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## FIELD EXPERIMENTS ON INTERSPECIFIC COMPETITION

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The study of interspecific competition has long been one of ecology's most fashionable pursuits. Stimulated in part by a simple theory (Lotka 1932; Volterra 1926; Gause 1934; Hutchinson 1959; MacArthur and Levins 1967), ecologists gathered numerous data on the apparent ways species competitively coexist or exclude one another (reviews in Schoener 1974*b*, 1983). As is typical in science, most of the early data were observational, and the few experimental studies were mostly performed in the laboratory rather than in the field.

Though never lacking its doubters, the belief in the natural importance of interspecific competition is now being severely questioned (review in Schoener 1982). Many of the putatively supportive observations have been challenged as being statistically indistinguishable from random contrivance. Most such attacks have been rebutted, but not without some modification of original conclusions (e.g., papers in Strong et al. 1983). New observations have been gathered for certain systems, suggesting a lack of competitively caused patterns and catalyzing the variable environment view of Wiens (1977) in which competition is seen as a temporally sporadic, often impotent, interaction. Other critics have charged that the lack of experimental field evidence for competition would preclude its acceptance regardless of the quality of observational data. Indeed, results of some of the earlier field experiments are in part responsible for competition's presently beleaguered state. Connell (1975), after reviewing the field experiments known to him through 1973, concluded that predation, rather than competition, appears to be the predominant ecological interaction and should be given "conceptual priority." Shortly afterward, Schroder and Rosenzweig (1975) showed experimentally that two species of desert rodents overlapping substantially in habitat did not appear to affect one another's abundances. This result was interpreted as contradicting a crucial assumption of competition theory, almost its linchpin: the greater the resource overlap between species, the greater the competition coefficient, a measure of the intensity of interspecific competition (relative to intraspecific competition; MacArthur and Levins 1967; review in Roughgarden 1979).

My purpose here is to synthesize the results from all field experiments so far done on interspecific competition and to ask what we have learned from them. For

the extreme skeptics, this is almost equivalent to asking what we know about interspecific competition in nature. For most, however, the question is more modest though still major, How do generalizations from field experiments compare with those from field observations, and to what extent are they in agreement, contradictory, or complementary? Specifically, I will address the issues raised above. How often do field experiments detect competition? What are the most important kinds of competition found? For which trophic types is competition most prevalent? Is there experimental evidence for temporal variability in the intensity of competition, such that often, if not most of the time, it is undetectable? To what extent do the experiments modify the domain of the simple theory, and when is the assumption that interspecific competition increases with ecological overlap appropriate, if at all? Finally, I will suggest some directions experimental field studies of competition might take in the future.

To try such an evaluation now might seem premature. After all, it has only been a few years since the experiments just referred to as "earlier" were performed. Indeed, in polling my ecological colleagues as to the number of field experiments on interspecific competition that they believed were now published, nearly all answers ranged from 10 to 50. In fact, such guesses are off by as much as an order of magnitude: The correct answer is over 150! Moreover, all such studies satisfied a rather strict set of criteria (see below). While certain competition experiments in plants are comparatively ancient (reviewed by Jackson 1981), about half those for animals were published in the past 5 yr. Indeed, when plotted, growth of all studies combined appears greater than exponential (*sensu* Watt 1968, pp. 9–10). By system, experiments are almost equally divided among terrestrial plants, terrestrial animals, and marine organisms, with freshwater organisms having about half as many as each of these.

#### WHAT IS A FIELD EXPERIMENT ON INTERSPECIFIC COMPETITION?

In defining the domain of this study two somewhat arbitrary decisions had to be made. First, under what circumstances does an experiment deal with competition, as opposed to some other interaction? Second, what is meant by "field"?

I consider an interspecific competition experiment to be a manipulation of the abundances of one or more hypothetically competing species. Such manipulations may be removals, introductions, or both. Removals most frequently take the form of physically transporting entire organisms from the study plot, but for plants also include "trenching," in which the roots of potentially competing trees are severed around a plot's boundaries. Introductions may consist of transporting certain individuals to areas inhabited by members of one or more other species, or clearing an area entirely, then introducing several species in various combinations. Manipulations of predators (or herbivores) alone are not considered competition experiments here. In cases in which predation (or herbivory) affects competing species differentially, such manipulations frequently result in changes at the prey level which can reveal much about how competition works (Paine 1966; Harper 1969). However, I have arbitrarily excluded these. I have also excluded experiments in which empty environments are created and their entirely natural

colonization followed. Again, successional events in such environments can reveal much about competition, but again, competitors are not manipulated directly. Finally, experiments obviously without proper controls are excluded, though here I have been rather liberal. I have included experiments in which treatments were performed at slightly different times or in slightly different places, provided such variation appeared unlikely to be related to the differences found.

When I began surveying the literature for this study, I had no idea that defining the "field" would be so difficult. However, seemingly unbroken continua exist between the laboratory and the field. For example, plant species can be grown together in small pots inside the greenhouse or grown there in large plots; the pots or plots can be taken outside but not placed in any kind of natural situation or can be moved into a natural habitat; or plants can be directly removed from or introduced into natural habitats. As a second example, experiments on freshwater organisms can be done in laboratory bottles, or the bottles can be taken outdoors and partly submerged in a lake; containers can be connected on one or more sides with the lake using mesh of various degrees of coarseness, and the container may be open at the top or not; or entirely unconfined introductions of organisms can be made into natural bodies of water.

Some headway can be made in determining where lines should be drawn if one asks why experiments are done at all. In an experiment, we dare nature to come up with some unknown factor that would foil our preconception about how things should work. If this were not so, we would never have to use real organisms and systems in our experiments, but we could simply test our models with a computer or scratch pad. In the laboratory, such natural twists are intrinsic to the organism itself, e.g., some unsuspected trait in behavior or physiology. Extrinsic factors are, optimistically at any rate, controlled. In the field, extrinsic, like intrinsic factors, are mostly uncontrolled, and these too can overturn our expectations. For example, the effect of competition might be greatly diminished by predators, by changes in the weather, by migration, and so forth. In short, we perform competition experiments in the field to find out if and how that process operates there in the presence of possibly overriding factors.

Consequently, I wish to define a field experiment as one in which some major natural factor extrinsic to the organisms of interest is uncontrolled. Greenhouses are thus ruled out, despite the fact that extraordinarily elegant experiments have been done therein (e.g., McClure 1980; Harper 1977). Fenced enclosures in natural habitats, on the other hand, are usually in, as are semipermeable containers in natural bodies of water, caged portions of the shoreline, and plots sown from scratch in natural (but not domestic) habitats. Of course, we shall take note of what the controls are, so that we can evaluate the importance of nature's major extrinsic factors.

The 164 studies surviving my definitional gauntlet, and of which I was aware through 1982, are given in table 1, the data base for all conclusions I will reach. Occasionally, several papers report one study, and sometimes several studies are reported in a single paper; designation of a "study" is somewhat arbitrary, but is based on differences in the pool of competitors, habitat, and/or experimental technique. Table 1 lists several characteristics of the species and systems, all of

which are straightforward: trophic type (determined from the papers cited or from other sources), habitat, and locale. In addition, certain characteristics of the experiments are given, not all of which are straightforward. First, the number of months the experiment ran is given; no special note is taken of additional manipulations after its beginning. Second, the number of species (or groups of species) that did and did not show an effect from the competition treatment is listed. Only species on the same trophic level as the manipulated species are considered as candidates for competition unless they clearly have the potential to compete for space. In particular, species affected indirectly are excluded. If a species showed an effect at one place but not another, or under some but not all treatments, this is denoted by an asterisk. Species showing competition in less than 10% of the treatments were counted as never showing competition and vice versa. All cases of temporal variability in the effect of competition are noted in the text; no asterisk is used for this case. When not explicitly mentioned, such temporal variability was sometimes surmised from the data given, though I may have misinterpreted here. Third, characteristics affected by competition, as well as those explicitly stated to be unaffected, are given. Fourth, the degree to which predators are excluded is assessed. For the most part, this consists primarily of giving information on enclosures; for many studies the degree of predator exclusion is simply impossible to determine. Fifth, the presence or absence of strong asymmetry in the reactions of species to competition is noted where appropriate. This situation automatically occurs when a study has species showing and not showing competition, but it may also occur among species that all show some competition. Sixth, an attempt is made to identify competitive mechanisms. Much uncertainty here is often expressed by investigators; rather than impose my own judgment, I have simply acted as interpreter, believing that the investigator should know his own system better than I. I used “??” for “most uncertain,” “?” for “fairly uncertain,” and no notation for “least uncertain;” rarely was an investigator without any uncertainty! Competitive mechanisms need not be shown in the particular experiment to be included. I am sure others would produce a somewhat different table.

#### EXISTENCE OF COMPETITION

An overwhelming fraction of experimental attempts to detect interspecific competition in the field did so: 148 of 164 studies, or 90%, demonstrate some competition. One-hundred ten of the 148 studies record changes in numbers through local births and deaths or migration. No statistically significant differences (by  $\chi^2$  tests) exist between systems: 91% of freshwater, 94% of marine, and 89% of terrestrial studies show some competition. In other ways, however, the studies performed are not a random sample. For example, nearly all were done in temperate regions, mostly on continents. Few studies are listed for folivorous insects, a group in which competition may be relatively infrequent (Lawton and Strong 1981). Moreover, in a few experiments densities are forced to levels somewhat higher than those occurring in nature (e.g., Werner and Hall's [1976, 1979] experiments with sunfish). Finally, some, perhaps many, investigators probably selected systems in

TABLE 1  
CHARACTERISTICS OF FIELD EXPERIMENTS ON INTERSPECIFIC COMPETITION

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
FRESHWATER							
Duckweed; lakes; CA, USA; McLay 1974	Pro	.2	1	Gro	Chem?	Encl	
Cattails; ponds; MI, USA; Grace & Wetzel 1981	Pro	5	1(1)	Dent(N), Hab	Over	NoEncl	Y
<i>Paramecium</i> ; seep; MI, USA; Gill & Hairston 1972	Omn	1.5	(1)	(Ext)		NoEncl	
Cladocerans (early season); ponds; MN, USA; Lynch 1978	Fil	1	1(1)	Ext, Siz	Cons(F)	Encl	Y-feeding efficiency?
Cladocerans (late season); ponds; MN, USA; Lynch 1978	Fil	1	2(1)	Dent(N), Rep	Cons(F)??	Encl	Y-feeding efficiency?
Cladocerans; ponds; WI, USA; Smith & Cooper 1982	Fil	.2-.3	2,1*	Dent(N)	Cons(F)	Encl	Y-niche overlap, larger sometimes superior
Snails; ponds; IN, USA; Brown 1982	Her, (Det)	2	1*(1)	Repr (Gro)	Cons(F)?, Chem?	Encl	Y
Sphaeriid clams; river; Ontario, Canada; Mackie et al. 1978	Fil	ca. 3?	2	Repr	Pre	Encl	
Corixids; rock pools; Finland; Pajunen 1982	Car	ca. 2?	2	Dent(W)	Cons(F), Enc (Agg, Avoi)	NoEncl	Y-larger superior
Insects; <i>Heliconia</i> bracts, wet forest; Costa Rica; Seifert & Seifert 1976	Her, (Det)	.1-.3	4*(2)	Dent(N)	Cons(F)?	NoEncl	Y
Insects; <i>Heliconia</i> bracts, wet forest; Venezuela; Seifert & Seifert 1979	Her, (Det)	.2-.3	2*(2)	Dent(N)	Cons	NoEncl	Y
Odonate nymphs; ponds; SC, USA; Benke 1978	Car	6	1(1)	Dent(N)	Enc(Pred)	Encl-fish removed	Y-larger superior
Mayflies; streams; WI, USA; Peckarsky & Dodson 1980	Her	.1	(1) <sup>8</sup>	(Imm)		"No" Encl—Preds. (when no preds., comp. occurs	

Mayflies; streams; CO, USA; Peckarsky & Dodson 1980	Her	.1	1 <sup>8</sup>	Imm	?	"No" Encl—Preds. (when no preds., comp. also occurs)	
Water boatmen; ponds; MI, USA; Is-tock 1973	Omn	2+	1(1)	Den(W)	Cons(F)?	Encl	Y-smaller superior
Sunfish; ponds; MI, USA; Werner & Hall 1976	Car	4	3	Gro, Hab, Foo	Cons (F), Enc(Agg)	NoEncl	Y
Sunfish; ponds; MI, USA; Werner & Hall 1977	Car	3	1(1)	Gro, (Sur)	Cons(F), Enc(Agg)?	NoEncl	Y (see above)
Sunfish; ponds; MI, USA; Werner & Hall 1979	Car	6	2(1)	Gro, Hab	Cons(F), Enc(Agg)?	NoEncl	Y-feeding efficiency
Trout; streams; MI, USA; Fausch & White 1981	Car	.1+	1	Hab	Ter	NoEncl	Y-even when sizes similar
Salamanders; temporary ponds; MI, USA; Wilbur 1972	Car	12	3	Dev, Sur, Siz	Cons(F)	Encl (birds & inverte- brate preds. excl.)	N
Tadpoles ( <i>Rana</i> ); ponds; MI, USA; DeBenedictis 1974	Omn, (Det)	24	2*	Sur, Den(W)	?	Encl (pred. reduced comp.)	N
Fish-ducks*; lakes; Sweden; Eriksson 1979	Car	36-60	1	Den(N)	Cons(F)	NoEncl	
MARINE							
Algae; intertidal; WA, USA; Dayton 1975	Pro	24-36	3*, 1	Den(N)	Over	NoEncl	Y*
Algae; shallow subtidal; AK, USA; Duggins 1980	Pro	24	1	Imm	Over (L,A)	Excl. urchins (stimulates otters)	Y*-shape & longevity
Algae; intertidal; New England, USA; Lubchenco 1980	Pro	36	2	Gro, Den(W)	Pre? Chem??	NoEncl (herbivores have only slight effect)	Y*
Algae; intertidal (early successional); CA, USA; Sousa 1979	Pro	4	1	Imm	Pre	NoEncl (affected by herbivores)	A succession

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Algae; intertidal (mid-successional); CA, USA; Sousa 1979 .....	Pro	4-6	3,3*	Imm, Gro	Pre	NoEncl	A succession
Algae*-mussels-barnacles*; low intertidal; New England; USA; Lubchenco & Menge 1978 .....	Pro, Fil	ca. 24	2	Den(N) Den(W)	Pre, Over	Encl (excl. preds., but like exposed places: pred. prevents comp.)	Y-growth form, larger mussels over barnacles
Sessile marine invertebrates*- <i>Botryllus</i> ascidians, epibenthos; ponds; MA, USA; Grosberg 1981 .....	Fil	.4	9(10)	Rec	Pre, Over	NoEncl	
Sea anemone-algae*, barnacles* polychaete*; intertidal; CA, USA; Taylor & Litterer 1982 .....	Pro, Fil	26	3(2), 2 = Fil	Den(N)	Pre, Over	Encl	Y-physiological traits
Barnacles*-mussels; exposed intertidal; NJ, USA; Peterson 1979 .....	Fil	ca. 5	1	Den(N)	Over, Pre	NoEncl (pred. important at protected site)	Y*-growth form, larger superior
Barnacles*-mussels; mid-intertidal; New England, USA; Menge 1976 ...	Fil	6-24	1*	Den(N)	Over	Encl (no pred. in exposed places; in protected, pred. prevents comp.)	Y*-growth form, larger superior
Barnacles; intertidal; Scotland; Connell 1961 .....	Fil	12	1	Den(N), Sur, Siz, Hab	Over	NoEncl (& Encl—when preds. excl., severity increased somewhat)	Y*-growth form
Anenones*-barnacles*, intertidal; San Juan Is., WA, USA; Dayton 1971 ..	Car, Fil	3-42	1(1 = barn)	Imm, Fis	Pre	NoEncl	Y
Anenones*-barnacles*-mussels-algae*; intertidal; ShiShi, WA, USA; Dayton 1971 .....	Car, Fil, Pro	36-48	2(1 = anem)	Imm	Pre	NoEncl (eventually, preds. ate barnacles)	Y



Gastropods; intertidal; <i>Cellana</i> experiments; S.E. Australia; Underwood 1978 .....	Her	3.8	2*(1)	Siz, Sur	Cons(F)	Encl (no important preds.)	Y-feeding rate, size, efficiency of energy extraction
Gastropods; intertidal; non- <i>Cellana</i> experiments; S.E. Australia; Underwood 1978 .....	Her	7.2	1(1)	Siz, Sur	Cons(F)	Encl (no important preds.)	Y-feeding rate, size, efficiency of energy extraction
Limpets; intertidal; CA, USA; Stimson 1970 .....	Her	.5-8	1	Imm	Ter	NoEncl	Y-larger superior
Limpets; intertidal; Rottneß Is., Australia; Black 1979 .....	Her	18-24	1(1 <sup>0</sup> )	Imm	Cons(F)	NoEncl	Y-feeding efficiency
Limpets; intertidal; CA, USA; Haven 1973 .....	Her	6-18	1,1*	Gro	Cons(F)	Encl	Y
Bryozoans*-tunicates*-other fouling organisms*; subtidal; NC, USA; Sutherland 1978 .....	Fil	ca. 36-48	4* (1 <sup>+</sup> )	Imm	Pre	NoEncl	Y
Starfish; intertidal; WA, USA; Menge 1972; Menge & Menge 1974 .....	Car	ca. 24	1	Siz, Act T	Cons(F), Enc(Agg)	NoEncl	Y*-larger
Hermit crabs; intertidal; Panama; Bertness 1981 .....	Det	.1	1(1)	Hab	Enc (Avoi)	NoEncl	Y-larger superior
Bivalves; subtidal; CA, USA; Peterson 1982 .....	Fil	24	(2*)	Repr, Rec (Gro)	Cons(F)	Encl	
Mud snails; estuaries; CA, USA; Race 1982 .....	Dep	2.5	1	Hab, Den(N)	Enc (Avoi, Pre)	Encl	Y*
Limpets; intertidal; N.S.W., Australia; Creese & Underwood 1982 .....	Her	3,6	2*, (1)	Sur, Gro, Siz	Cons(F)	Encl	Y-feeding method
Sea pansy*, sand dollar; subtidal; CA, USA; Kastendiek 1982 .....	Fil	.5	1	Den(N)	Pre, Enc(Agg)	NoEncl	Y*
Sea urchins; sublittoral; AK, USA; Duggins 1981 .....	Her	6-11	(2)	(Den, Con)		NoEncl	
Polychaetes; soft-bottom; WA, USA; Woodin 1974 .....	Dep	4-6,9	1	Imm, Den(N)	Pre	Encl	Y-niche overlap
Bivalves; soft-bottom; CA, USA; Peterson & Andre 1980 .....	Fil	2-3	1*(1)	Gro	Enc (Act L?), Cons(F)?	Encl	

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Fishes; coral reefs; Gr. Barrier Reef; Low 1971	Her	ca. .1	3	Imm	Ter	NoEncl	
Fishes; reefs; Panama; Robertson et al. 1976	Her	ca. .05	5	Imm, Act L	Ter	NoEncl	Y*
Fishes; reef; CA, USA; Hixon 1980a	Car	ca. 3	1(1)	Imm, Hab	Enc (Agg, Avoi)	NoEncl	Y-sizes similar
Pomacentrid fishes; reefs; Heron Is., Australia; Sale 1974	Her	13	1	Imm	Ter	NoEncl	N
Rockfish; reefs; CA, USA; Larson 1980	Car	30	2	Den(N), Hab	Ter? Pre?	NoEncl	Y-sizes similar
Damselfish; reefs; Jamaica; Williams 1978	Her	ca. 10 <sup>-3</sup>	1	Imm	Ter	NoEncl	
Sea urchins; reefs; Jamaica; Williams 1981	Her	.5	2	Den(N)	Cons(F)	NoEncl (encl. show little effect of preds., but affected by competing damselfish)	Slight
Urchins*-damselfish; reefs; Jamaica; Williams 1981	Her	.4	2	Den(N)	Ter	NoEncl (see previous entry)	Y*
<b>TERRESTRIAL PLANTS</b>							
Grasses*-mesquite; mid-elevation grassland; AZ, USA; Kincaid et al. 1959	Pro	156	1	Den(N, W)	?	NoEncl	
Herbaceous dicots-grasses; fields; MI, USA; Werner 1977	Pro	48	1(1)	Den(P)	Cons (W, N)	NoEncl	Y-niche overlap
Herbaceous vegetation*-aspen; upper elevation woodland; UT, USA; Ellison & Houston 1958	Pro	36	4	Den(W)	Cons(W)?	NoEncl (livestock excl.)	
Herbaceous perennials; meadow, mt.; CO, USA; Waser 1978	Pro	24	2	Repr	Enc, Cons <sup>9</sup>	NoEncl	Y
Teasel*-plant litter; fields; MI, USA; Werner 1975	Pro	14	1	Ger	Chem	NoEncl	
Clover*-other vegetation; pasture; UK; Turkington et al. 1979	Pro	12	1	Ger, Sur, Siz	?	No Encl (light grazing)	
Various plants; field; NC, USA; Fowler 1981	Pro	ca. 24	12*(3)	Den	Pre	NoEncl (mowed)	Y

<i>Verbascum</i> *-other vegetation; field; MI, USA; Gross 1980	Pro	ca. 24	1	Ger, Sur(J)	Cons(W) Over, Pre?	NoEncl	
Biennial plants; old fields; MI, USA; Gross & Werner 1982	Pro	36	4	Ger, Est, Gro(J) (Gro(A))	?	NoEncl	
Plants; old field; OH, USA; Hills & Vankat 1982	Pro	4.5	(3g)	(Den(W))		NoEncl	
Annuals* <i>Artemisia</i> ; desert; Israel; Friedman et al. 1977	Pro	9	lg	Den(N,W)	Chem, Cons(W)	NoEncl?	
<i>Ambrosia</i> *-winter annuals; early suc- cessional field; IL, USA; Raynal & Bazzaz 1975	Pro	36	1	Den(W), Repr, Siz	Over, Cons(N), Chem	NoEncl	
<i>Medicago</i> *-vegetation; desert; Israel; Friedman & Orshan 1974	Pro	3.7	1*	Repr	Cons(W) ??, Chem??	Encl? ("animals" excluded)	
Forbs*-grasses; old field; SC, USA; Pinder 1975	Pro	2	lg	Siz	Cons(W)?	NoEncl	
Plants; old field; MI, USA; Kroh & Stephenson 1980	Pro	<4?	4*	Den(W)	?	NoEncl	
Plants; old field; NJ, USA; Allen & Forman 1976	Pro	2	6*(3)	Den	Over?, Cons?	NoEncl	Y-larger superior, growth form
Grasses; grassland; WA, USA; Harris 1967	Pro	6	1	Con, Siz, Sur (J)	Cons(W)	NoEncl, semi-domestic	Y-growth rate
Sorrels; grassland; UK; Putwain & Harper 1970	Pro	ca. 12	1*	Den(N), Ger	?	NoEncl (grazed by sheep)	
Sorrels; grassland; UK; Putwain & Harper 1970	Pro	ca. 12	1*	Den(N), Ger	?	Encl (sheep excl.)	
Grasses*-sagebrush; mid-elevation sagebrush; AZ, USA; Robertson 1947	Pro	36	lg	Repr, Den(P), Siz, Con, (Ger)	Cons(W)?	NoEncl (livestock excl.)	
Grasses*; sagebrush; NV, USA; Robertson & Pearse 1945	Pro	36	lg	Den(W), Siz	Cons(W)	NoEncl (livestock excl., rabbits present)	Y-species differ in response

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Grasses; prairie; NE, USA; Clements et al. 1929 .....	Pro	24-36	11(2)	Gro, Repr. Siz	Cons(W,N), Over?	NoEncl	Y-root depth
<i>Plantago</i> * & grasses; fields; UK; Sagar & Harper 1961 .....	Pro	ca. 12	2,1*	Ger, Den(N)	?	NoEncl (site with most grazing shows least comp.)	N
Aster*-broomsedge; fields; NC, USA; Keever 1950 .....	Pro	3	1	Sur, Siz	Cons(W)	NoEncl	
Various plants; heath; UK; Miles 1972 .....	Pro	ca. 6	11*(7)	Ger, Sur, Est	?	NoEncl (rabbits ate 1 sp.)	
Annual plants; desert; AZ, USA; Inouye 1980 .....	Pro	1.5	1g <sup>8</sup>	Ger	Pre	Part Encl	
Annual plants; desert; AZ, USA; Inouye et al. 1980 .....	Pro	ca. 2	3 <sup>8</sup>	Gro, Den(W), Repr	Cons(W), Over?	Part Encl (pred. affects den. and repr.; comp. still exists)	
Annual plants*- <i>Ambrosia</i> ; fields; IL, USA; Abul-Fatih & Bazzaz 1979 .....	Pro	3.5	1g	Den(W,N)	Over(L)	NoEncl	Y*-growth rate
Shrubs; desert; CA, USA; Fonteyn & Mahall 1978, 1981 .....	Pro	11	2	Con	Cons(W)? Chem?	NoEncl	N
Shrubs; desert; Israel; Friedman 1971	Pro	24	1	Est, Gro, (Sur(A))	Cons(W)	NoEncl	
<i>Plants-Rhus</i> * shrubs; forest-prairie; OK, USA; Petranka & McPherson 1979 .....	Pro	ca. 12	1g	Ger, Est	Chem, Over	NoEncl	Y*-larger superior, toxins
Secondary plants ( <i>Callunetum</i> ); UK; Miles 1974 .....	Pro	11	2,5* (1)	Est, Sur	Over?	NoEncl	
Understory plants; pinewoods; UK; Watt & Fraser 1933 .....	Pro	24	2	Den(W)	Cons(N)?	"No" Encl (encl. after 18 mo.)	
Understory plants; white-pine forest; NH, USA; Toumey & Kienholz 1931	Pro	96	1g	Den, Ext, Siz	Cons(W)	NoEncl	

Trees; 2 forest types; Germany; Fricke 1904; in Toumey & Kienholz 1931 ..	Pro		2	Ger, Sur, Gro	Cons(W)	Prob NoEncl
Understory plants; Scotch-pine forest; Sweden; Hesselman 1929 in Toumey & Kienholz 1931 ..	Pro	24	(1)			Prob NoEncl
Trees; spruce forest; Germany; Fabricius 1929 in Toumey & Kienholz 1931 ..	Pro	24	1	Den(N), Siz	Cons(W)	Prob NoEncl
Understory plants; red spruce; NH, USA; Baldwin 1930 in Toumey & Kienholz 1931 ..	Pro	60	1	Den, Ext	Cons(W)	Prob NoEncl
Understory plants; 7 forest types; NC, USA; Korstian & Colle 1938 ..	Pro	36-48	7g	Den(N,W), Ext, Est, Gro	Cons(W)	NoEncl
Understory plants; white-pine forest; NH, USA; Craib 1929 ..	Pro	36 +	1	Den, Ext	Cons(W)	NoEncl
Jack pine; forest; MI, USA; Brown 1967 ..	Pro	24	1*	Ger	Chem	NoEncl (some herbivore damage)
Trees; rainforest; Queensland, Australia; Cannon et al. 1961 ..	Pro	1.2	(1)	(Ger)		NoEncl
Alder; woodland; UK; McVean 1956	Pro	ca. 12	1*	(Siz not affected by root competition; light important)	Over	NoEncl
Loblolly pine; mixed forest; LA, USA; Chapman 1945 ..	Pro	36	1	Est, Sur, Siz	Over	NoEncl
Conifers*-aspen; aspen forest; MN, USA; Shirley 1945 ..	Pro	48	4	Ger, Sur, Siz, Den(W), Con	Cons (W,N), Over	Encl
Conifers*-jackpine; forest; MN, USA; Shirley 1945 ..	Pro	48	4 <sup>8</sup>	Siz, Den(W), Sur, Con	?	Encl
Spruce, spruce forest; BC, Canada; Barr 1930 ..	Pro	3.5	1*	Ger	Cons(W)	Encl
Trees; tropical forest; S. Africa; Phillips 1928 ..	Pro	≤6	3	Est, (Ger)	Cons(W)	Encl

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Pine* & birch; forest; NH, USA; Toumey 1929 in Toumey & Kienholz 1933 .....	Pro	48	1g	Siz	Cons(W)	Prob NoEncl	
Fungus*-rodents; desert; AZ, USA; Inouye 1981 .....	Her(G)	84 <sup>10</sup>	1	Den(N)	Cons(F)	Partial Encl	
TERRESTRIAL ANIMALS							
Spiders; forest; MD, USA; Wise 1981a	Car	4	(2)	(Sur, Repr, Hab)		NoEncl	
Sheet-web spiders; bog & lake shore; Germany; Schaefer 1978 .....	Car		(1)	(Den(N))		NoEncl	
Lycosid spiders; salt marsh; Germany; Schaefer 1975 .....	Car	ca. 4	(2)	(Den(N))		NoEncl	
Orb-weaving spiders; salt marsh; CA, USA; Spiller, in prep. ....	Car	6	2	Gro, Sur, Repr, Fee, Hab	Cons (F), Enc (Agg Pred)	NoEncl	Y-larger can be superior
Orb-weaving spiders; old fields; MD, USA; Horton & Wise, in press .....	Car	24	(2)	(Gro, Sur, Hab, Fee, For)		NoEncl	
Darkling beetles; dry woodland, 2,250 m; NM, USA; Wise 1981b .....	Omn	36	(4)	(Den(N)), (Siz)		Encl	
Stenodemine bugs; sward; UK; Gibson & Visser 1982 .....	Her	.6	1*	Sur, Dev	Cons(F)	"No" Encl (crawling insects excl.)	
Hispine beetles; <i>Heliconia</i> ; Costa Rica; Strong 1982a, 1982b .....	Her	.03-.06	(3)	(Imm, Foo)		NoEncl	
Ants; mangrove islands; FL, USA; Cole, in press .....	Det, Car	6.7	4	Ext	Ter (Agg, Avoi)	NoEncl	Y
Ants; steppe; Siberia; Stebaev & Reznikova 1972 .....	Det, Car		1	Act T	Ter	NoEncl	

Ants; meadows; MA; USA; Adams & Trianello 1981	Det	<.004	1	Imm	Chem	NoEncl	Y
Ants, <i>Lasius</i> * & <i>Myrmica</i> ; fields; UK; Pontin 1969	Car	24	1	Den(P-alate queens)	Cons(F), Enc(F)	NoEncl	
Ants, <i>Lasius</i> only; fields; UK; Pontin 1969	Car	36	2	Den(P-alate queens)	Cons(F), Ter	NoEncl	
Ants; fields; UK; Pontin 1960	Car	36	1	Den(P-alate queens)	Cons(F), Ter	NoEncl	
Ants-rodents; desert; AZ, USA; Brown et al. 1979	Her(G)	48	2g	Den(N,W)	Cons(F)	Part Encl (rodent excl. fenced)	Y-larger superior
Bees; meadow; CO, USA; Inouye 1978	Her(N)	ca. .03	2	Imm	Cons(F)	NoEncl	N
Hummingbirds-bees*; meadow; CA, USA; Carpenter 1979	Her(N)	ca. 1	1	Imm	Cons(F), Enc(Agg)	Part Encl	
Bees; coast; ME, USA; Morse 1977	Her(N)	<10 <sup>-4</sup>	1	Hab	Enc (Avoi)	Encl	Y*-larger superior
Bees; forest-savanna; French Guiana; Roubik 1978	Her(N)	ca. 1	1* g	Den(N), Act P (Repr, Con, For)	Enc (Avoi)	NoEncl	Y*-larger foragers and colonies superior
Syrphid flies*-bumblebees; pasture rose; ME, USA; Morse 1981	Her(N)	<10 <sup>-3</sup>	1g	Den(N)	Enc(Agg)	Encl (1 experiment)	Y*-larger superior
Carrion flies; riparian woodland; CA, USA; Denno & Cothran 1976	Det	<1	1	Den(N)	Cons	Encl (excludes vertebrates)	
Frogs; rainforest; Borneo; Inger & Greenberg 1966	Car	8-11	3	Den(N), Imm	?	NoEncl	Slight
Salamanders; woodland & talus; VA, USA; Jaeger 1971, 1972, 1974; Wrobel et al. 1980	Car	3	1(1)	Sur	Ter (Shel)? Cons(F)?	Encl (birds not excl.)	Y-smaller superior
Salamanders; forest; NC, USA; Hairston 1980a, 1981	Car	60	2(4)	Den(N), Sur(J)	Pre(N)?	NoEncl	Y-larger superior
Lizards; desert; TX, USA; Dunham 1980	Car	48	2	Den(N), Gro, Con, For, Sur (J.A)	Cons(F)	NoEncl	Y-larger superior

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Lizards; woodland; AZ, USA; Tinkle 1982 .....	Car	24	(1)	(Hab, Den(N), Sur Siz)		NoEncl	
Lizards; pine-oak woodland; AZ, USA; Smith 1981 .....	Car	24-36	2	(Den(N)) (Sur(A)) Gro, Sur(J)	Cons(F)	NoEncl	Slight
Lizards; islands; Lesser Antilles; Pacala & Roughgarden 1982, 1983 ..	Car	4	1(1)	Gro, Hab, Repr, Foo, For	Cons(F) Enc(Agg)	"No" Encl (most preds. not excl.)	Y-niche overlap
Lizards; islands; Bahamas; Schoener & Schoener, in prep. ....	Car	48-60	2	Den(N), (Ext)	Cons(F), Enc(Agg)	NoEncl	Y-varies with site
Titmice; forest; Belgium; Dhont & Eyckerman 1980 .....	Omn	24	1	Den(N)	Ter (Shel), Cons(F)?	NoEncl	Y*-larger superior
Titmice; woodland; UK; Minot 1981 ..	Car	ca. .5	1	Con	Cons	NoEncl	
Jackdaws & magpies*; grassland & trees; Sweden; Hogstedt 1980 .....	Omn	24	1	Repr	Cons(F)	NoEncl	
Sparrows; old fields; CA, USA; Davis 1973 .....	Her(G)	3	1	Imm	Enc(Agg)	NoEncl	Y*-larger superior
Sparrows; suburbia; CA, USA; Mewaldt 1964 .....	Her(G)	24	4 <sup>8</sup>	Imm		NoEncl	
Birds spruce-fir forest; ME, USA; Stewart & Aldrich 1951 .....	Car	.8	1g <sup>8</sup>	Imm	Ter	NoEncl	
Bark-foraging birds; woodland; IL, USA; Williams and Batzli 1979 .....	Her(G), Her(G), Omn(G)	ca. 12	2,1*	Imm, Hab	Ter(Agg)	NoEncl	Y*-larger superior
Moose-hare; forest; Isle Royale, MI, USA; Belovsky, in press .....	Her	ca. 27.5 <sup>10</sup>	2	Hab, Den(N), Equi	Cons(F)	Partial Encl	Y-larger superior; has more exclusive resource



Chipmunks; pine & sagebrush; CA, USA; Chappell 1978 .....	Her(G, F)	3	I,1*	Imm	Enc(Agg)	NoEncl	Y-larger superior
Rodents; secondary growth; S.E. TX, USA; Joule and Jameson 1972 .....	Her, Her, Omn	3-7	I(2)	Siz, (Den(N))	?	NoEncl (only roads)	Y-smaller superior
Rodents; grassland & woods; Sas- katchewan, Canada; Morris and Grant 1972 .....	Her	24	1	Hab	Ter(Agg, Encl, Avoi)		
Rodents; grassland & woods; Quebec, Canada; Grant 1969 .....	Omn, Her	4-2	I(1)	Den(N), Hab	Ter(Agg, Avoi)	Encl	Y-larger superior
Rodents; grassland & woods; Quebec, Canada; Grant 1971 .....	Omn	24	1	Den(N), Hab	Ter(Agg, Avoi)	Encl	Y*-larger superior
Mice; fields; CA, USA; DeLong 1966	Omn	5-6	1	Sur(J)(Gro, Repr, Sur(A))	Enc (Pred, Agg)	NoEncl	
Voles; grassland; MT, USA; Koplin & Hoffman 1968 .....	Her	12	1	Imm	Enc (Agg)?	NoEncl	
Cricetine rodents; pine-oak-grass; AZ, USA; Holbrook 1979 .....	Omn	ca. 6	2(1)	Hab, Act L	?	NoEncl	Y-smaller superior (1 pair)
Mice; grassland & woods; Sweden; Hoffmeyer 1973 .....	Omn	.1	I <sup>11</sup>	Hab*	Enc (Avoi)	Encl	Y*-larger superior
Heteromyid rodents; desert-grassland; AZ, USA; Price 1978 .....	Her(G)	.5-1	4	Hab	?	Encl	N
Kangaroo rats; desert; NM, USA; Schroder & Rosenzweig 1975 .....	Her(G)	7-8	(2)	(Imm)		NoEncl	
Rodents; prairie, CO, USA; Abramsky et al. 1979 .....	Omn	ca. 6	1	Imm	?	NoEncl	Y*-habitat overlap?
Mice; grassland & forest; British Col- umbia, Canada; Sheppe 1967 .....	Omn	ca. 1	1	Imm	Enc (Agg)?	NoEncl (semi-domestic)	
Rodents; grassland; British Columbia, Canada; Redfield et al. 1977 .....	Omn	36	1	Sur-Emi, Rec	?	NoEncl	
Rodents; mixed woodland; UK; Mont- gomery 1981 .....	Omn	7	2	Repr T, Hab, Den(N), Siz	Const(F)?	NoEncl	Y-smaller superior

(Continued)

TABLE 1 (Continued)

Group <sup>1</sup> ; Habitat; Locality; Source	Trophic Type <sup>2</sup>	Duration (mo)	Species or Groups Affected <sup>3</sup>	Effects <sup>4</sup>	Mechanism <sup>5</sup>	Enclosures, Predators <sup>6</sup>	Asymmetry <sup>7</sup>
Small rodents*—large rodents—ants; desert; AZ, USA; Munger & Brown 1981 .....	Her(G) Omn	33	I(1) (1 = Omn)	Den(N)	Cons	Partial Encl	Y-niche overlap
Rodents; coastal prairie; TX, USA; Kincaid & Cameron 1982; Cameron 1977; Cameron & Kincaid 1982 ....	Omn, Her	36	I(1)	(Den(N), Foo), Hab	Enc (Avoi)	NoEncl	Y*-larger superior
Gerbilline rodents; coastal dunes; Israel; Abramsky & Sellah 1982 .....	Her(G)	13	(1)	(Den(N))	Cons(F)	NoEncl	
Rodents; forest; Poland; Gliwicz 1981	Omn	6	1	Den(N), Sur(J), Sur(A) or Emi, Repr		NoEncl	

<sup>1</sup> \* = Experimental subject.

<sup>2</sup> Trophic types of treated species or groups only; if treated species or groups are not all of same trophic type, types correspond to order in column 1. Pro = producer, Car = carnivore, Her = herbivore (G = granivore, N = nectivore [and pollen], F = frugivore), Fil = filter feeder, Omn = omnivore, Det = detritivore or scavenger, Dep = deposit feeder.

<sup>3</sup> Number of species or groups (g) showing competition is unenclosed; number of species or groups not showing competition is enclosed by parentheses. \* = for all major effects, showing competition in certain sites or with certain treatments but not all, (\*) denotes showing competition in <10% of treatments, o = inferred from observations only.

<sup>4</sup> If effect is in parentheses, it was tested but did not occur. If not in parentheses, it occurred in at least one species. Den = density (N = number of inds., W = weight, P = production), Sur = survival (J = juvenile, A = adult), Gro = individual growth, Siz = individual size, Fis = fission rate, Ger = germination, Est = establishment, Dev = developmental rate, Con = condition or weight, For = foraging success, Rec = recruitment rate, Hab = habitat shift, Imm = immigration rate, Emi = emigration rate, Act T = activity time, Act L = activity level, Repr = reproduction products, Repr T = reproductive time, Ext = extinction, Equi = new species equilibrium other than extinction. Foo = food type or size.

<sup>5</sup> Cons = consumptive (F = for food, W = for water, N = for nutrients), Pre = preemptive (Shel = for shelter sites, otherwise for space per se), Over = overgrowth (light almost always involved for plants), Chem = chemical, Ter = territorial (Agg = aggression, Avoi = avoidance, Shel = for shelter, N = for nest sites), Enc = encounter (Agg = aggression, Avoi = avoidance, Pred = predation).

<sup>6</sup> Encl = enclosure, NoEncl = no enclosure, preds. = predators, pred. = predation, comp. = competition, excl. = excluded.

<sup>7</sup> Y = substantial asymmetry among test species or groups, N = no substantial asymmetry among test species or groups, Y\* = not tested experimentally in the field, but one or more subjects concluded to belong to asymmetrical species or group from field-observational or laboratory-experimental evidence.

<sup>8</sup> Some intraspecific competition included.

<sup>9</sup> Competition involves pollinators: heterospecific pollen reduces seed set and pollinator time is in short supply.

<sup>10</sup> Only censused at end of period.

<sup>11</sup> Not entirely in the field.

<sup>12</sup> Only 1st-order interactions given.

which they expected to find competition, though devil's advocacy in this area has recently become fashionable. Therefore, these numbers cannot tell us what fraction of all interactions in all systems involve competition; insect foliovores for example comprise 25% of the earth's known species (D. Strong, personal communication). Yet considering the recent skepticism concerning competition's existence in nature, 90 is a very high percentage indeed!

Not all of the 148 positive studies show competition among all species, or at all places, or during all times. Of the 390 species (or groups) subjected to possible competition, 76% showed competition at least sometimes (asterisked species in table 1 included here), and 57% showed competition under all circumstances tested (asterisked species excluded). Again, systems are strikingly alike in frequency of competition: 71% of freshwater, 71% of marine, and 79% of terrestrial species at least sometimes showed competition; the figures for species always showing competition are 52%, 56%, and 59%, respectively. None of these systems is significantly different from any other in  $\chi^2$  tests.

Figures for species are perhaps less interesting than those for studies, since the former are sometimes confounded by deliberate artifacts in study design. For example, investigators deliberately test species in some of which they expect to find competition and in others of which they do not (e.g., Pacala and Roughgarden 1982, 1983; Munger and Brown 1981); competition theory does not predict that all possible combinations of species should show substantial competition! On the other hand, there exists a pattern in this interspecific variation that accords well with certain biologically sensible hypotheses, as I shall discuss below.

#### MECHANISMS OF COMPETITION

Traditionally, competition is divided into two classes of mechanisms. In *exploitative* competition, individuals, by using resources, deprive others of benefits to be gained from those resources. *Interference* competition (*sensu* Park 1962) is more direct: Individuals harm one another by fighting, producing toxins, and so on. Though the two kinds of competition can be defined precisely in mathematical models (Schoener 1973, 1974a, 1976, 1978), some confusion afflicts their everyday usage, especially as regards competition for space. Space, like any resource, can be used to deprive others of its benefits, yet most cases of space competition involve active interference behavior.

To avert ambiguity, I will use here a taxonomy that distinguishes six kinds of competition. Some of my terms are already in the literature; others are new and describe the actual mechanisms (according to the dictionary, at least) more exactly than "exploitative" or "interference."

1. *Consumptive* competition occurs when some quantity of resource (e.g., food, water, a nutrient) is consumed by an individual, thereby depriving other individuals of it.

2. *Preemptive* competition occurs when a unit of space is passively occupied by an individual, thereby causing other individuals not to occupy that space before the occupant disappears; it occurs primarily in sessile organisms.

3. *Overgrowth* competition occurs when another individual or individuals grow over or upon a given individual, thereby depriving that individual of light (as in plants) or access to water-borne food (as in sessile, filter-feeding animals), and possibly harming that individual by some consequence of physical contact (e.g., abrasion, undercutting).

4. *Chemical* competition occurs when an individual produces some chemical (toxin) which diffuses into the medium or substrate and harms other individuals.

5. *Territorial* competition occurs when an individual aggressively defends, or by its behavior signals its intention to defend, a unit of space against other individuals; it occurs primarily in mobile organisms.

6. *Encounter* competition occurs as a result of an interaction between mobile, nonspatially attached individuals, in which some harm comes to one or more; such harm can include time or energy losses, theft of food, injury, or death by predation, fighting, or mere accident.

In all cases, the deprivation or harm, by the definition of competition, decreases the victims' population size by decreasing their survival or reproduction or both. In actuality, such decreases are sometimes inferred from other injurious effects, as summarized below.

Of these terms, type 1 clearly lies within the old category of "exploitation," whereas types 4 and 6 are clearly "interference." The others, which cover various kinds of competition for space, are more ambiguous. Types 3 and 5 are usually considered interference. Type 2 is closer to exploitation; it is like 1 except that, unlike most food items, units of space can be reused once relinquished. Inasmuch as 2 involves avoidance, however, it includes an aspect of interference.

Table 2 gives the distribution of the six competitive mechanisms among systems and taxa. Notice that consumptive competition, the purest form of exploitation, is the commonest among all but marine organisms, in which preemptive competition is the most common. In marine systems, overgrowth, territorial, and consumptive competition are each somewhat less common and about equally frequent. Territorial competition prevails among fishes, whereas overgrowth and preemptive mechanisms occur mainly among sessile organisms. Consumptive competition occurs mainly among top carnivores, such as starfish, and among herbivores, especially gastropods. In freshwater systems, consumptive competition is by far the most common; the only other common type is encounter competition; this takes the form of aggression, avoidance, and even predation. Among terrestrial plants, consumptive competition is very common; it is apparently mainly for water, implicated, among other ways, in the trenching experiments mentioned above. While also quite conceivable, competition for nutrients is mentioned in only 5 of the 28 studies in which consumptive competition is proposed as a mechanism. In many terrestrial plant studies, however, the mechanisms are apparently so uncertain that they are not speculated upon at all, and very possibly often several exist simultaneously in particular cases. Among terrestrial animals, consumptive competition is most common, and two interference mechanisms, territorial and encounter competition, are also very common. The latter takes the form of aggression or avoidance and is sometimes difficult to distinguish from the former.

TABLE 2

MECHANISMS OF INTERSPECIFIC COMPETITION PROPOSED FOR SUBJECTS OF FIELD EXPERIMENTS (table 1)\*

GROUP	MECHANISM						Totally Unknown
	Consumptive	Pre-emptive	Over-growth	Chemical	Territorial	Encounter	
Freshwater							
Plants ...	0	0	1	1	0	0	0
Animals ..	13	1	0	1	1	5	2
Marine							
Plants ...	0	6	4	1	0	0	0
Animals ..	9	10	6	0	7	6	0
Terrestrial							
Plants ...	28	3	11	7	0	1	9
Animals†	21	1	0	1	11	15	6
Total ..	71	21	22	11	19	27	17

\* If several mechanisms are proposed for a particular situation, all are counted.

† Includes an herbivorous fungus.

Even considering the uncertainty surrounding the determination of competitive mechanisms, classical exploitative competition is considered likely in many studies: 28 cases in plants and 43 in animals are consumptive. There is a strong showing for consumptive competition despite the fact that all other kinds of competition save chemical are frequently directly observable; consumptive competition is not. Moreover, it is often argued that certain interference mechanisms, especially territoriality (review in Hixon 1980*b*), are adaptations to secure food. Classical interference competition (excluding preemptive) is, in total, detected about as often: 25 cases in plants and 34 cases in animals. In 15 cases in plants and 36 in animals, only interference mechanisms are proposed; the same figures for consumptive competition are 18 and 27. In a substantial number of studies (10 in plants and 16 in animals), both consumptive and interference mechanisms are proposed. These last points are theoretically important, and we shall return to them below.

#### TEMPORAL VARIABILITY IN COMPETITION

Wiens's (1977) currently prominent hypothesis concerning competition holds that it acts rarely in certain systems, during so-called resource "crunch" years. Observations with which Wiens supports his hypothesis come mainly from the North American shrub-steppe, an arid, continental vegetation (e.g., Rotenberry 1980; Rotenberry and Wiens 1981; Wiens and Rotenberry 1980).

What is presently known from field experiments concerning temporal variability in competition intensity? Rarely in the studies of table 1 does an investigator mention such variability one way or the other. When it is mentioned, or when ascertainable from the data, year-to-year variability in the effect of competition not obviously caused by the experimenter occurs in 11 cases (Robertson 1947; Robertson and Pearse 1945; Friedman 1971; Chapman 1945; Mewaldt 1964;

Sutherland 1978; Clements et al. 1929; Dunham 1980; Smith 1981; Morris and Grant 1972; Eriksson 1979) and possibly three others (DeBenedictis 1974; Dayton 1971; Pontin 1969), whereas it fails to occur in 12 cases (Werner 1977; Pontin 1960; Brown et al. 1979; Dhondt and Eyckerman 1980; Hogstedt 1980; Redfield et al. 1977; Lubchenco 1980; Larson 1980; Munger and Brown 1981; Peterson 1982 [recruitment]; Raynal and Bazzaz 1975; Fonteyn and Mahall 1981). Moreover, at least four studies in which competition was never detected continued for more than 1 yr (Wise 1981a; Horton and Wise 1983; Tinkle 1982; Peterson 1982 [growth]; and possibly Hesselman 1929 [in Toumey and Kienholz 1931]). Within-year variability occurs in one case (Lynch 1978) and conspicuously fails to occur in two others (Woodin 1974; Fonteyn and Mahall 1981). In only two, possibly three, of the 11 cases clearly showing temporal variability per se does competition appear to be totally absent during certain years but not others: two studies of desert lizards (Dunham 1980; Smith 1981) and possibly one of rodents in a forest-meadow situation (Morris and Grant 1972) all involve drought. In another study (Eriksson 1979), differences between treatments are always high, but they are statistically significant in only two of three years. In all other cases of variability, competition appears never actually absent (though statistical procedures vary widely). Of these, three are in desert (Robertson 1947; Robertson and Pearse 1945; Friedman 1971), one is in prairie and is often clearly drought related (Clements et al. 1929), and another is in a Louisiana pine forest and again involves drought (Chapman 1945). The one certain case of variability in a marine system is among a subtidal fouling community where the species composition of larval recruitment varies from year to year (Sutherland 1978). The other possible marine cases have other explanations, such as internal self-damping (Dayton 1971). Finally, a freshwater system of microcrustacea shows a seasonal reversal in the competitively superior species (Lynch 1978). In summary, (1) variability in the existence of competition is rare; (2) much year-to-year variability in competition's existence and intensity occurs among terrestrial organisms in dry, continental habitats or is otherwise related to drought; and (3) variability is especially rare in most marine systems.

Despite the large total number of studies, however, one might argue that few have gone on long enough to test Wiens's hypothesis properly. Excluding explicitly behavioral experiments, a substantial fraction of studies exceed 1 yr (fig. 1). Because of long generation times, lags, and so on, however, even several years may not suffice. Moreover, those studies failing to detect any competition could be consistent with Wiens's scheme: Only noncrunch years, which Wiens argues are especially frequent, may have been studied. For these reasons I do not wish to emphasize the percentage of studies not showing conspicuous variability; but certainly a substantial number of cases do not show it, and some pattern seems to be emerging for those that do.

#### DIFFERENTIAL OCCURRENCE OF COMPETITION BETWEEN TROPHIC LEVELS

In 1960, Hairston, Smith, and Slobodkin published a hypothesis (hereafter denoted HSS) specifying how competition should be distributed among trophic

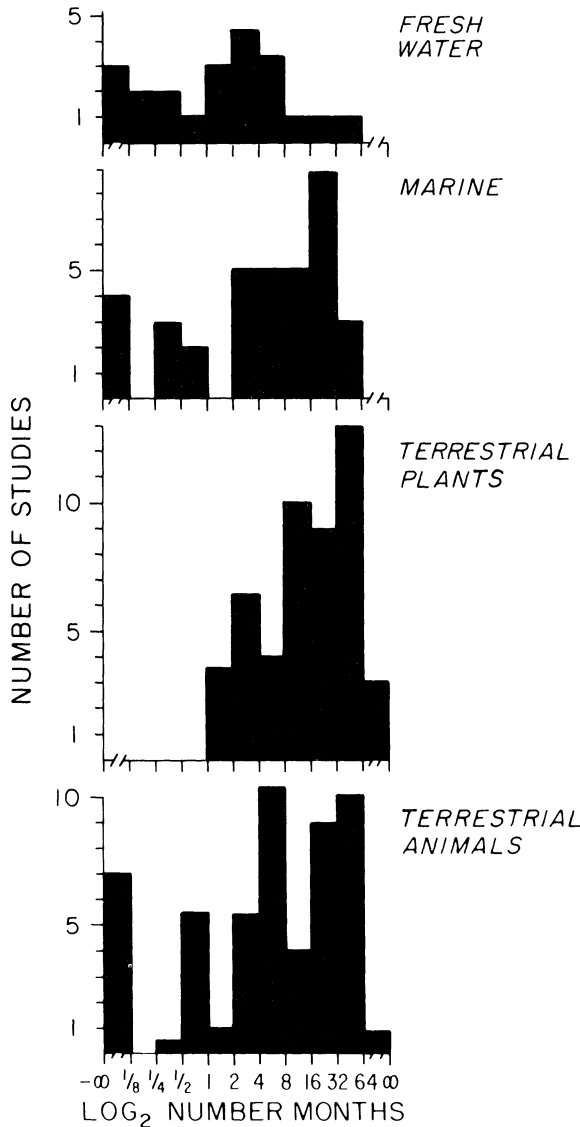


FIG. 1.—Duration of field-experimental studies on interspecific competition.

levels. It proposes that carnivores should actively compete, as should producers and decomposers. In contrast, herbivores should not compete but, because of their intermediate position in the food web, should have their populations held down by predators. The idea that predation can enhance coexistence of competing prey has received much support both empirically (e.g., Paine 1966; Connell 1975; Lubchenco 1978) and theoretically (e.g., Cramer and May 1972; Roughgarden and Feldman 1975; Hassell 1978).

In a later paper (Slobodkin et al. 1967), the same authors clarified their definition of herbivores to include phytophagous species only; they argued that nectivores, granivores, and frugivores behave as carnivores. Omnivores are ambiguous, but in my opinion obligatory omnivores would generally act as predators and facultative ones as herbivores. Although the HSS predictions were made for levels as a whole, they should apply, on average, to species within levels. Moreover, although proposed with terrestrial systems in mind, some of the logic may generalize, and we shall examine the HSS predictions for marine and freshwater systems as well.

Tables 3 and 4 show to what extent field experiments support these predictions. In these tables, cases showing competition are tabulated in two ways, by species and by study. In the first way, each species subjected to possible competition is scored as to whether or not it is affected; species affected by some treatments or in some places but not others (denoted by asterisks in table 1) are placed in a third class. In the second kind of tabulation, three classes of studies are recognized: (1) All treated species show competition at least sometimes (all species are outside of parentheses in table 1); (2) no treated species shows competition (all species are inside parentheses in table 1); and (3) at least one species in the study always or sometimes shows competition, and at least one never does. Because enclosures may keep out predators, the tables distinguish experiments with and without them (7th column, table 1; "Partial Encl" is counted as enclosed). It is, however, worth doing comparisons both including and excluding enclosed experiments for two reasons. First, enclosures do not necessarily exclude all predators. Second, densities inside enclosures are often contrived to be those occurring naturally, and such natural densities may reflect some reduction by predators.

Because the third class in each type of tabulation is ambiguous, I performed comparisons in three ways: Comparison A.—The third class is added to the first and the total contrasted with the second. Comparison B.—The third class is added to the second and the total contrasted with the first. Comparison C.—The first class is contrasted with the second; the third is excluded.

In testing HSS for marine and freshwater systems, I counted herbivores in two ways: phytophagous herbivores only and phytophagous herbivores plus filter feeders. Although the latter are generally omnivorous to some degree, the extension of HSS by Menge and Sutherland (1976) places filter feeders in the group which, on average, should not show competition.

Species were classified into trophic types on the basis of information in the second column of table 1. When a species belonged to more than one type, it was assigned to its primary type (not in parentheses). I was fairly conservative about the "omnivore" class among terrestrial organisms in particular; many mice, for example, were assigned to this class. Note also that trophic type may change with season for a given species (e.g., in certain songbirds).

All comparisons for freshwater species show the trend predicted by HSS. Compilations excluding filter feeders show a stronger trend than those including them (table 4). Compilations excluding enclosed experiments show a stronger trend than those including them (table 4). Moreover, in an experiment with nymphal mayflies, which are herbivorous, competition occurred in only one



locality where predators were not excluded but in both where they were deliberately excluded (Peckarsky and Dobson 1980). All comparisons of types B and C, but not A, are statistically significant (All experiments—Phytophagous herbivores and filter-feeders: A:  $\chi^2 = 1.161$ ,  $P > .10$ ; B:  $\chi^2 = 8.869$ ,  $P < .005$ ; C:  $\chi^2 = 3.600$ ,  $P < .05$ . Phytophagous herbivores only: A:  $\chi^2 = 2.072$ ,  $P < .10$ ; B:  $\chi^2 = 17.486$ ,  $P \ll .001$ ; C:  $P = .005$  [exact test]. No enclosures only—[the two comparisons above are identical here] A:  $P > .10$ ; B:  $P = .001$ ; C:  $P = .024$  [exact tests]).

Marine species show substantially weaker support for HSS, though only 2 of the 12 possible contingency tables testing it give the opposite trend. In this system, when filter feeders are excluded from the group not expected to show competition, the percentage of species showing competition actually rises (table 4); this is largely because of 10 species of herbivorous fishes, all of which show competition. Excluding studies done in enclosures increases slightly the contrast between species expected and not expected to show competition. Only one contingency table is significant at the 5% level (1-tailed tests): comparison A, filter feeders included, no enclosures ( $\chi^2 = 2.724$ ,  $P < .05$ ). Another comparison (B, filter feeders excluded, no enclosures) gives a  $\chi^2$  value of 2.778, but its trend is against HSS. Three other comparisons, all supporting HSS, are nearly significant ( $.05 < P < .10$ ). If fishes are deleted from comparisons, significance generally rises substantially: two tables are significant at the 5% level or better and five additional ones are nearly significant ( $.05 < P < .10$ ); none of these tables goes counter to HSS.

A variety of reasons can be suggested for the very weak correspondence of marine species to HSS. First, some of the marine experiments are designed deliberately to mimic predator-free situations (e.g., Lubchenco and Menge 1978; Duggins 1980). Second, as reviewed by Menge and Sutherland (1976) for the North American intertidal, whether or not particular trophic types compete often depends upon the presence and absence of strong predation, and the latter can vary substantially from one locality to another. Indeed, predators are known to be uncommon on certain of the herbivores tested, e.g., the gastropods studied by Underwood (1978) and Creese and Underwood (1982) and the reef fishes (see below).

Terrestrial species are highly supportive of HSS. Every comparison save two is statistically significant at the 5% or better level, and all are in the direction supporting HSS (All experiments—A:  $\chi^2 = 6.874$ ,  $P < .005$ ; B:  $\chi^2 = 1.375$ ,  $P > .10$ ; C:  $\chi^2 = 4.970$ ,  $P < .025$ . Nonenclosed experiments—A:  $\chi^2 = 7.223$ ,  $P < .005$ ; B:  $\chi^2 = 2.523$ ,  $P < .10$ ; C:  $\chi^2 = 5.740$ ,  $P < .01$ ). If anything, producer species show less competition on average than do nonproducer species, though both show substantial competition. If producers are deleted, overall statistical significance rises (same 6 cases as above, in same order:  $\chi^2 = 3.112$ ,  $P < .05$ ;  $\chi^2 = 4.295$ ,  $P < .025$ ,  $\chi^2 = 3.730$ ,  $P < .05$ ;  $\chi^2 = 3.361$ ,  $P < .05$ ;  $\chi^2 = 5.099$ ,  $P < .025$ ;  $\chi^2 = 4.449$ ,  $P < .025$ ). Except for certain types of plant studies, enclosures are not commonly used in terrestrial experiments. As the figures show, if enclosed experiments are excluded, trends are only slightly clearer than before, and qualitative conclusions for a significance level fixed at 5% are unaltered.

In terrestrial systems, a large number of species, mostly rodents, are listed as

TABLE 3  
TROPHIC TYPES: PRESENCE AND ABSENCE OF COMPETITION AS DETECTED BY FIELD EXPERIMENTS

SYSTEM	PRODUCERS			HERBIVORES† (P, G, N)			OMNIVORES			FILTER FEEDERS			CARNIVORES			SCAVENGERS DETRITIVORES			DEPOSIT FEEDERS		
	No		Encl	No		Encl	No		Encl	No		Encl	No		Encl	No		Encl	No		Encl
	Encl			Encl			Encl			Encl			Encl			Encl			Encl		
By SPECIES OR GROUP																					
Freshwater																					
Always present	....	1	1	0	1	0	0	0	7	0	0	4	10	0	0	0	0	0	0	0	
Always absent	....	0	1	1	5	0	1	1	2	0	0	1	2	0	0	0	0	0	0	0	
Sometimes present		0	0	1	6	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Marine																					
Always present	....	5	8	2	16 <sup>ll</sup>	...	...	...	3	13	0	5 <sup>#</sup>	0	0	1	2	0	0	0	0	
Always absent	....	2	0	3	3	...	...	...	3	12	0	2**	0	0	1	0	0	0	0	0	
Sometimes present		0	6	5	0	...	...	...	2	4	0	0	0	0	0	0	0	0	0	0	
Terrestrial																					
Always present	....	15	59	(3,8,3)	(2,8,2)	3	12	...	...	...	1	20	1	6	...	...	...	...	...	...	
Always absent	....	0	22	(1,0,0)	(5,3,0)	5	2	...	...	...	1	13	0	0	...	...	...	...	...	...	
Sometimes present		3	42	(0,0,0)	(1,1,1)	0	1	...	...	...	0	0	0	0	0	0	0	0	0	0	
By STUDY																					
Freshwater																					
Present at least																					
sometimes in all																					
species or groups	..	1	0	1	0	1	0	0	2	0	1	4	0	0	0	0	0	0	0	0	
Never present in																					
any species or																					
group	.....	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	

Mixed: never present in some, sometimes or always in others ...	0	1	1	2	1	2	0	1	2	0	0	0	0
Marine													
Present at least sometimes in all species or groups ..	2	5	1	7‡	...	...	3	4	0	3§	0	2	0
Never present in any species or group .....	0	0	0	1	...	...	1	1	0	1	0	0	0
Mixed: never present in some, sometimes or always in others ...	1	0	3	1	...	...	1	2	0	1§	0	1	0
Terrestrial													
Present at least sometimes in all species or groups ..	9	31	(3,4,3)	(1,4,2)	3	10	...	...	0	10	1	3	...
Never present in any species or group .....	0	3	(0,0,0)	(3,2,0)	2	1	...	...	0	5	0	...	...
Mixed: never present in some, sometimes or always in others ...	0	6	(0,0,0)	(1,0,0)	0	1	...	...	1	2	0	...	...

\* Use numbers in col. 4 of table 1.  
† Numbers in parentheses refer to phytophagous herbivores, granivores and nectarivores, respectively.  
‡ Includes 4 fish studies.  
§ Includes 1 fish study.  
|| Includes 10 fishes.  
# Includes 3 fishes.  
\*\* Includes 1 fish.

TABLE 4  
EXPECTATIONS OF THE HSS HYPOTHESIS COMPARED TO DATA (All figures percentages, compiled from table 3)

	By Species			By Study		
	Predicted to Show Competition	Predicted Not to Show Competition	Her† & Fil†	Predicted to Show Competition	Predicted Not to Show Competition	All Species
	All species	Her Only		All Species	All Species	
FRESHWATER						
A. All experiments	N = 20	N = 23	N = 14	N = 10	N = 9	
Competition present* . . . .	80.0	34.8	7.1	60.0	33.3	
Competition absent . . . .	20.0	34.8	42.9	0	11.1	
Mixed . . . . .	0	30.4	50.0	40.0	55.6	
B. No enclosures only						
Competition present . . . .	N = 13	N = 12	N = 12	N = 7	N = 2	
Competition absent . . . .	77.0	8.3	8.3	57.1	0	
Mixed . . . . .	23.0	41.7	41.7	0	0	
	0	50.0	50.0	42.9	100	
MARINE						
A. All experiments	All species	Her & Fil	Her Only	All Species	Her & Fil	Her Only
Competition present . . . .	N = 30	N = 66	N = 29	N = 14	N = 25	N = 13
Competition absent . . . .	63.3	51.5	62.1	71.4	60.0	61.5
Mixed . . . . .	16.7	31.8	20.7	7.1	12.0	7.7
	20.0	16.7	17.2	21.4	28.0	30.8



omnivores and so have not been included in the preceding comparisons. Most of the omnivorous rodents show competition. One might argue that some of the rodents classified as omnivores in fact are species HSS would expect to show competition because they eat mostly either seeds or arthropods. Those genera most likely to belong here are *Onychomys*, *Peromyscus*, and *Apodemus* (the others are *Neotoma*, *Clethrionomys*, *Reithrodontomys*, and *Mus*). Of the former group, two species (or groups) did not show competition and seven did, almost exactly the percentages for all nonproducers expected to show competition (table 4). Moreover, of the two cases not showing competition, one (Munger and Brown 1981) was deliberately included because it was not expected to show competition with the manipulated species because of low niche overlap. Hence, if anything, inclusion of more omnivorous rodents would strengthen our conclusions for terrestrial organisms.

Despite the strong support that HSS receives from terrestrial experiments, one class, that of carnivores, is far from overwhelmingly supportive. The main reason is experiments on spiders: Four of five such experiments listed in table 1 failed to detect competition, and another unpublished one is also negative (review in Wise 1983). In fact, as in marine systems (Menge and Sutherland 1976), terrestrial predators at an intermediate trophic level, such as spiders (cf. Schoener and Toft 1983), might be variable in their vulnerability to predation on themselves, sometimes resembling herbivores. Intermediate-level predators are typically small, and Connell (1975) and Schoener (1974*b*), among others, have suggested that small animals should compete less, on average, either because they can be overcome by a greater variety of predators or because they are more sensitive to mortality from harsh climatic conditions or physical disturbance. In fact, taken as a whole, small terrestrial heterotrophs (all arthropods except one fungus) show competition significantly less frequently than do the larger vertebrates in two of three possible comparisons. (A: 22 of 36 small species always or sometimes show competition; 51 of 67 large species always or sometimes do;  $\chi^2 = 2.555$ ,  $P < .10$ . B: 20 of 36 small species always show competition; 49 of 67 large species always do;  $\chi^2 = 3.272$ ,  $P < .05$ . C:  $\chi^2 = 2.899$ ,  $P < .05$ .) In particular, certain exceptions to the tendency for phytophagous herbivores not to show competition occur among large mammals; the phytophagous moose is probably less likely to be eaten than many insectivorous lizards, for example. Freshwater animals show a similar pattern for size, though only one comparison is statistically significant (A: 20 of 31 small species always or sometimes show competition; 13 of 15 large species always or sometimes do;  $\chi^2 = 2.446$ ,  $P < .10$ . B: 12 of 31 small species always show competition; 11 of 15 large species always do;  $\chi^2 = 4.847$ ,  $P < .025$ . C: exact  $P = .054$ ). Size may also be important in marine systems, though here all the very large species are fishes, 13 of 14 of which always show competition. Marine fishes show competition significantly more often than other marine animals, no matter which comparison is used A: ( $\chi^2 = 3.150$ ,  $P < .05$ ; B:  $\chi^2 = 8.951$ ,  $P < .005$ ; C:  $\chi^2 = 4.836$ ,  $P < .025$ ). The fishes studied all inhabit reefs, and such species have been noted as being relatively free of predators once they reach a certain size (e.g., Sale 1977). Certain marine invertebrates can also "escape in size" from predators (Dayton 1971; Connell 1975), and possibly some finer size discrimina-

tion would produce significant results within that group. Given the substantial variability in size of many marine species during the competition experiments, however, I do not feel informed enough to make the effort.

Size, however, cannot be the whole story so far as terrestrial animals are concerned. Among bees and ants, as small or smaller than spiders, 5 of 5 and 11 of 11 species, respectively, sometimes show competition; of these, only one bee does not always show it. Bees and ants are noxious in various ways, and this must reduce their vulnerability to predation. (Moreover, the ants occur in large groups, so may be fairly resistant to moderate predation.) Similarly, many terrestrial plants can be inedible because of compounds they produce; indeed, this explanation for lack of control by herbivores has been argued as being as or more important than that the herbivores are held down by predators (Murdoch 1966; Ehrlich and Birch 1967), though the authors of HSS do not agree (Slobodkin et al. 1967).

If studies, rather than species, are examined, sample sizes are substantially lower but trends are mostly the same. The four possible freshwater comparisons go in the direction predicted by HSS (table 4), but none is statistically significant. In marine systems, 11 of 12 comparisons support HSS and the one exception is only slightly reversed (table 4); again, nothing is significant. In terrestrial systems, all 12 comparisons go in the direction predicted by HSS. Of these, comparisons including producers give stronger trends than those excluding them, in contrast to species comparisons: All such comparisons are significant at the 5% or better level whereas none of the others is. (Producers included. All experiments—A:  $\chi^2 = 4.952$ ,  $P < .025$ ; B:  $\chi^2 = 3.912$ ,  $P < .025$ ; C:  $\chi^2 = 5.347$ ,  $P < .025$ . Nonenclosed experiments—A:  $\chi^2 = 8.138$ ,  $P < .005$ ; B:  $\chi^2 = 7.144$ ,  $P < .005$ ; C:  $\chi^2 = 9.605$ ,  $P < .005$ . Producers excluded. All experiments—A:  $\chi^2 = 1.314$ ,  $P > .10$ ; B:  $\chi^2 = 1.620$ ,  $P > .10$ ; C:  $\chi^2 = 1.561$ ,  $P > .10$ ; Nonenclosed experiments—A:  $\chi^2 = 2.461$ ,  $P < .10$ ; B:  $P = .065$  [exact test]; C:  $P = .096$  [exact test].)

Finally, we can ask whether enclosures significantly increase the proportion of species showing competition. In terrestrial plants, they do in all three possible comparisons (A:  $\chi^2 = 3.815$ ,  $P < .05$ ; B:  $\chi^2 = 8.410$ ,  $P < .005$ ; C:  $\chi^2 = 4.034$ ,  $P < .025$ ). Moreover, in a study of *Plantago*, competition was undetectable only in an area where competing grasses were heavily grazed (Sagar and Harper 1961). Enclosed experiments are also less likely to show competition among those terrestrial trophic types supposed to show it according to HSS (A:  $\chi^2 = 2.998$ ,  $P < .05$ ; B:  $\chi^2 = 3.788$ ,  $P < .05$ ; C:  $\chi^2 = 3.220$ ,  $P < .05$ ). In all comparisons, terrestrial phytophagous herbivores compete more frequently within enclosures; while trends are strong, the numbers are never large enough to achieve statistical significance. Curiously, in terrestrial omnivores the trend is actually reversed, in one comparison (A) nearly significantly so ( $P = .053$  [exact test]). In marine systems, enclosures seldom have a significant effect in toto, but the trend is often opposite from that expected. Significantly opposite trends occur in herbivores (B:  $\chi^2 = 11.474$ ,  $P \ll .001$ ; C:  $\chi^2 = 4.126$ ,  $P < .025$ ). To some extent, as explained above, the marine results must be artifacts of the experimenters' intentions. Freshwater experiments show no obvious trends, but sample sizes are small.

In conclusion, HSS receives significant support from terrestrial and freshwater

systems and no significant contradiction from marine ones. Nonetheless, exceptions are always frequent: For very few cases, including herbivores, does the number of species or studies never showing competition fall above 50%, and the highest percentage is 62.5 (table 4; but see above for possible biases). Note also that it is crucial to the success of HSS in terrestrial systems that nectivores and granivores not be counted as typical herbivores. Finally, exceptions in all systems appear related to characteristics reducing predation, such as large size and noxious qualities. Since trophic type and these latter characteristics are themselves nonindependent, the various trends are somewhat confounded. Once more data become available, effects can perhaps be discriminated with multivariate analysis.

#### COMPETITION AND ECOLOGICAL OVERLAP

In the first mathematical paper relating similarity in resource use to competitive exclusion, MacArthur and Levins (1967) proposed that the competition coefficient could be computed as a measure of ecological overlap. This coefficient,  $\alpha_{ij}$ , is the competitive effect on the growth of species  $i$  of an individual of species  $j$  divided by the same effect of an individual of species  $i$ . (The outcome of competition is also determined by carrying capacities,  $K$ 's, and in more-than-two-species systems, by the intrinsic rates of increase,  $r$ 's [Strobeck 1973].) The MacArthur-Levins formulation is:

$$\alpha_{ij} = \frac{\sum_k p_{ik} p_{jk}}{\sum_k p_{ik}^2} \quad (1)$$

where  $p_{ik}$  is the fraction of the total resource use by species  $i$  from resource  $k$ . For example,  $p_{ik}$  might be the fraction of the diet comprised of prey type  $k$ , or the fraction of the time habitat  $k$  is utilized. As was pointed out several times subsequently (Colwell and Futuyma 1971; Vandermeer 1972), great ecological overlap need not indicate great competition but may result from interspecific tolerance, whereas low overlap may result from aggressive exclusion, among other things. Despite such possible problems, many ecologists have continued to find equation (1) useful.

Certain field experiments can give us some insight into where equation (1) or a similar expression is likely to work. In six experiments, low ecological overlap was associated with low competition and vice versa (Abramsky et al. 1979; Pacala and Roughgarden 1982, 1983; Reynoldson and Bellamy 1970; Munger and Brown 1981; Peterson and Andre 1980; and Werner 1977). In four of these, overlap involved food type (the first 4 listed), and in three it involved microhabitat—perch characteristics (Pacala and Roughgarden 1982, 1983) or depth in sediment (Peterson and Andre 1980) or soil (Werner 1977). Only one (Abramsky et al. 1979) involved macrohabitat, and this only in part. In all six experiments, two pairs of species (or groups) were included; one comprised species which overlapped



broadly and one did not. The experiments of Pacala and Roughgarden and Munger and Brown, in particular, were designed to test explicitly the proposition that competition increases with degree of food and/or microhabitat overlap. Moreover, in a reef experiment in which an omnivorous fish species was removed, five species overlapping in diet responded, but two species with nonoverlapping diets did not (Robertson et al. 1976). These results are in contrast to the typical situation for macrohabitat overlap. Studies of this dimension involving several pairs of species are unavailable, but we can look at experiments done with a single pair. Four experiments on mammals (Grant 1969, 1971; Koplin and Hoffmann 1968; Schroder and Rosenzweig 1975) showed that low macrohabitat overlap implies low competition or vice versa. Similarly, sharp zonation along marine shorelines has been experimentally associated with high competition (e.g., Connell 1961; Bertness 1981). Moreover, three sets of experiments on intraspecific variation in competitive ability, one on salamanders (Hairston 1980*a*, 1980*b*) and two on plants (Turkington and Harper 1979; Martin and Harding 1981 [a laboratory experiment]), bear on this question. They show that a given species is harmed less by individuals of a second species from localities where the species broadly overlap spatially than by individuals from allopatric localities. Apparently coexistence mechanisms have coevolved where spatial contact is great. Thus with one partial exception, macrohabitat overlap is inversely, and other ecological overlap is directly, related to experimentally demonstrated competition.

I am now going to argue that all this is consistent with the only derivation of equation (1) from resource overlap known to me. This derivation, performed by MacArthur (1968) and elaborated by Schoener (1974*c*) and Abrams (1980), shows that an equation like (1), but more complicated, results when a certain consumer-resource system reaches equilibrium. The system assumes that consumers encounter resource types according to their proportions in the whole system (or assumes some other encounter schedule that amounts to this condition). This assumption is very likely to be violated if the resource types are particular macrohabitats, especially where territorial competition is present (though territoriality did not occur in all macrohabitat experiments mentioned above; moreover, in the Schroder-Rosenzweig experiment, apparently some habitats were simply way stations rather than feeding areas). It is much less likely to be violated for microhabitats or food types, given the scale of territoriality and movement. Whether territoriality occurs or not, if habitats are the arenas of competition rather than categories of resources, habitat segregation can result from competition and the appropriate models are very different from MacArthur's equations (Schoener 1974*a*). Indeed, table 1 gives 22 cases in which habitat segregation was produced experimentally.

Certain field experiments pose other inconsistencies with equation (1). Lynch (1978) showed that one or another species of microcrustacean was competitively dominant at different times of the year, despite no obvious change in food overlap. He suggested that changes in relative feeding efficiency with changes in temperature might be responsible. In fact,  $\alpha$ 's derived from MacArthur's equations could reflect this shift, even though equation (1) cannot. The MacArthur expression is:

$$\alpha_{ij} = \frac{\sum_k a_{ik} a_{jk} [(b_{ik} K_k)/r_k]}{\sum_k a_{ik}^2 [(b_{ik} K_k)/r_k]}$$

where  $b_{ik}$  represents the net energy per item of resource  $k$  extractable by an individual of consumer  $i$ ;  $a_{ik}$  is a consumption rate of resource  $k$  by consumer  $i$ ;  $r_k$  is the intrinsic rate of increase of resource  $k$ ; and  $K_k$  is its carrying capacity. In particular, the  $a$ 's incorporate the abilities of consumers to eat particular prey. (Details are given in Schoener [1974c].) When the resource kinds are habitats,  $p$ 's can be substituted for  $a$ 's in equation (2) provided that the whole expression is multiplied by  $(T_j/T_i)$ , which gives the relative overall consumption times (or some related quantity) for the two species. When the resource kinds are prey types, the  $p$ 's from the diet must be divided by relative frequencies of the prey types in the environment, and again, a ratio  $(T_j/T_i)$  is present, where the  $T$ 's now refer to the total number of items consumed by the species. Under this interpretation, the greater the consumption rate of species  $j$  relative to species  $i$ , the greater  $\alpha_{ij}$ . Equation (2), but not equation (1), may also be consistent with Black's (1979) data on two species of limpets. Here,  $\alpha$ 's measured from habitat utilizations are about equal, even though one species appears competitively superior. Again, a difficulty in using habitat to estimate  $\alpha$  may be involved, but as just shown, a difference in the relative consumption rates could easily account for the inconsistency.

Alternatively, a linear (Lotka-Volterra) competition model may be inappropriate, and a nonlinear one may be necessary. For example, G. Belovsky (personal communication) found a nonlinear model to fit field-population data on grasshopper competition better than the linear model, and only the nonlinear model predicted the actual outcome of competition. In another field experiment, Belovsky (1983) found that only a nonlinear model correctly predicted the relative per capita effects of the competitors (moose and hare) on one another; equation (1) was insufficient. Note that the nonlinear models can be explicitly models of food overlap (Schoener 1974a, 1976, 1978), just as is the two-level model giving rise to equation (2). Thus, inconsistency of data with equations (1) and (2) does not necessarily imply that ecological overlap is irrelevant, nor that resource competition is not occurring.

#### ASYMMETRICAL COMPETITION

Table 1 contains a number of cases in which only some of a group of treated species are affected, or strongly affected, by competition. Indeed, asymmetry in such sensitivity is rather common; when explicitly tested, species are strongly asymmetrical in 51 studies and relatively equal in only 10. Moreover, 24 other studies mention that the experimental subject appears to belong to an asymmetrical species pair or group. Asymmetry is especially notable in the marine intertidal, where certain species are referred to as "competitive dominants" (Paine 1980).

In general, the species included in a particular study are identical in trophic

role, locale, and time of experimentation. How then can such variation be explained?

First, as just reviewed, a major reason for some but not other species to be sensitive to competition is the degree to which their resource use overlaps with that of the species to which they are exposed.

Second, particularly among terrestrial vertebrates, the larger species tend to be less affected by competitors. In all systems combined, substantially larger competitors are superior in 14 experiments, small ones in 5 ( $P = .032$ ); if we add cases where observation was used to establish the direction of superiority, the figures are 27 to 5 ( $P < 10^{-4}$ ). Theoretically, asymmetry resulting from size differences can arise through exploitation or some form of aggressive competition or both (Roughgarden 1972; Wilson 1975; Schoener 1975). Note from the previous section that the term  $T_j/T_i$  to which  $\alpha_{ij}$  is directly proportional is larger, the larger an individual of species  $j$  relative to  $i$ , provided consumption rates increase with increasing body size. In addition to the field experimental results, various field observations and laboratory experiments have documented the usual, but not universal, tendency for large animals to dominate in competitive situations (Miller 1967; Grant 1970).

Other apparent reasons for superiority include (1) differences in feeding parameters for a variety of kinds of organisms; (2) differences in recruitment abilities and a more rapid or destructive growth pattern in sessile marine organisms; and (3) physiological traits, such as response to desiccation, which cause differential responses to competitor removal (table 1).

#### FUTURE DIRECTIONS

An unequivocal conclusion of the foregoing review is that interspecific competition has now been established experimentally in a great variety of natural systems and among a great variety of organisms. For those not accepting observational evidence of competition at all, this has been an essential task. In my opinion, however, experimental data will never replace observational data, since the latter can be gathered far more quickly, so can encompass far more individuals, species, localities, and times. Ideally, once a large amount of observational data is available, crucial situations can be selected for experiment. Such experimentation may support or recast inferences made from observations, and the resulting edifice of knowledge will be more substantial than either approach alone can provide. Thus I see the two approaches as complementary rather than successional.

Furthermore, I would argue that field experiments have only begun to be exploited for the great variety of information which they are capable of generating, information that goes well beyond simply establishing competition. To illustrate, I will consider four shortcomings of the present studies in toto and will try to show how a more quantitative, theoretically guided approach might both resolve them and lead to new discoveries. I do not wish, however, to discuss methodological or statistical problems, even though these can be major, given the difficulties of working under natural conditions.

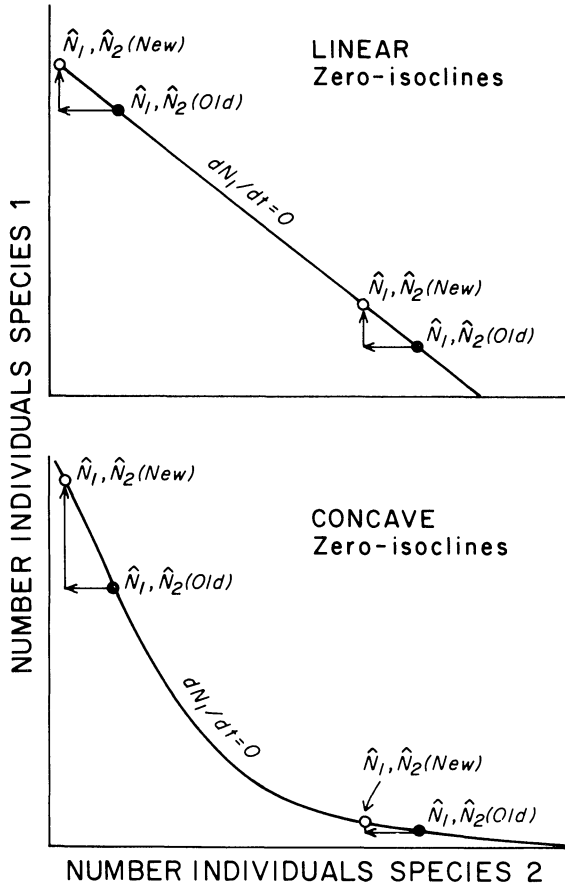


FIG. 2.—Hypothetical change in equilibril abundances of two species resulting from a sustained experimental reduction of species 2. *Top*, Lotka-Volterra, linear-isocline model. Whether species 1 is common or rare before perturbation (old equilibrium), a fixed decrement in species 2 produces a fixed increase in species 1. *Bottom*, Concave, nonlinear isocline model. If species 1 is rare, a fixed decrement in species 2 (the common species) causes almost no change in species 1. If species 1 is common, the opposite holds. Obviously, the argument can be reversed for experimentally maintained increases in the abundance of one of the species.

*1. Detection of competition.*—Competition may be very difficult to detect in nature. How detectable it is depends, among other things, on the underlying population dynamics. If competition follows Lotka-Volterra dynamics, an experimentally maintained fixed increment in the population of species  $j$  will produce a fixed decrement in the equilibrium population of species  $i$ , regardless of the initial population size of species  $i$  (fig. 2a). On the other hand, if competition follows a concave-isocline model (Schoener 1974a, 1976, 1978; Ayala et al. 1973), the less numerous species  $i$  is to begin with, the more individuals of species  $j$  will be required to depress its equilibrium a certain amount (fig. 2b). In other words, competitive effects on rare species may be slight and very difficult to measure

while effects on common species are the opposite. In experiments with salamanders, Hairston (1981) could detect an effect of competition only on the two commonest species and not on the four rarest ones. Because all species overlapped substantially in food type, he concluded that food probably was not the object of competition among any of the species, including the two most common ones. This conclusion may be perfectly correct. An alternative explanation, however, is that all species compete for food (or perhaps in some other way), but that the effect of the treatment on the rare species was so small as to be undetectable.

Competition models producing concave isoclines incorporate a variety of exploitative and/or interference mechanisms, and they have been found more suitable in describing certain laboratory data than the Lotka-Volterra model (Ayala et al. 1973). Field tests of these models are almost nonexistent; I know only of the several experiments of Belovsky described above.

2. *Degree of competition.*—Field experiments have detected a great variety of effects of interspecific competition (table 1). These are, however, often behavioral or physiological. Even when number of individuals is affected, the degree to which the species composition of the community can be altered is often not investigated. For example, a community resistant to invasion by a small number of individuals of a competing species might be successfully invaded with a large number. This possibility exemplifies the phenomenon of multiple stable points, theoretically likely if resource overlap is great and strong interspecific interference exists (Schoener 1976, 1978). The phenomenon may characterize marine fouling systems (Sutherland 1974), among others. In short, while many competition experiments have now been performed, few, except in certain marine systems, try to perturb communities to new states or go on long enough to give much insight into whatever equilibrium structure exists.

3. *Mechanisms of competition.*—Determining the mechanisms of competition is almost as elusive using simple field experiments as from mere observation. Indeed, even in experiments most interference mechanisms are surmised from observation, and rarely is an attempt made to determine their quantitative importance. Hence their importance might be distorted relative to the much less observable exploitative competition. Consumptive competition can be implicated by monitoring resources, or better, by artificially increasing them for one category of treatments. When space is the object of competition, new units of space can be introduced; this is especially useful in demonstrating preemptive competition, in which behavior is often unobservable. For example, empty settling substrate can be periodically introduced to determine the availability of larval colonists for sessile marine organisms (Sutherland and Karlson 1973; Schoener and Schoener 1981), or empty shells can be used to determine the scarcity of that resource for hermit crabs (Abrams 1981).

Regardless of the quality of evidence, most investigators give some opinion about mechanism. Here I would like to point out that certain mechanisms or combinations are in theory more likely than others (Schoener 1974a, 1976, 1978). In particular, competition for habitat-homogeneous space if costs are low is by itself unlikely to allow coexistence. If an individual of one species invests more

energy in territorial competition than a heterospecific individual and thereby acquires more space, coexistence is more likely. Coexistence is especially likely if both consumptive and some kind of interference competition is going on, given the possibilities of trade-offs between costs and benefits; species could then coexist even under high resource overlap. Thus in nature, exploitative and interference competition are likely to be coupled from a population-stability point of view, just as the former is likely to select for the latter over evolutionary time.

4. *Ecological overlap and competition.*—As discussed, competition is theoretically least likely to increase with overlap in macrohabitat, as indeed it usually does not in field experiments. Moreover, the simple MacArthur-Levins overlap measure (eq. [1]) may be inadequate even if consumptive competition is the only mechanism acting; the more complicated, theoretically justifiable versions of equation (2) may be much better, or nonlinear models may be necessary. Here I wish to urge experimentalists not to throw the baby out with the bathwater: Failure of equation (1) to describe an experiment does not imply that resource competition is not going on, and in particular that no overlap-type measure is appropriate. In very few cases have alternative overlap measures (Abrams 1980) or alternative competition models even been cursorily evaluated.

In conclusion, field experiments have already revealed much about the natural domain of interspecific competition. Yet unlike the case for laboratory experiments, strong links between field experiments and the theory of competition have mostly yet to be forged, a major task that remains for the future.

#### SUMMARY

Rare until recently, field-experimental studies of interspecific competition now number well over 150. Competition was found in 90% of the studies and 76% of their species, indicating its pervasive importance in ecological systems. Exploitative competition and interference competition were apparent mechanisms about equally often. Few experiments showed year-to-year variation in the existence of competition, though more did in its intensity; many were not long-term. The Hairston-Slobodkin-Smith hypothesis concerning variation in the importance of competition between trophic levels was strongly supported for terrestrial and freshwater systems. In particular, producers, and granivores, nectarivores, carnivores, and scavengers taken together, showed more competition than did phytophagous herbivores and filter feeders. In marine systems, virtually no trend was detectable one way or the other. Large heterotrophs competed more than small ones in most comparisons, and other properties possibly deterring predation, such as stinging behavior, seemed also characteristic of species competing frequently. Among terrestrial plants and certain terrestrial animals but not all, experiments carried out in enclosures were more likely to show competition than unenclosed experiments. A greater ecological overlap implied a greater tendency to compete, as determined experimentally, when niche dimensions were food type or microhabitat; the opposite was true for macrohabitat. A substantial number of studies showed asymmetry in their species' response to competition; larger species were significantly more often superior than smaller ones, though a variety

of other apparent reasons for asymmetry also existed. The integration of competition theory into field experimentation has only just begun.

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