover of algae and *Phragmatopoma*, and on no. of barnacles. Type 1: algae 3 spp. @ 1/1, 2 spp. @ 0/1; animals 2 spp. @ 1/1. No pairing. Positive responses of 2 spp. algae to anemone.
 64. Tinkle 1982. Terrestrial predatory lizard, 1 sp. 2 yr. Type 1: With data on annual variation: density 0/2 yr, survival 0/2 yr, yearling body size 0/2 yr, older body size 0/2 yr. Without data on variation: habitat use 0/1. No pairs. No positive responses.
 65. Turkington et al. 1979. Terrestrial plant, 1 sp. on 4 sites each having a different species of competitor, in pasture grazed by sheep for 60 yr. Type 1: seed sown, seedling emergence 4/4; transplanted seedlings, survival 4/4, yield 4/4. No pairing.
 66. Underwood 1978. Marine herbivorous snails in cages, mortality (mort.) and weight (wt.) change. C. = *Cellana*, N. = *Nerita*, B. = *Bembicium*. Experiments: 100 days all 3 spp., 200 days, N. and B. only; each fraction refers to exp. between a particular pair of species shown by the abbreviations. The number of experiments for each species is as follows: for mortality, 1 exp. replicated in time; for wt., 2 exp. at different seasons, each having as replicates the different individuals measured. The author provided the analyses for the 2 different times, since these data had been pooled in the published paper. Type 1: C., mort. 1/1 N., 0/1 B., wt. 2 seasons: 2/2 N., 0/2 B.; N.: mort. 0/1 C., 0/2 B., wt. 0/2 C., 0/2 B.; B.: mort. 1/1 C., 1/2 N., wt. 2/2 C., 2/2 N. No positive responses. Temporal (seasonal) variation in wt.: C.: 0/2, 0/2; N.: 0/2, 0/2; B.: 2/2, 2/2. Type 2: C.: mort., intra = with N., intra > with B.; wt., intra = with N., intra > with B.; N.: mort., 200 days intra > with B., wt., 200 days intra > with B.; B.: mort., 100 days inter > from C., 200 days intra = with N.; wt. 100 days inter > from C., 200 days intra = with N. Pairs: mort.: N. > C. asym., N. > B. asym. or neither, C. > B. asym.; growth: N. > C. asym., N. > B. asym., C. > B. asym. Three-species transitive hierarchy; no reversals within pairs.
 67. Werner, E., and Hall 1977. Freshwater predaceous fish, juveniles only, placed in experimental ponds, 2 spp., estimated only the relative strength of intraspecific competition vs. interspecific. Results: survival, intra = for both spp.; growth, bluegill inter >, green sunfish intra =; food type, intra = for both spp.; food size, intra = for both spp.
 68. Werner, P. 1977. Terrestrial plant productivity in second-yr and third-yr fallow old fields. Effect of experimental introduction of a different colonizing sp. on 2 taxa (grasses, herbaceous dicots); 3 sites, 2 yr. Type 1: var. space: grasses 0/3 s; variation time: grasses 0/2 yr, dicots 2/2 yr. Total: grasses 0/6, dicots 2/2. No pairing. No positive results.
 69. Williams 1981. Marine herbivorous echinoderm density, 2 spp. Type 1: removed fish, 1/1, 1/1; removed other sp. of echinoid 1/1, 1/1. Total 2/2, 2/2. One pair, both.
 70. Wise 1981a. Terrestrial predatory spiders in open frames, density, 2 spp. B. = *basilica* (*Mecynogea lemniscata*), L. = *labyrinth* (*Meteteira labyrinthea*). Type 1: all 4 variables (see below) 0/1 for each sp. Type 2: survival, L. intra >; rate of egg production, no competition either sp.; eggs per sac, B. intra >. Web height B. intra >. Pair: neither. No positive responses.

71. Wise 1981*b*. Terrestrial omnivorous insect density, 3 yr, 4 spp., effect of removal of fifth sp. Type 1: 4 spp. @ 0/3 yr. No pairs. Some positive responses which were inconsistent throughout a yr.
72. Woodin 1974. Marine deposit-feeding omnivorous annelid density in cages. Type 1: Burrowing sp. increased when the total of 3 spp. of tube-builders was reduced at 2 depths: 2/2 s. No pairing.

APPENDIX B

ON TESTING COMPETITION THEORY

The character and intensity of biological interactions have undoubtedly been modified during evolution. Direct evidence of such coevolution comes from studies of parasite-host interactions between pathogens and their plant hosts (Van der Plank 1968). Similar coevolution may have occurred between species of competitors, reducing the intensity and frequency of interspecies competition.

In a recent paper (Connell 1980) I discussed the adequacy of the existing evidence concerning the coevolution of competitors. Contrary to the statements in Pacala and Roughgarden (1982, p. 444) and Roughgarden (1983, p. 583), my paper did not criticize competition theory; it was critical only of the adequacy of the evidence that had been marshalled to test the theory of coevolution of competitors. As did Grant (1972, 1975), I concluded that the existing evidence was weak. I also argued that coevolution would be more likely to occur between populations on different trophic levels (predator-prey, parasite-host, etc.) than between competitors. My reasoning was that since predators or parasites are dependent upon their hosts for food, there would be continual interactions as the natural enemies sought out and fed on their prey. In contrast, since neither competitor is dependent upon the other, there would be less reason for the two to co-occur, so that one would expect more variability in this interaction than between natural enemies and their prey. Since variability in the interaction has been directly observed to reduce the possibility of coevolution between wheat and the pathogenic rust attacking it (Van der Plank 1968), we might also expect the same reduction in selection pressure for coevolution between competitors when competition is variable. The evidence given in the present paper suggests that interspecific competition is very variable.

Since direct evidence is preferable to reasoning by analogy, I suggested (Connell 1980) some designs for field experiments to test for competitive coevolution. My reasoning and experimental suggestions have been criticized by Roughgarden (1983) on several grounds. First, he argues that no single experimental protocol can guarantee that competition actually occurs in a system because the circumstances, mechanisms of competition, and population structure all vary. Since the success of any experiment depends upon how well it is executed, as discussed above, I agree that there is no guarantee that an experiment that followed mine or any other single protocol will demonstrate the existence of competition. Also, since the intensity of competition varies, a single experiment may fall in a period when competition intensity is very weak, and so give negative results. However, the point of doing replicated experimental manipulations with associated controls is to reduce the effects of the external contingencies and environmental variations by including them in the experiment. Properly arranged treatments and controls are open to the same degree of environmental variation, and replication is done to ensure that the results are not heavily influenced by a single extreme case, as described earlier. So within an experiment, variation is controlled for, given sufficient replication.

Roughgarden (1983) makes four other detailed criticisms of my experimental protocol; I will refer to them by the letter designations used by him. Point A: Divergence through time is only one possible outcome of coevolution, and a rather unlikely one. Possibly so, in theory; however, the theoretical argument given by Roughgarden to support this point specifies no assumptions or equations, so that there is no way to judge its applicability to reality. In any case, I stated that my protocol applies only to populations that show such divergence; they are the ones most often used to illustrate competitive coevolution and

seemed to me to provide the best situation to use for a field experimental test. (The same uncertainties apply to his other use [pp. 589, 590] of a theoretical argument against my contention that predators are effective in some conditions in reducing competition by keeping populations below the level at which they compete. In any case, his argument does not apply to the situation described in my paper, since in it, prey populations do compete.) Point B: The protocol focused on niche compression and expansion, not on niche shifts. This is true; elsewhere in my paper I had referred to niche divergence; it is easily included by adding the appropriate wording. Point C suggests that, since competition is greatly reduced after coevolutionary divergence has occurred, it would tax the resolution of my experimental protocol so the recommended test is unworkable. However, this is wrong; my experiments were designed precisely to address this problem, by transplanting the allopatric population that had not yet diverged. Point D states that detecting a genetic basis is difficult. I agree, but nothing in the subsequent discussion shows that the method I suggested would not be effective. Roughgarden's remarks (pp. 589, 590) on the problems of interpreting experimental results from intertidal systems are well taken, but I was not proposing that such intertidal systems be used to test the theory. Rather the example (of J. R. E. Harger's work) was used because it was the only one I knew in which both a transplant from allopatry to sympatry and a field experiment on competition had been done.

Roughgarden (p. 590) states that my experiments are "biased toward the detection of interference mechanisms." While this may be so, it should not actually introduce bias, since he also suggests that "exploitative competition should cause the evolution of interference mechanisms." If so, then detecting interference mechanisms should also provide indirect evidence of exploitation. He states that the lack of direct evidence concerning exploitative mechanisms "is an artifact of studies focused on the observation of inter-individual interactions." Whether this lack indicates that exploitation is actually of little importance or is an artifact of improper focus, no one knows.

To sum up, I feel that whether the theory concerning the coevolution of competitors is true or not, it has only begun to be adequately tested in the field. Roughgarden (1983, pp. 593, 583) states that his paper is a response to the "antitheoretical rhetoric" in Connell (1980) and two other papers. "These criticisms imply that competition theory, including its extension to the coevolution of competitors, is irrelevant to natural processes and is unworthy of testing regardless of whether the testing is feasible." In regard to my paper, these assertions are wrong; I did not criticize competition theory nor imply that it is unworthy of testing; in fact I proposed experimental tests. The only way I know to decide whether competition theory is relevant or irrelevant is to formulate testable hypotheses and test them, using either field experiments or statistical analyses such as Dunham et al. (1979) have done.

Ecological theory does not establish or show anything about nature. It simply lays out the consequences of certain assumptions. Only a study of nature itself can tell us whether these assumptions and consequences are true. My attitude to ecological theory is not to suggest that theory as such is worthless, but to test it.

Roughgarden also states that mine and the other two papers "criticize the evidence for competition" (p. 583) and that my paper "maintains a view downgrading the importance of competition in nature" (p. 590). It is certainly true that I criticized the quality of the existing evidence concerning the coevolution of competitors. However, my intent was neither to downgrade nor upgrade the importance of competition in nature, but simply to evaluate the evidence for it.

Roughgarden (p. 593) asserts that I maintain a view "biased against the existence of competition." Here he is confusing a specific bias with a general skepticism; I am skeptical of the existence of anything until there is evidence of it. However, it is difficult to counter an allegation of bias, since as Salt (1983) points out, unconscious bias is almost unavoidable. In his autobiography, Charles Darwin said, "I had, also, during many years followed a golden rule, namely, that whenever a published fact, a new observation or thought came across me, which was opposed to my general results, to make a memorandum of it without

fail and at once; for I had found by experience that such facts and thoughts were far more apt to escape from the memory than favourable ones'' (Darwin 1898, p. 71). The best one can do is to follow Darwin's golden rule and take steps to guard against unconscious bias. I tried to do this in the literature survey in this present paper by strictly defining the criteria for inclusion of studies and, instead of using my own bibliography of references, started from scratch and took the sample from a particular set of journals over a certain span of time.

Since I wrote my 1980 paper I have found two examples of the use of field experiments to investigate the evolution of competitors. Turkington and Harper (1979) experimented with clones of white clover that had coexisted with four different grass species in different sites in a permanent pasture. They transplanted cuttings of each clone to the four different field sites and found that usually transplants grew significantly better in the site in which each had originally lived, both in the presence and absence of the competing grass. Thus local differentiation had apparently occurred in response to both the physical nature of the site and to the species of local competitor. In the greenhouse the cuttings were grown with each of the four grass species using the same soil in all treatments so that only the species of competitor was varied. In three of the four treatments, the clone grew best with the species of grass it had lived with in the field. While it has not yet been established that this differentiation has a genetic basis, it seems likely, given other studies of white clover (references in Turkington and Harper 1979).

The second study (Hairston 1980a) is an extension of the work on competition in salamanders cited earlier (Hairston 1980b, study no. 24). Having established that interspecific competition was less strong in the site where altitudinal overlap was greater, at both sites Hairston replaced local populations of one species with transplants of the same species from the other site. The hypothesis was that where overlap was greater, adaptations that reduced the intensity of competition had been evolved to a greater extent than where overlap was small. The experimental results were consistent with this hypothesis. As in the paper by Turkington and Harper (1979) it has not yet been established that there is a genetic basis for this difference. However, these two papers provide excellent examples of well-designed field experiments that give evidence from natural populations concerning the evolution of competitors.

My views concerning competition have undergone a sea change over the past 20 yr. My first marine research indicated that interspecific competition was an important process in reducing the abundance and reproductive output of the barnacle *Chthamalus* in Scotland (Connell 1961). When I began to study what appeared at first to be a very similar situation in Washington, I was convinced that I would find competition between the barnacles to be of similar importance there. But to my surprise I did not; it was prevented by very intense predation (Connell 1970, 1971, 1975). In both studies, competition was neither upgraded nor downgraded (see Roughgarden 1983), it was simply evaluated along with other interactions in a particular community. Clearly we should withhold judgment until the evidence is more complete. The purpose of the present paper and the experiments suggested in Connell (1980) is to help make the evidence concerning competition both more complete and more rigorous.

LITERATURE CITED

- Abramsky, Z., M. I. Dyer, and P. D. Harrison. 1979. Competition among small mammals in experimentally perturbed areas of the shortgrass prairie. *Ecology* 60:530-536.
- Abramsky, Z., and C. Sellah. 1982. Competition and the role of habitat selection in *Gerbillus allenbyi* and *Meriones tristrami*: a removal experiment. *Ecology* 63:1242-1247.
- Adams, E. S., and J. F. A. Traniello. 1981. Chemical interference competition by *Monomorium minimum* (Hymenoptera: Formicidae). *Oecologia (Berl.)* 51:265-270.
- Allen, E. B., and R. T. T. Forman. 1976. Plant species removal and old-field community structure and stability. *Ecology* 57:1233-1243.

- Bertness, M. D. 1981. Competitive dynamics of a tropical hermit crab assemblage. *Ecology* 62:751–761.
- Birch, L. C. 1957. The meanings of competition. *Am. Nat.* 91:5–18.
- Black, R. 1979. Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *J. Anim. Ecol.* 48:401–411.
- Brown, K. M. 1982. Resource overlap and competition in pond snails: an experimental analysis. *Ecology* 63:412–422.
- Burkholder, P. R. 1952. Cooperation and conflict among primitive organisms. *Am. Sci.* 40:601–631.
- Buss, L. W. 1980. Competitive intransitivity and size frequency distributions of interacting populations. *Proc. Natl. Acad. Sci. USA* 77:5355–5359.
- Chappell, M. A. 1978. Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*). *Ecology* 59:565–579.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- . 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40:49–78.
- . 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer and G. R. Gradwell, eds. *Dynamics of numbers in populations. Proceedings of the Advanced Study Institute on dynamics of numbers in populations*, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen.
- . 1974. Field experiments in marine ecology. Pages 21–54 in R. Mariscal, ed. *Experimental marine biology*. Academic Press, New York.
- . 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. Cody and J. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- . 1976. Competitive interactions and the species diversity of corals. Pages 51–58 in G. Mackie, ed. *Coelenterate ecology and behavior*. Plenum, New York.
- . 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- Connell, J. H., and M. J. Keough. 1983. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In S. T. A. Pickett and P. S. White, eds. *Natural disturbance: an evolutionary perspective*. Academic Press, New York (in press).
- Creese, R. G., and A. J. Underwood. 1982. Analysis of inter- and intraspecific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53:337–346.
- Darwin, F., ed. 1898. *The life and letters of Charles Darwin*. Vol. I. D. Appleton, New York.
- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45:137–159.
- DeBenedictis, P. A. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: an experimental field study. *Ecol. Monogr.* 44:129–141.
- Dhondt, A. A., and R. Eyckerman. 1980. Competition between the great tit and the blue tit outside the breeding season in field experiments. *Ecology* 61:1291–1296.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size selective predation. *Limnol. Oceanogr.* 15:131–147.
- Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61:447–453.
- . 1981. Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia* 48:157–163.
- Dunham, A. E. 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. *Ecol. Monogr.* 50:309–330.
- Dunham, A. E., G. R. Smith, and J. N. Taylor. 1979. Evidence for ecological character displacement in western American catostomid fishes. *Evolution* 33:877–896.
- Eriksson, M. O. G. 1979. Competition between freshwater fish and goldeneyes *Bucephala clangula* (L.) for common prey. *Oecologia (Berl.)* 41:99–107.
- Fonteyn, P. J., and B. E. Mahall. 1981. An experimental analysis of structure in a desert plant community. *J. Ecol.* 69:883–896.
- Fowler, N. 1981. Competition and coexistence in a North Carolina grassland. II. The effects of the experimental removal of species. *J. Ecol.* 69:843–854.

- Friedman, J., and G. Orshan. 1974. Allopatric distribution of two varieties of *Medicago laciniata* (L.) Mill. in the Negev desert. *J. Ecol.* 62:107–114.
- Friedman, J., G. Orshan, and Y. Ziger-Cfir. 1977. Suppression of annuals by *Artemisia herba-alba* in the Negev desert of Israel. *J. Ecol.* 65:413–426.
- Gill, D. E. 1972. Intrinsic rates of increase, saturation densities, and competitive ability. I. An experiment with *Paramecium*. *Am. Nat.* 106:461–471.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am. Nat.* 118:463–474.
- Grant, P. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4:39–68.
- . 1975. The classical case of character displacement. *Evol. Biol.* 8:237–337.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old field in Michigan: experiments on the effects of vegetation. *J. Ecol.* 68:919–927.
- Gross, K. L., and P. A. Werner. 1982. Colonizing abilities of “biennial” plant species in relation to ground cover: implications for their distribution in a successional sere. *Ecology* 63:921–931.
- Hairston, N. G. 1980a. Evolution under interspecific competition: field experiments on terrestrial salamanders. *Evolution* 34:409–420.
- . 1980b. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* 61:817–826.
- . 1981. An experimental test of a guild: salamander competition. *Ecology* 62:65–72.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. *Am. Nat.* 94:421–425.
- Harger, J. R. E. 1970a. Comparisons among growth characteristics of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. *Veliger* 13:44–56.
- . 1970b. The effect of species composition on the survival of mixed populations of the sea mussels *Mytilus californianus* and *Mytilus edulis*. *Veliger* 13:147–152.
- . 1972. Competitive co-existence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. *Veliger* 14:387–410.
- Harper, J. L. 1969. The role of predation in vegetational diversity. *Brookhaven Symp. Biol.* 22:48–62.
- . 1977. Population biology of plants. Academic Press, London.
- Hils, M. H., and J. L. Vankat. 1982. Species removals from a first-year old-field plant community. *Ecology* 63:705–711.
- Hixon, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61:918–931.
- Holbrook, S. J. 1979. Habitat utilization, competitive interactions, and coexistence of three species of cricetine rodents in east-central Arizona. *Ecology* 60:758–769.
- Hurlberg, L. W., and J. S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions on sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.* 37:1130–1139.
- Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology* 59:672–678.
- Inouye, R. S. 1981. Interactions among unrelated species: granivorous rodents, a parasitic fungus and a shared prey species. *Oecologia* 49:425–427.
- Jackson, J. B. C. 1979. Overgrowth competition between encrusting ectoprocts in a Jamaican cryptic reef environment. *J. Anim. Ecol.* 48:805–824.
- . 1981. Interspecific competition and species distributions: the ghosts of theories and data past. *Am. Zool.* 21:889–901.
- Kastendiek, J. 1982. Factors determining the distribution of the sea pansy, *Renilla kollikeri*, in a subtidal sand-bottom habitat. *Oecologia* 52:340–347.
- Kay, A. M., and M. J. Keough. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia* 48:123–130.
- Keough, M. J. 1983. Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* (in press).
- Kroh, G. C., and S. N. Stephenson. 1980. Effects of diversity and pattern on relative yields of four Michigan first year fallow field plant species. *Oecologia* 45:366–371.
- Larson, R. J. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecol. Monogr.* 50:221–239.

- Lawton, J. H., and M. P. Hassell. 1981. Asymmetrical competition in insects. *Nature* 289:793–795.
- Levine, S. H. 1976. Competitive interactions in ecosystems. *Am. Nat.* 110:903–910.
- Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344.
- Lynch, M. 1978. Complex interactions between natural coexploiters—*Daphnia* and *Ceriodaphnia*. *Ecology* 59:552–564.
- McClure, M. S., and P. W. Price. 1975. Competition among sympatric *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on American sycamore. *Ecology* 56:1388–1397.
- Mackie, G. L., S. U. Qadri, and R. M. Reed. 1978. Significance of litter size in *Musculium securis* (Bivalvia: Sphaeriidae). *Ecology* 59:1069–1074.
- McLay, C. L. 1974. The distribution of duckweed *Lemna perpusilla* in a small southern California lake: an experimental approach. *Ecology* 55:262–276.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46:355–393.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *Am. Nat.* 110:351–369.
- Miles, J. 1974. Effects of experimental interference with stand structure on establishment of seedlings in callunetum. *J. Ecol.* 62:675–687.
- Minot, E. O. 1981. Effects of interspecific competition for food in breeding blue and great tits. *J. Anim. Ecol.* 50:375–385.
- Montgomery, W. I. 1981. A removal experiment with sympatric populations of *Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior) (Rodentia: Muridae). *Oecologia* (Berl.) 51:123–132.
- Morse, D. H. 1981. Interactions among syrphid flies and bumblebees on flowers. *Ecology* 62:81–88.
- Neill, W. E. 1974. The community matrix and interdependence of the competition coefficients. *Am. Nat.* 108:399–408.
- Pacala, S., and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science* 217:444–446.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.* 14:710–719.
- Peterson, C. H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* 39:1–24.
- . 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monogr.* 52:437–475.
- Peterson, C. H., and S. V. Andre. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecology* 61:129–139.
- Petranks, J. W., and J. K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology* 60:956–965.
- Pinder, J. E. 1975. Effects of species removal on an old-field plant community. *Ecology* 56:747–751.
- Price, M. V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921.
- Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *Am. Nat.* 122:602–617.
- Race, M. S. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologia* 54:337–347.
- Rahman, M. S. 1976. A comparison of the ecology of *Deschampsia cespitosa* (L.) Beauv. and *Dactylis glomerata* (L.) in relation to the water factor. I. Studies in field conditions. *J. Ecol.* 64:449–462.
- Raynal, D. J., and F. A. Bazzaz. 1975. Interference of winter annuals with *Ambrosia artemisiifolia* in early successional fields. *Ecology* 56:35–49.
- Redfield, J. A., C. J. Krebs, and M. J. Taitt. 1977. Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal British Columbia. *J. Anim. Ecol.* 46:607–616.
- Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57:1208–1220.
- Roughgarden, J. 1983. Competition and theory in community ecology. *Am. Nat.* 122:583–601.

- Rubin, J. A. 1982. The degree of intransitivity and its measurement in an assemblage of encrusting cheilostome bryozoans. *J. Exp. Mar. Biol. Ecol.* 60:119–128.
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* 53:12–19.
- Salt, G. W. 1983. Roles: their limits and responsibilities in ecological and evolutionary research. *Am. Nat.* 122:697–705.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- . 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240–285.
- Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia* 19:9–28.
- Seifert, R. P., and F. H. Seifert. 1976. A community matrix analysis of *Heliconia* insect communities. *Am. Nat.* 110:461–483.
- . 1979. A *Heliconia* insect community in a Venezuelan cloud forest. *Ecology* 60:462–467.
- Simberloff, D. 1983. Competition theory, hypothesis-testing, and other community ecological buzzwords. *Am. Nat.* 122:626–635.
- Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *Am. Nat.* 101:109–124.
- Smith, D. C. 1981. Competitive interactions of the striped plateau lizard (*Sceloporus virgatus*) and the tree lizard (*Urosaurus ornatus*). *Ecology* 62:679–687.
- Smith, D. W., and S. D. Cooper. 1982. Competition among *Cladocera*. *Ecology* 63:1004–1015.
- Smith-Gill, S. J., and D. E. Gill. 1978. Curvilinearities in the competition equations: an experiment with ranid tadpoles. *Am. Nat.* 112:557–570.
- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49:227–254.
- Strong, D. R. 1982. Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. *Ecology* 63:1039–1049.
- Sutherland, J. P. 1978. Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. *Ecology* 59:257–264.
- Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology* 63:135–146.
- Tinkle, D. W. 1982. Results of experimental density manipulation in an Arizona lizard community. *Ecology* 63:57–65.
- Turkington, R., M. A. Cahn, A. Vardy, and J. L. Harper. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. III. The establishment and growth of *Trifolium repens* in natural and perturbed sites. *J. Ecol.* 67:231–243.
- Turkington, R., and J. L. Harper. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. *J. Ecol.* 67:245–254.
- Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185–202.
- Underwood, A. J., and E. J. Denley. 1983. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, N.J.
- Van der Plank, J. E. 1968. *Disease resistance in plants*. Academic Press, New York.
- Vandermeer, J. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *Am. Nat.* 116:441–448.
- Werner, E. E., and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* 58:869–876.
- Werner, P. A. 1977. Colonization success of a “biennial” plant species: experimental field studies of species cohabitation and replacement. *Ecology* 58:840–849.
- Wiens, J. A. 1977. On competition and variable environments. *Am. Sci.* 65:590–597.
- Wilbur, H. M. 1972. Competition, predation and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* 53:3–21.

- Williams, A. H. 1981. An analysis of competitive interactions in a patchy back-reef environment. *Ecology* 62:1107–1120.
- Wise, D. H. 1981*a*. Inter- and intraspecific effects of two orb-weaving spiders (Araneae: Araneidae). *Oecologia (Berl.)* 48:252–256.
- . 1981*b*. A removal experiment with darkling beetles: lack of evidence for interspecific competition. *Ecology* 62:727–738.
- Wit, C. T. de 1960. On competition. *Versl. Landbouwk. Onderz. (Agric. Res. Rep.)* no. 66, 8. Wageningen, Netherlands.
- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecol. Monogr.* 44:171–181.