Predation, Competition, and Prey Communities: A Review of Field Experiments

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Ecology Research Group, T. H. Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506

INTRODUCTION

A central controversy in ecology addresses the relative importance of competition and predation in determining the characteristics of organisms (e.g. behavior, life history), populations (e.g. population size, stability), and communities (e.g. species diversity, total and relative abundance patterns). Through the early 1970s the "competition school" appeared to dominate (e.g. 19, 20, 107, 109, 166). However, in recent years a discernible shift has occurred towards the notion that predation often has the greater impact, sometimes by reducing the importance of competition (e.g. 16, 22, 133, 134, 206).

A related controversy concerns the techniques used to evaluate the importance of a given factor. Before the 1970s, field ecologists relied primarily on observation. More recently, experiments have become part of the standard protocol in field studies. Each approach has benefits and drawbacks. Controlled experiments produce stronger inferences than do observations alone; however, experiments are often impractical, particularly where the questions are broad in scope (e.g. on a geographic or an evolutionary scale). Observational techniques can address broad questions but are more open to alternative interpretations.

*Current address: Department of Zoology, Michigan State University, East Lansing, Michigan 48824

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The recent burst of experimental work allows the use of a third method: the review and statistical analysis of the results of a large number of field experiments. Connell (24) and Schoener (167) recently surveyed field competition experiments. Although the tone of their conclusions differed markedly, both showed that competition often occurs.

The frequent occurrence of competition, however, does not imply that competition is more important than predation. At minimum, one must do a similar survey of the experimental work on predation. We summarize the results of such a survey. The organization of the paper is as follows: (a) definitions and methodology; (b) results, including tests of previously suggested trends; (c) analyses on the overall relative importance of predation and competition; (d) a survey of studies that include experiments on both competition and predation; and (e) suggestions for future study. Brief summaries at the end of each results section emphasize major gaps in the studies to date and so suggest fruitful directions for future research.

DEFINITIONS AND METHODOLOGY

What is predation? In its broadest sense, predation includes any interaction in which energy flows from one organism to another. By that definition all animals and some plants are predators. We somewhat arbitrarily decided to exclude carnivorous plants, detritivores, parasites, and pathogens, limiting our survey to animal carnivores, herbivores, omnivores, and seed predators. A rather fuzzy line separates some organisms that we included from those that we excluded (e.g. nearly all herbivorous insects can be considered parasites). Our decision was based primarily on our perception that most of the ideas concerning the effects of predation come from studies of the included groups.

What is a field experiment? We followed Schoener's (167, p. 242) definition that a field experiment is a manipulation (here, of predator density) "in which some major natural factor extrinsic to the organisms of interest is uncontrolled." This kind of manipulation includes both removals and additions, as well as removal with restocking of predators at controlled densities. Both fenced enclosures/exclosures and experiments with no artificial barriers to predator movement were included in our analysis.

We initially hoped to consider only studies with no obvious design problems. However, many studies lacked either proper controls, sufficient replication (many were pseudoreplicated—see 69a), or statistical analyses. Ideally, treatments and controls should be performed at the same time and place, so that the two experience the same uncontrolled environmental variations. We included studies in which controls and treatments were close enough that we believed the controls to be reliable. We excluded studies with no controls or with no

replication, but included those with pseudoreplication or low replication. Finally, a surprisingly large proportion of the studies lacked any statistical analysis of the data. We excluded these studies if they provided no measures of the variation among replicates. Where results included standard errors but no statistical tests, we attempted to judge the statistical significance of any apparent differences. Although we may have made some errors, these are unlikely to have changed our qualitative conclusions. Overall, our tack was to include flawed studies but to record their problems to permit analyses comparing results based on all studies to those with or without problems.

We did not attempt an exhaustive review of all field experiments on predation. Instead, we followed Connell's (24) basic protocol. We surveyed 20 years (1965–1984; not including the last two months of 1984) of seven journals: *American Naturalist, Ecology, Ecological Monographs, Journal of Ecology, Journal of Animal Ecology, Limnology and Oceanography, and Oecologia.* This systematic and, we hope, unbiased survey yielded 139 papers. Unfortunately, this procedure left out some important studies of predation, including a few inadvertently missed within the bounds of our survey. We apologize for these oversights.

Analyses were done on both a "by study" and a "by comparison" basis. Deciding how a series of experiments should be divided into distinct "studies" is not straightforward. We defined a single study as including all experiments discussed in a single paper. We feel confident that any other definition of a study would not alter major qualitative conclusions.

A given study can include dozens of comparisons between experimental treatments and controls for different taxa or response variables. For example, a study might look at the effects of predator removal on prey species diversity, total prey abundance, and on the abundance of each of 10 prey taxa. Such a study would include 12 comparisons. If the study was repeated in two different years, we have 24 comparisons, and so on. The 139 studies included 1412 comparisons. Each comparison was categorized in the following ways (see Table 1): by latitude, by ecosystem type, by predator and prey taxa, by predator trophic level, by type of experimental manipulation, by type of response, and by magnitude of response. To produce adequate sample sizes for statistical analysis we were forced to combine groups that might be rather dissimilar; for example, the terrestrial system includes experiments done in tropical and temperate forests, grasslands, deserts, and tundra. This procedure is conservative: it might mask interesting differences but is unlikely to produce speciously significant results. Our full data set is briefly summarized in Table 2.

Most of the classifications listed in Table 1 and used in Table 2 are self-explanatory, but a few require additional explanation.

In describing the types of experiments, we use *fenced* to signify any type of

Table 1   Classification variables and categories resulting from categorizing experiments, the contrasts performed on each classification variable, and the response variables for which the contrasts were performed

Classification variables	Categories	Contrasts
Latitudinal zone	Temperate (TM) Tropical (TR) Polar (PO)	TM × others TR × PL
System	Intertidal (INT) Other marine (MAR) Lotic (LOT) Lentic (LEN) Terrestrial (TER)	TER × others INT&MAR × LOT&LEN INT × MAR LOT × LEN
Predator type	Mammal (MA) Bird (BI) Reptile or amphibian (HP) Fish (FI) Arthropod (AR) Mollusc (MO) Other invertebrate (IN)	MA&BI&HP&FI × AR&MO&IN AR × MO&IN
Predator trophic level	Herbivore (HB) Primary carnivore (CA1) Secondary carnivore (CA2) Omnivore (OM) Seed predator (SE) Other (OT) Unknown (UK)	HB × CA1 CA2 CA1 × CA2
Experiment type	Removal fenced (RF) Removal unfenced (RUF) Stocked fenced (SF) Stocked unfenced (SUF) Addition fenced (AF) Addition unfenced (AUF)	RF&RUF × SF&SUF&AF&AUF RF × RUF AF&SF × AUF&SUF

Response variables

Species diversity (SD)
Total prey abundance (TO)
Relative prey abundance (RE)
Population size (PO)
Size structure (SI)
Prey fitness (FT)
Prey growth rate (GR)
Prey feeding rate (FR)
Prey behavior (BE)
Other (OT)

artificial barrier to predator movement. This includes both obvious barriers such as cages and more subtle ones such as "sticky fences" to keep ants off plants, or copper paint to limit the dispersal of intertidal gastropods.

Different measures of prey abundance (including number, density, biomass, percent cover) were used in the studies: (*a*) Some investigators quantified the abundance of one or more prey taxa (species, genus, or sometimes higher levels) but did not report total prey abundance. We termed the abundance of each taxon *prey population size,* even though in many instances the taxa quantified were of a higher level than species. (*b*) Some papers reported the abundance of both separate prey taxa and the summed abundance of all prey. The abundance of each taxonomic grouping is *prey population size,* whereas the sum is *total prey abundance.* (*c*) Finally, some studies examined the abundance of only one prey grouping. If this grouping represented only a small fraction of the predator's overall diet, we referred to their abundance as *prey population size,* but if the grouping included most of the available prey for that predator, we called it *total prey abundance.* Although some subjectivity is involved, we found the distinction between these two categories was usually clear.

Several other categories of prey response also deserve discussion. *Species diversity* includes species richness as well as measures of diversity that in-corporate both the number of species and their equitability. *Relative prey abundance* refers to the proportion of prey in each category. *Size structure* refers to the distribution of the sizes of prey individuals. *Individual fitness* includes any measure of the survivorship or fecundity of prey individuals. *Individual growth* includes prey growth rate and size at a particular stage. *Behavior* includes habitat use, diet, activity level, and time of activity.

An *expected response* takes place when a higher density of predators results in a reduction in either prey species diversity, total prey abundance, prey population size, individual prey fitness, individual prey growth rate, or prey feeding rate. An *unexpected response* is the opposite, in each case. The *keystone* predator effect (133, 134) is thus an *unexpected* effect in this sense. The keystone effect goes against the straightforward expectation that predation should reduce prey populations and, by driving some prey locally extinct, reduce prey species diversity. Prey relative abundance, size structure, and behavior can only be classified as "expected" or "unexpected" if some details on the predator-prey interaction are available; for example, to have an expecta-tion about the effects of predators on relative prey abundance and size structure, we must know something about predator preferences for different prey taxa or sizes.

Finally, we attempted to estimate roughly the magnitude of prey responses to predator manipulations. An increase or decrease by at least a factor of two (i.e.

Table 2 A classification of field experiments on predation from seven research journals[a], 1965–1984

Reference	Latitude[b]	System[c]	Predator taxa[d]	Predator trophic level[e]	Experiment type[f]	Response type[g]	Effect[h]	Large[i]	Unexpected[j]
Addicott 1974	TM	LEN	AR	CA1	SUF	SD TO RE	Yes	Yes	No
Allan 1982	TM	LOT	FI	CA2	RF	TO PO	Yes	Yes	Yes
Andrew & Choat 1982	TM	MAR	FI IN	HB CA1	RF RUF	PO SI	Yes	UK	Yes
Bärlocher 1980	TM	LOT	AR	OT	RE	SD	Yes	Yes	No
Benke 1978	TM	LEN	AR	CA1	AF	PO	Yes	No	Yes
Bertness 1984	TM	INT	MO	HB	RF	PO	Yes	Yes	Yes
Bishop & Daly 1984	TM	TER	MA	HB	RF	PO FT	Yes	Yes	No
Black 1976	TM	INT	MO	HB	RUF	OT	Yes	Yes	Yes
Bochert & Jain 1978	TM	TER	MA	SE	RF	FT	Yes	Yes	No
Carroll & Risch 1984	TR	TER	AR	SE	RF	FT	Yes	Yes	No
Cattaneo 1983	TM	LEN	AR MO IN	HB	AF	TO	Yes	Yes	No
Choat & Kingett 1982	TM	MAR	FI	CA1	RF	PO	Yes	No	Yes
Connell 1970	TM	INT	MO	CA1	RF AF	FT	Yes	Yes	No
Connell et al 1984	TR	TER	UK	HB SE	RF	FT	Yes	Yes	No
Cooper 1984	TM	INT	FI	CA2	RUF AUF	BE	Yes	Yes	No
Cowen 1983	TM	MAR	FI	CA1	RUF	PO SI	Yes	No	No
Crowder & Cooper 1982	TM	LEN	FI	CA2	SF	TO RE SI OT	Yes	Yes	No
Cubit 1984	TM	INT	MO	HB	RUF	TO	Yes	Yes	No
Cuker 1983	PL	LEN	MO	HB	SF	TO SI	Yes	Yes	No
Davidson & Barbour 1977	TM	TER	MA	HB	RF	FT	No	No	No
Dayton 1971	TM	INT	MO IN	CA1	RF	PO	Yes	Yes	Yes
Dayton 1975	TM	INT	IN	HB	RUF	SD TO	Yes	Yes	No
Dayton et al. 1974	PL	MAR	IN	CA1	SF	GR	Yes	Yes	No
Dethier & Duggins 1984	TM	INT	MO	HB	RUF	PO	Yes	Yes	Yes
Dodson 1974	TM	LEN	MO	CA1	SF	PO	Yes	Yes	Yes

Study	PL						Yes	UK	UK
Dodson & Eggers 1980	TM	LEN	BI	CA1	RF	SI	Yes	UK	UK
Drenner et al 1982	TM	LEN	FI	CA2	SUF	PO	Yes	Yes	No
Duggins 1980	TM	INT	IN	HB	RUF	SD TO PO	Yes	Yes	No
Duggins 1983	TM	MAR	IN	CA1	AUF	PO BE	Yes	Yes	No
East 1974	TM	TER	MA	OK	RF	SI	Yes	No	No
Eickwort 1977	TM	TER	AR	CA1	RF	FT	Yes	No	No
Flint & Goldman 1975	TM	LEN	AR	OK	SUF	PO	Yes	Yes	Yes
Fraser & Cerri 1982	TM	LOT	FI	CA1	SF	FT	Yes	No	No
Fulton 1984	TR	MAR	IN	CA1	SF	TO RE	Yes	Yes	No
Garrity & Levings 1981	TM	INT	MO	CA1	RUF	BE	Yes	Yes	No
Gashwiler 1967	TM	TER	MA BI	HB	RF	FT	Yes	Yes	No
Gilinsky 1984	TM	LEN	FI	CA2	SF	SD TO PO	Yes	Yes	Yes
Gradwohl & Greenberg 1982	TM	TER	BI	CA1	RF	TO PO SI	Yes	No	Yes
Hay et al 1983	TR	MAR	FI	HB	RF	TO	Yes	Yes	No
Heads & Lawton 1984	TM	TER	AR	CA1	RF	PO	Yes	Yes	Yes
Himmelman et al 1983	TM	MAR	IN	HB	RUF	SD PO	Yes	Yes	Yes
Horvitz & Schemske 1984	TR	TER	AR	HB	RUF	FT	Yes	Yes	No
Hunter & Russell-Hunter 1983	TM	TER	MO	HB	RF SF	SD TO	Yes	Yes	No
Hurd & Eisenberg 1984	TM	TER	AR	CA1	AUF	SD TO SI	Yes	Yes	Yes
Inouye 1981	TM	TER	MA	HB	RF	OT	Yes	UK	No
Inouye et al 1980	TM	TER	MA AR	SE	RF RUF	SD TO PO	Yes	Yes	Yes
Islam & Crawley 1983	TM	TER	AR	HB	SUF	FT	Yes	Yes	No
Jaksic & Fuentes 1980	TR	TER	MA	HB	RF	TR	Yes	Yes	Yes
Jara & Moreno 1984	TM	INT	MO	HB	RUF AUF	SD PO	Yes	Yes	Yes
Jupp & Spence 1977	TM	LEN	BI	HB	RF	PO	Yes	No	No
Kareiva 1982	TM	TER	AR	HB	RF	OT	Yes	Yes	No
Keller 1983	TR	MAR	FI IN	CA1	RF	OT	No	Yes	No
Keough 1984	TM	TER	FI MO IN	CA2	RF	PO	No	No	No
Kitting 1980	TM	INT	MO	HB	RUF	PO	Yes	No	No
Kneib & Stiven 1982	TM	MAR	FI	CA1	SF	PO	Yes	No	Yes
Koptur 1984	TR	TER	AR	CA1	RF	OT	Yes	Yes	No
Lamberti & Resh 1983	TM	LOT	AR	HB	RUF	TO	Yes	Yes	No

Table 2 A classification of field experiments on predation from seven research journals[a], 1965–1984

Reference	Latitude[b]	System[c]	Predator taxa[d]	Predator trophic level[e]	Experiment type[f]	Response type[g]	Effect[h]	Large[i]	Unexpected[j]
Lock 1972	TR	TER	MA	HB	RF	TO PO OT	Yes	Yes	Yes
Longhurst et al 1967	TM	MAR	AR	HB	SF	PO	Yes	Yes	No
Louda 1982a	TM	TER	AR	HB	RUF	FT	Yes	Yes	No
Louda 1982b	TM	TER	AR	HB	RUF	FT	Yes	Yes	No
Louda 1983	TM	TER	AR	HB	RUF	FT OT	Yes	Yes	Yes
Louda 1984	TM	TER	AR	HB	RUF	FT GR	Yes	Yes	No
Lubchenco 1980	TM	INT	MO	HB	RF	PO	Yes	Yes	No
Lubchenco 1983	TM	INT	MO	HB	RF	PO	Yes	Yes	Yes
Lubchenco & Cubit 1980	TM	INT	MO	HB	RF	PO	Yes	Yes	No
Lubchenco & Menge 1978	TM	INT	MO IN	HB CA1	RF SF	PO	Yes	Yes	Yes
Luecke & O'Brien 1983	PL	LEN	AR	CA1	SF	PO SI	Yes	Yes	Yes
Lynch 1979	TM	LEN	FI	CA2	SF	PO SI FT	Yes	Yes	Yes
Lynch & Shapiro 1981	TM	LEN	FI	CA2	SF	TO PO	Yes	Yes	Yes
MacKay 1982	TM	TER	AR	CA1	RUF	FR	Yes	Yes	No
May et al 1970	TM	INT	MO	HB	RUF	SD PO	Yes	Yes	No
McBrien 1983	TM	TER	AR	HB	RUF	PO	Yes	UK	Yes
McCauley & Briand 1979	TM	LEN	AR	HB	RF	SD	Yes	No	Yes
Menge 1976	TM	INT	MO	CA1	RF	PO	Yes	Yes	Yes
Menge 1982	TM	INT	MO	CA1	RUF	PO	Yes	Yes	No
Menge & Lubchenco 1981	TR	INT	FI	CA2	RF	PO	Yes	Yes	Yes
Mills 1983	TM	TER	MA AR	HB	RF	FT	Yes	UK	UK
Morin 1983	TM	LEN	HP	CA1	SUF	RE FT GR OT	Yes	Yes	Yes
Morin 1984a	TM	LEN	FI	CA2	RF	PO	Yes	Yes	Yes
Morin 1984b	TM	LEN	FI	CA2	RF	PO	Yes	Yes	Yes
Morin et al 1983	TM	LEN	HE	CA1	SUF	TO	Yes	UK	UK

Reference									
Murdoch et al 1984	TM	LEN	AR	CA1	RF AF	PO SI FT	Yes	Yes	No
Murphy 1984	PL	LEN	AR	HB	RF AF	TO OT	Yes	Yes	No
Neill 1981	TM	LEM	AR	CA1	RF AF	PO	Yes	Yes	No
Neill 1984	TM	LEN	AR	CA1	RF AF	PO	Yes	Yes	Yes
Nicotri 1977	TM	MAR	MO	HB	RF SF	SD TO PO	Yes	Yes	Yes
Oberndorfer et al 1984	TM	LOT	AR	CA1	SF	PO OT	Yes	Yes	No
O'Dowd & Gill 1984	TM	TER	MA	SE	RF	FT	No	No	No
Paine 1971	TM	INT	IN	CA1	RUF	PO	Yes	Yes	No
Paine 1974	TM	INT	IN	CA1	RUF	PO	Yes	Yes	Yes
Paine 1976	TM	INT	IN	CA1	RUF	SI	Yes	Yes	No
Paine 1984	TM	INT	MO	HB	RF	PO	Yes	Yes	Yes
Paine & Vardas 1969	TM	INT	IN	HB	RUF	SD	Yes	UK	Yes
Parker 1984	TM	TER	AR	HB	RF	GR OT	Yes	No	No
Peckarsky & Dodson 1980	TM	LOT	AR	CA1	SF	PO	Yes	Yes	No
Peterson 1979	TM	INT	AR	CA1	RF	PO	Yes	Yes	No
Peterson 1982	TM	MAR	MO UK	CA1	RF	PO FT	Yes	Yes	No
Petraitis 1983	TM	INT	MO	HB	SF	PO	Yes	Yes	Yes
Porter 1972	TM	LEN	AR	HB	RF	PO	Yes	Yes	Yes
Quammen 1984	TM	MAR	BI AR	CA1 CA2	RF	PO	Yes	Yes	No
Rausher 1981	TM	TER	UK	CA1	RF	TO	Yes	Yes	No
Rausher & Feeny 1980	TM	TER	BI	HB	SUF	PO	No	No	No
Reichman 1979	TM	TER	MA AR	SE	RUF	FT	Yes	Yes	No
Risch & Carroll 1977	TR	TER	AR	CA2	RF	TO	Yes	Yes	Yes
Robles 1982	TM	INT	AR MO	HB	RF	SD TO PO	Yes	Yes	Yes
Robles & Cubit 1981	TM	INT	AR	HB	RF SUF	PO	Yes	Yes	No
Room 1972	TR	TER	AR	CA1	RF	FR	No	No	No
Ross et al. 1970	TM	TER	MA	HB	RF	PO	Yes	Yes	No
Schiel 1982	TM	MAR	IN	HB	RUF	PO	Yes	Yes	No
Schmitt 1982	TM	MAR	AR MO IN	CA1	SUF	FT	Yes	Yes	No
Schroeter et al 1983	TM	MAR	IN	CA1	AUF	BE	Yes	No	UK
Sih 1982	TM	LOT	AR	CA2	RUF AUF	BE	Yes	Yes	No

Table 2 A classification of field experiments on predation from seven research journals[a], 1965–1984

Reference	Latitude[b]	System[c]	Predator taxa[d]	Predator trophic level[e]	Experiment type[f]	Response type[g]	Effect[h]	Large	Unexpected[i]
Skinner & Whittaker 1981	TM	TER	AR	CA1	RF	PO	Yes	Yes	No
Smith 1983	TM	LEN	AR	CA1	RUF AUF	PO	Yes	Yes	No
Smith & Cooper 1982	TM	LEN	AR	CA1	SF	PO FT	Yes	Yes	No
Smith & Odum 1981	TM	TER	BI	HB	RF	TO OT	Yes	Yes	No
Sousa 1979	TM	INT	AR MO	HB	RF SF	PO	Yes	Yes	Yes
Stephenson 1982	TM	TER	AR	CA1	RF	FT	Yes	No	No
Taylor & Littler 1982	TM	MAR	IN	HB CA1	RF	TO PO	Yes	Yes	Yes
Thorp & Bergey 1981	TM	LEN	HP FI	CA2	RF	SD TO PO	Yes	Yes	Yes
Thorp & Cothran 1984	TM	LEN	AR	CA1	SF	SD TO RE PO	Yes	No	Yes
Turner 1983	TM	INT	MO	HB	RF	PO	Yes	Yes	No
Underwood 1980	TM	INT	MO	HB	RF	PO	Yes	Yes	No
Underwood et al 1983	TM	INT	MO	CA1	RF	PO	No	No	No
Valiela 1969	TM	TER	AR	CA1	SF	FT	Yes	Yes	No
Van Blaricom 1982	TM	MAR	FI AR IN	CA1	RF SF	TO RE PO FT	Yes	Yes	No

Study	Latitude[b]	System[c]	Predator taxa[d]	Predator trophic level[e]	Experiment type[f]	Response type[g]	Effect[h]	Large[i]	Unexpected[j]
Vance 1979	TM	MAR	IN	HB	RUF	PO	Yes	Yes	Yes
Van Dolan 1978	TM	MAR	FI AR	CA1	RF	PO	Yes	No	Yes
Van Dyne 1967	TM	TER	MA	HB	RF	PO GR	Yes	Yes	Yes
Vimstein 1977	TM	MAR	FI AR	CA1	RF SF	SD TO DO	Yes	Yes	No
Vogel et al 1984	PL	TER	MA	HB	RF	TO PO	Yes	Yes	Yes
Walde & Davies 1984	TM	LOT	AR	CA1	RF SF	PO	Yes	Yes	Yes
Watzin 1983	TM	MAR	AR IN	UK	AF	TO PO	Yes	No	Yes
Wellington 1982	TR	MAR	FI	CA2	RF	FT GR	Yes	Yes	No
Werner et al 1983	TM	LEN	FI	CA2	SF	GR BE	Yes	No	Yes
Whittaker 1982	TM	TER	AR	HB	RUF	FT GR	Yes	Yes	No
Wilbur 1972	TM	LEN	HP	CA2	SF	FT GR	Yes	Yes	Yes
Wilbur et al 1983	TM	LEN	HP	CA1	SUF	PO	Yes	Yes	No

[a] The American Naturalist, Ecological Monographs, Ecology, Limnology and Oceanography, Journal of Animal Ecology, Journal of Ecology, Limnology and Oceanography, and Oecologia.
[b] Latitude: TE, temperate; TR, tropical; PL, polar.
[c] System: INT, marine intertidal; MAR, other marine; LOT, freshwater lotic; LEN, freshwater lentic; TER, terrestrial.
[d] Predator taxa: MA, mammals; BI, birds; HP, amphibians and reptiles; AR, arthropods; MO, molluscs; IN, other invertebrates.
[e] Predator trophic level: HB, herbivores; CA1, primary carnivores; CA2, secondary carnivores; OM, omnivores; SE, seed predators; OT, others; UK, unknown.
[f] Experiment type: RF, removal fenced; RUF, removal unfenced; SF, stocked fenced; SUF, stocked unfenced; AF, addition fenced; AUF, addition unfenced.
[g] Response type: SD, species diversity; TO, total prey abundance; RE, relative prey abundance; PO, population size; SI, size structure; FT, fitness; GR, growth rate; FR, feeding rate; BE, behavior; OT, other.
[h] Effect (Did the predator manipulation yield any significant effects?): Yes; No.
[i] Large (Did it yield any effects 2(?): Yes; No; UK, unknown.
[j] Unexpected (Did any prey benefit significantly at higher predator densities?): Yes; No; UK, unknown.

$+ > 100\%$ or $- > 50\%$) we called a large change, and inversely, an increase or decrease of less than a factor of two we called a small change.

Statistical analyses consisted primarily of G-tests (with the Williams correction—see 205a) on the numbers of (a) responses vs no responses; (b) large vs small responses; and (c) expected vs unexpected responses. These tests compare responses to predator manipulations following the classification schemes listed in Table 1. Tests were done on both a "by study" and "by comparison" basis. For each classification variable we decomposed the overall effects in a predetermined way designed to preserve orthogonality. The contrasts used are also shown in Table 1. The significance level for all tests is 0.05.

In some cases we observed cross-correlations that can make it difficult to determine whether a statistically significant trend reflects a causal relationship. For example, the marine intertidal system has a disproportionately large number of studies on herbivores and nonarthropod invertebrates. This system shows significantly larger predation effects than do other systems. However, this trend might not reflect anything special about the intertidal system; instead, it might be due to herbivores having larger effects than carnivores, or nonarthropod invertebrates having larger effects than other predator taxa. We did not attempt to tease apart the effects of cross-correlations between contingency tables in the statistical analysis; but where we can identify cross-correlations, we discuss their potential importance.

RESULTS AND DISCUSSION

Distribution of Effort

The number of papers on experimental manipulations of predators has increased in a roughly sigmoid fashion over the past 20 years. From 1967 to 1976 the mean number of studies per year was 2.4. This increased to 5.3 for 1977–1979, 10.5 for 1980–1981, and 24 in 1982. However, the numbers may be approaching a plateau with 25 in 1983 and 29 in 1984. About half of these papers, 69 out of 139, appeared in *Ecology*. *Oecologia* with 26 and *Ecological Monographs* with 19 were also well represented. Only 25 studies appeared in the other 4 journals.

The great majority of the field experimental studies on predation have been done in the temperate zone—120/139 studies or 86%. The overall effort (as based on the number of comparisons) is roughly evenly divided among five major systems (with a slight underrepresentation of lotic freshwater), and among three main predator taxonomic groupings: vertebrates, arthropods, and nonarthropod invertebrates. Also, about equal effort has been devoted to herbivore and primary carnivore manipulations, while only about half that amount has been focused on secondary carnivores. The numbers of comparisons and the percentage in some subcategories (e.g. system vs taxa, and

system vs predator-trophic level) are shown in Table 3. Some notable trends are
as follows. In the intertidal, a disproportionate number of comparisons involve
manipulations of herbivores relative to other predator trophic levels—
particularly the predator taxa, molluscs and echinoderms. In the terrestrial
environment, manipulations of arthropod herbivores are overrepresented. In
freshwater, most of the comparisons involve carnivorous vertebrates, usually
fish and amphibians. To some extent, these trends reflect the high relative
abundance (or biomass) of these predators in these systems. Besides the lack of
experimental work in nontemperate regions, perhaps the most glaring gaps are
the almost total lack of manipulations of herbivores in freshwater and of
nonarthropod invertebrates in freshwater and on land. To date, we have very
little experimental evidence on how zooplankton affect phytoplankton com-
munities or on how the numerous freshwater and land molluscs affect the
organisms on which they feed.

Table 4 shows the distribution of effort by response type. The apparent
paucity of studies examining the effects of predators on patterns of relative prey
abundance is misleading. In fact, these effects are usually recorded but not
explicitly analyzed. For example, many studies show that when predators are
removed, some prey increase and others decrease in abundance, or that some
prey populations increase more than do others. These changes are analyzed on a
species-by-species basis. Although relative abundances clearly change, no
statistical analyses are done to address this change specifically. In contrast, the
lack of studies on the details of individual prey responses to predators is real.
Surprisingly few experimental field studies have been published addressing the
effects of predators on prey behavior and prey feeding rates (but see 27, 44, 52,
169, 170, 201).

To summarize this section (a) Most published experimental studies on
predation have appeared in the last three years; many in the journal *Ecology*. (b)
Most of the work has been done in temperate regions. (c) Marine experiments
have been primarily on nonarthropod invertebrate herbivores; terrestrial work
has primarily been on arthropod herbivores; and freshwater work has con-
centrated on vertebrate carnivores. (d) Manipulations of herbivores have rarely
been done in freshwater; on land and in freshwater, few studies have looked at
the effects of nonarthropod invertebrates on their prey. (e) The effects of
predators on prey behavior and prey feeding rates have relatively rarely been
examined experimentally in the field.

Problems

A surprisingly high proportion of the studies in our survey had obvious prob-
lems with lack of replication (only one replicate) or lack of statistical analysis.
In several other instances, low replication in a highly variable system may have
caused a trend to be nonsignificant (184a); in some cases, prey were ten times

Table 3 The proportion comparisons by system, predator taxon, and predator trophic level (%)

System	Predator trophic level			Predator taxon		
	Herbivore[b]	Primary carnivore	Secondary carnivore	Vertebrate	Arthropod	Nonarthropod
Intertidal (289)[a]	59.9	34.6	5.5	4.8	15.6	79.6
Other marine (343)	42.0	53.1	5.0	30.5	9.3	60.2
Lotic (181)	2.8	23.2	74.0	68.5	31.0	0.5
Lentic (232)	6.9	70.3	22.8	62.3	36.5	1.2
Terrestrial (267)	65.2	16.9	18.0	30.2	69.8	0.0
Grand mean (1312)	39.0	40.5	20.4	35.9	31.7	32.4

[a]Numbers in parentheses are number of comparisons.
[b]*Broken vertical lines* indicate contrasts that were made; *asterisks* indicate a significant difference (alpha = 0.05). For example, the lines for lotic vs lentic comparisons indicate significantly different proportions across trophic levels but not across predator taxa.

Table 4   Distribution of predation and competition studies by response type

Classification	Predation	Competition[a]
Species diversity	19	0
Total prey abundance	30	12
Relative prey abundance	4	0
Population size	79	95
Size structure	11	2
Individual fitness	30	55
Prey growth rate	9	41
Prey feeding rate	1	6
Prey behavior	6	30

[a]From Schoener (167).

more abundant in the absence of predators, but this difference was not signifi-
cant. Although such studies may suffer from insufficient replication, we did not
classify them as poorly replicated if they contained more than one replicate.
Similarly, we did not judge the quality of the statistical analyses performed; we
merely recorded cases where no statistics were done. To be fair, in some
instances, the effect of the predator manipulation was so striking that statistical
analyses would have seemed superfluous. For example, several studies did not
include statistical analyses when a complete switch from 100% of one prey
species to 100% of another prey species occurred following the removal of
predators.

Using the above guidelines of 139 studies, 40% showed low (1 or 2 repli-
cates) or pseudoreplication; 35% included no statistical analyses of predation
effects; and 53% had one or both of these problems. The trend, however, is
toward improved designs and analyses. Before 1982, 45/61 or 74% of the
studies had one problem or the other. For 1982–1984, this proportion dropped
to 29/78, or 37%. This difference is statistically significant ($G = 18.63, p <$
.01). The problem of low replication can be logistically difficult to solve, as, for
example, in studies of whole lake dynamics. The lack of statistical tests is less
defensible. The seven journals surveyed appear to have greatly reduced their
acceptance of papers without such analyses over the last three years. [The
proportion of predation experiments without statistical tests was 35/61 (57%)
before 1982, and 14/79 (18%) for 1982–1984.]

Summarizing this section, we find a surprisingly high proportion of the
experimental studies on predation had problems with low replication or lack of
statistical analysis. This problem has been greatly reduced in the last three
years.

Analyses by Study

Virtually every report of experimental field studies on predation showed some
significant effects (132/139 or 95.0%). Large responses by prey were very

common; 112/131 studies or 85.5% had at least one comparison where prey showed a large response to predator manipulations (eight studies did not have information on the magnitude of effects). A sizable fraction (54/135 or 40.0%) showed at least one unexpected effect.

Table 5 shows the percentage of studies that yielded any significant effects, any large significant effects, and any unexpected significant effects, depending on latitude, system, predator taxon or trophic level, response type, and experiment type. In some instances where sample sizes were very small, classifications were either dropped (e.g. only three trophic levels were analyzed) or were combined (e.g. community effects include species diversity, total prey abundance, and relative prey abundance; individual effects include effects on fitness, feeding rate, growth rate, and behavior).

The outstanding feature of Table 5 is the paucity of significant differences among categories. Except for contrasts involving prey response type, only 1 of 48 G-tests was statistically significant. Manipulations in aquatic environments showed significant effects more often than did experiments on land. Since many tests were performed and only this one test was significant at the 0.05 level, this single "significant" effect is probably not biologically meaningful.

For response type, community-level responses were generally not as common and not as large as at the population- and individual-levels. However, this is probably an artifact of the analysis. A typical community study might examine the effects of predators on prey species diversity, prey total abundance, and the population size of 10 prey species. Our analysis would then show 2 community comparisons and 10 population size comparisons. In fact, the average number of comparisons per study was: 2.42 for community level effects, 5.39 for individual effects, and 11.21 for population size effects. Although in studies with more comparisons a lower proportion was significant ($r^2 = 0.11$, $p < 0.001$; proportions were arcsine transformed), studies with more comparisons were more likely to have at least one comparison with either some effect or a large effect.

The negative correlation between the number of comparisons per study and the proportion showing significant effects might reflect an interesting bias. Investigators examining only one or few species may tend to choose species likely to show effects. In contrast, studies examining many prey species may yield a more unbiased (and lower) estimate of the likelihood that a randomly chosen prey species will respond to predator manipulations (see 24 for a similar analysis of competition studies). For predation experiments this bias appears to be weak; the number of comparisons explains only 11% of the variance in the proportion of studies yielding significant effects.

Summarizing this section (*a*) Almost all of the studies showed some significant effects, and the great majority showed some large effects. (*b*) When analyzed by study, predation effects appeared consistent regardless of latitudinal zone, system, predator trophic level, predator taxon, or experiment type.

Table 5 The proportion of studies that yielded any significant effects, large significant effects, and unexpected significant effects for various categories of studies (%)

Classification	Effect[a,e]	Large[b]	Unexpected[c]
Latitude			
Temperate	95.0 (120)[d]	84.1 (113)	41.4 (116)
Tropical	100.0 (13)	91.7 (12)	30.8 (13)
Polar	100.0 (6)	100.0 (6)	33.3 (6)
System			
Intertidal	94.4 (36)	91.1 (34)	40.0 (35)
Other marine	100.0 (25)	75.0 (24)	32.0 (25)
Lotic	100.0 (17)	70.6 (17)	47.1 (17)
Lentic	100.0 (22)	90.5 (21)	47.6 (21)
Terrestrial	89.7 (39)	75.7 (37)	22.2 (36)
Predator type			
Vertebrate	91.3 (46)	70.0 (40)	42.9 (42)
Arthropod	98.0 (49)	79.2 (48)	30.6 (49)
Other invertebrate	94.2 (52)	88.2 (51)	37.3 (51)
Predator trophic level			
Herbivore	94.9 (59)	86.8 (53)	38.6 (57)
Primary carnivore	96.4 (56)	74.1 (54)	31.5 (54)
Secondary carnivore	100.0 (16)	93.3 (15)	50.0 (16)
Response type			
Community	80.0 (60)	60.9 (46)	19.1 (47)
Population	97.4 (76)	84.9 (73)	50.0 (76)
Individual	93.5 (46)	68.2 (44)	13.6 (44)

[a] Studies with any significant effects as a percentage of all studies.
[b] Studies with large significant effects as a percentage of all studies with significant effects.
[c] Studies with unexpected significant effects as a percentage of all studies with significant effects.
[d] Numbers in parentheses are the number of total studies.
[e] *Broken vertical lines* indicate contrasts that were made; *asterisks* indicate comparisons that are significantly different.

Analyses by Comparison

The previous section had the perhaps uninteresting theme that the intensity of predation is the same regardless of where you are, what you study, or how you do your studies. This conclusion, however, does not hold when analyses are done by comparison rather than by study. The important differences between these analyses are that (*a*) tests using all comparisons have much larger sample sizes; and (*b*) tests using all comparisons weight the studies in proportion to their numbers of comparisons. We feel that the following analyses using all comparisons provide a better test of various ideas concerning the relative importance of predation under different circumstances.

FREQUENCY AND MAGNITUDE OF EFFECTS   Table 6 shows the frequency of significant effects and of large significant effects depending on the latitude,

Table 6   The proportion of comparisons that yielded significant effects and large significant effects (%)

Classification	Effect[a]	Large[b]
Latitude		
Temperate	59.3 (1241)[c,d]	71.9 (658)
Tropical	66.2 (139)	77.3 (44)
Polar	56.3 (32)	66.7 (15)
System		
Intertidal	66.1 (289)	79.1 (187)
Other marine	48.6 (354)	80.1 (146)
Lotic	54.6 (183)	74.0 (73)
Lentic	70.5 (244)	66.2 (133)
Terrestrial	55.8 (294)	69.6 (158)
Predator type		
Vertebrate	58.5 (482)	59.9 (227)
Arthropod	57.2 (425)	69.5 (226)
Other invertebrate	60.9 (435)	84.3 (255)
Predator trophic level		
Herbivore	65.4 (512)	80.1 (327)
Primary carnivore	57.5 (532)	64.0 (261)
Secondary carnivore	47.4 (268)	73.3 (101)
Response type		
Population size	52.6 (852)	70.5 (308)
Community	70.3 (145)	66.3 (83)
Individual	64.5 (248)	69.7 (155)
Grand mean	59.9 (1412)	72.1 (717)

[a]Comparisons with any significant effect as a percentage of all comparisons.
[b]Comparisons with any large effect as a percentage of those with significant effects.
[c]Numbers in parentheses are the total number of comparisons.
[d]*Broken vertical lines* indicate contrasts that were made; *asterisks* indicate comparisons that are significantly different.

system, predator taxa, predator trophic level, response type, and experiment type involved.

By latitude   One of the classic unresolved issues in ecology is the explanation of latitudinal trends in species diversity (e.g. 87, 143, 144). One popular explanation for high diversity in the tropics stipulates that predation generally increases species diversity and that predation is more intense in the tropics (e.g. 23, 74, 133). However, few studies have specifically attempted to compare the relative intensity of predation in temperate versus tropical regions (but see 9). Our survey indicates a slight trend towards both more frequent and stronger effects of predation in tropical latitudes; however, this trend was not statistically significant (Table 6). The problem may lie in the paucity of experimental studies on predation in the tropics. Although the existing data set does not convincingly support the popular notion that predation is stronger in the tropics, this issue requires more data before a strong conclusion can be drawn.

By system   The role of predation has been heavily emphasized in marine systems, particularly in the rocky intertidal (e.g. 22, 98, 100, 117, 133, 134, 135, 137), and in freshwater, particularly in lakes (e.g. 14, 58, 82, 207). In contrast, the importance of predation has not been emphasized as often in flowing water systems or on land. Is predation really less important in lotic and terrestrial systems, or have lotic and terrestrial ecologists simply ignored the evidence at hand?

Predation may indeed be somewhat more important in rocky intertidal and lentic systems than elsewhere (Table 6). Predator manipulations have effects more frequently in both the rocky intertidal system and in lakes than in other systems. In addition, marine systems in general show larger effects of predator manipulations than do other systems. The marine intertidal system appears to stand out as showing stronger effects of predation than any other system. Notice, however, that the difference between the various systems in frequency and magnitude of effects is not striking. Thus our survey provides a hint (but not a strong suggestion) that predation paradigms emerging from the intertidal or from lakes may not hold as well elsewhere because predation is not as strong elsewhere.

Why does predation seem to be more important in the intertidal and in lakes than it is elsewhere? Our survey did not gather the information required to address this question rigorously. Although cross-correlations could be responsible, we suspect that the answer lies in the lower structural heterogeneity typically found in these habitats. Compared to other systems, the openwater habitat of lakes and the rocky surfaces of the intertidal system are generally thought to be structurally simple. Both theory and data suggest that structural complexity reduces the effectiveness of predation. In a later section, we discuss

some experimental field studies that directly address the effects of structure on predation.

By predator trophic level   In one of the most widely cited ecological papers of the 1960s, Hairston, Smith & Slobodkin (57) suggested that (*a*) plants are not herbivore-limited, but that they compete; (*b*) herbivores are not food-limited but are limited by carnivores; and (*c*) carnivores, in turn, compete for limited animal food. After some serious debate concerning the logic behind these generalities (46, 124, 174), researchers let the ideas fade from the forefront until a recent revival in the competition reviews of Schoener (167) and Connell (24; see also 56a, 168a). In the current context, the Hairston, Smith & Slobodkin (hereafter termed HSS) predictions are that (*a*) herbivore manipulations should have relatively little effect on plant communities; (*b*) primary carnivore manipulations should have a strong effect on herbivores; and (*c*) secondary carnivore manipulations should have a weak effect on primary carnivores. We emphasize that the HSS hypothesis was originally designed to fit terrestrial environments ("the world is green" applies more obviously on land than underwater). It may be somewhat unfair (though instructive) to test it with a data set dominated by data from aquatic systems (56a).

In a similar vein, Menge & Sutherland (117; hereafter MS) predicted that predation should be more important on lower trophic levels, i.e. that the effects of experimental manipulations on prey communities should decrease as we go from herbivores to primary carnivores to secondary carnivores. The two sets of hypotheses make opposing predictions concerning the relative effects of herbivores and primary carnivores. The ranking of their effects on prey should be, according to HSS: herbivore < primary carnivore; according to MS, herbivore > primary carnivore. Chance, of course, would predict no overall difference between the effects of manipulations of herbivore vs primary carnivore.

Our survey provides strong support for the predictions of Menge & Sutherland (117). The ranking for the frequency of significant effects is herbivore > primary carnivore > secondary carnivore. All three are significantly different from one another. For the magnitude of effects, the ranking is herbivore > primary carnivore = secondary carnivore. The combined effect strongly suggests that herbivores have stronger effects on plant communities than carnivores have on animal communities.

Interestingly, a breakdown of trophic level analyses by system shows that the trend predicted by MS appears to hold in all five systems (Table 7). Conversely, the HSS prediction that herbivores should have a weaker effect than primary carnivores is not upheld for any system. But since freshwater ecologists have manipulated herbivores only rarely, the crucial test of MS versus HSS predictions could not be done. Nonetheless, the overall consistent tendency for lower trophic levels to have larger effects on their prey than do higher levels is in striking agreement with Menge & Sutherland (117).

Table 7 The proportion of studies showing any significant effects and large significant effects as a function of predator trophic level and system (%)

System	Effect			Large		
	Herbivore	Primary carnivore	Secondary carnivore	Herbivore	Primary carnivore	Secondary carnivore
Intertidal	67.7 >[a]	57.8[b]		84.2 >	70.1[b]	
	(173)[c]	(116)		(120)	(67)	
Other marine	59.0 >	40.7[b]		95.1	68.4[b]	
	(144)	(199)		(82)	(57)	
Lotic		66.7 >	49.3		72.7	75.0
		(42)	(134)		(22)	(95)
Lentic		73.0	64.2		61.3	55.2
		(163)	(53)		(106)	(29)
Terrestrial	63.2 >	53.3 >	28.6	74.1	61.1	
	(174)	(45)	(49)	(112)	(36)	

[a]Results of G-tests; > indicates the contrasts are significantly different.
[b]All carnivores pooled.
[c]Numbers in parentheses are sample sizes.

By prey and predator taxa   Several authors have suggested that predators should have a stronger effect on prey of smaller size (e.g. 22, 24, 167). Connell (24) and Schoener (167) tested the competition corollary of this prediction by comparing vertebrates and invertebrates. Unfortunately, we cannot perform an analogous comparison because virtually no studies have manipulated predators of vertebrate prey.

Although we did not analyze the effects of prey taxa, we did look at patterns relative to predator taxa. Predator taxa did not significantly influence the frequency of predation effects. However, nonarthropod invertebrates had larger effects than did arthropods or vertebrates. To our knowledge this had not been previously predicted or noticed. Unfortunately, this trend is at least partially explained by a cross-correlation with system type and predator trophic level. Of the comparisons involving manipulations of nonarthropod invertebrate predators, 99% were performed in marine systems. These are primarily experiments involving molluscan (e.g. limpets, chitons, snails) and echinoderm (e.g. sea urchins) herbivores, although several classic carnivore experiments (e.g. Paine's studies of *Pisaster*) are also included. We suspect that nonarthropod invertebrates are not unusually effective predators but that they appear so because they are often herbivores (recall that herbivores are more effective than carnivores in every system) in systems with relatively few prey refuges. Further inferences on this question will require more experiments on nonarthropod invertebrates outside the marine environment and appropriate statistical analysis for teasing apart correlated variables in multiple contingency tables.

By response type   The above analyses pooled data examining a number of very different prey characteristics ranging from community traits, such as species diversity, to population size or individual fitness parameters. Only for population size were there sufficient data to allow analyses using exclusively that response type. Qualitative trends using only the data on prey population size do not differ substantially from those discussed above.

Differences among response types in the frequency and magnitude of predation effects are shown in Table 6. Studies addressing population size do not yield significant effects as often as do studies addressing community or individual prey responses. Community and population responses may differ for two reasons: (*a*) a community response can result when only one or a few of the prey species respond strongly; or (*b*) consistent but nonsignificant population-level responses can yield significance in a more powerful test at the community level. That populations do not appear to respond as frequently as do the individuals within them probably reflects a bias among investigators. When monitoring population sizes, ecologists often include all populations captured by a given sampling technique without regard to whether the species appear to be affected by predators. This is a relatively unbiased means of choosing the groups to be examined. However, when studying individual prey responses to predators, practical limitations usually dictate that the investigator concentrate on one or a few prey species. If these species were chosen at random, the frequency of response for population and individual prey parameters should be similar; that is, changes in prey population size are usually associated with some change in individual fitness parameters, and vice versa. That individual-level studies show a higher frequency of response suggests that investigators choose (consciously or not) to do detailed studies on prey that appear to be affected by predators. This bias is not surprising and not unwise but it does perhaps yield an inflated impression of the importance of predation.

By experiment type   This analysis addresses some potentially important methodological questions. Is the apparent importance of predation affected by whether the manipulation involves predator removal or addition, or fenced or unfenced conditions?

Our a priori guess was that removal experiments would yield smaller effects than addition or stocking experiments. For example, if natural predator densities are low, then predator removals might have no effect. However, predator additions or stocking at higher than natural density might still show an effect. We further reasoned that fenced enclosures of predators would result in particularly strong predator effects. Predator enclosures often use unnaturally high predator densities (at times, enclosures are small enough that even one predator

is an unnaturally high density) and also prevent predator dispersal. The latter may force predators to feed in areas from which they would normally disperse.

Neither of these notions was upheld (Table 8). Although removal experiments showed a lower frequency of effects (as predicted), they also resulted in a higher frequency of large responses. These offsetting trends suggest that the overall importance of predation does not differ substantially between addition and removal experiments. The comparisons of fenced versus unfenced experiments also showed significant trends but in a direction opposite to that predicted. Both enclosures and exclosures of predators yielded weaker predation effects than did experiments with no fencing. We know of no obvious explanation for this result.

To summarize: (a) Predation effects did not differ among latitudinal zones. (b) Predation appears to be more important in the marine intertidal and in lakes than in other systems. (c) Herbivores have greater effects than do carnivores. This concurs with the predictions of Menge & Sutherland (117) but not with those of Hairston, Smith & Slobodkin (57). (d) Nonarthropod invertebrate predators have larger effects on their prey communities than do other taxa, but this might be due to cross-correlations with the marine system and with herbivory. (e) The overall importance of predation appears to be lower when fencing is used (though we can offer no plausible explanation for this).

UNEXPECTED EFFECTS   Some workers have defined predation as a "negative-positive" interaction, because predators are expected to have a negative effect

Table 8   The proportion of comparisons yielding significant effects and large significant effects by experiment type (%)

Type of experiment	Effect	Large
All addition-stocked	63.4 (470)[a,b]	65.9 (270)
All removal	56.0 (895)	75.8 (447)
All fenced	53.6 (995)	70.0 (466)
All unfenced	71.6 (370)	76.1 (251)
Addition-stocked		
Fenced	58.4 (334)	69.5 (174)
Unfenced	75.7 (136)	59.4 (96)
Removal		
Fenced	51.3 (661)	70.2 (292)
Unfenced	69.2 (234)	86.5 (155)

[a]Numbers are total number of comparisons.
[b]*Broken vertical bars* indicate contrasts that were made; *asterisks* indicate comparisons that were significant.

on prey and prey are expected to have a positive effect on predators (e.g. 76, 159). For the present analysis, an unexpected effect occurs when predators have a positive effect on prey. This includes cases where predators cause an increase in prey feeding or growth rate, survivorship, or reproduction that increases the population size of one prey species or of all prey species summed, or increases the diversity of prey.

Unexpected effects probably occur when positive effects through indirect pathways override the direct negative effect of mortality caused by predation. Two positive indirect effects of predators have often been mentioned. A keystone predator effect (133) takes place when a predator reduces the density of the competitively dominant prey to the point that poor competitors are released from the negative effects of competition. Although this concept is usually applied to cases where predators increase prey species diversity, we will use it to include any positive effect on prey via release from competition. A three-trophic-level effect occurs when a top predator consumes a middle-level predator and thus releases the prey at the bottom trophic level from intermediate-level predation. For example, a vertebrate predator might consume large numbers of invertebrate predators to the point that invertebrate prey enjoy a positive effect.

These two mechanisms clearly have similarities. In both cases, predators have a negative effect on a prey species A that has negative effects on another prey species B. The product of these two negative effects is an indirect positive effect. The indirect positive effect is more likely to outweigh the direct negative effect of predation if (a) predators prefer species A (e.g. the competitive dominant) over species B (e.g. 39, 98, 133, 134, 135, 190); (b)predation intensity is not too strong (e.g. 1, 47, 59, 98, 138); and (c) species A (the competitive dominant or the middle-level predator) has potentially strong negative effects on species B in the absence of the predator (1, 141).

In our survey 40% (54/135) of all studies yielded some unexpected effects and 24.7% (190/770) of all relevant comparisons showed unexpected effects. Unexpected effects did not tend to be large (by the factor-of-two criterion) as often as did expected effects—76.0% (417/549) of expected compared to 59.5% (100/168) of unexpected effects were large, $G = 16.40$, $p < 0.01$. Nonetheless, unexpected and presumably indirect predator-mediated effects appear to be common. The frequency of unexpected effects varied with response type, latitude, system, predator trophic level, and predator taxa (see Table 9). Although some theory concerning indirect effects has been developed (e.g. 65, 81, 82, 89, 90, 191), most of the patterns we observed are trends in search of an explanation.

By response type   Total prey abundance stands out as having fewer unexpected effects than do other response types. This seems reasonable. Whereas

Table 9 The proportion of comparisons yielding unexpected effects (%)

Classification	Unexpected	Classification	Unexpected
Latitude		Predator trophic level	
Temperate	25.5 (710)[a,b]	Herbivore	17.2 (331)
Tropical	11.4 (44)	Primary carnivore	31.3 (278)
Polar	25.0 (16)	Secondary carnivore	20.7 (179)
System		Response type	
Intertidal	24.7 (190)	Species diversity	29.7 (37)
Other marine	9.9 (171)	Total prey abundance	3.7 (448)
Lotic	40.9 (93)	Population size	24.6 (448)
Lentic	39.7 (156)	Individual parameters	20.8 (159)
Terrestrial	16.9 (160)		
Predator taxon			
Vertebrate	39.4 (269)		
Arthropod	13.5 (230)		
Other invertebrate	20.2 (262)		

[a]Numbers in parentheses are sample sizes.
[b]Broken vertical lines indicate contrasts that were made; asterisks indicate comparisons that are significant.

predators can indirectly benefit some prey by consuming their enemies, it is not clear what circumstances would result in predators having an indirect positive effect on the total abundance of prey. Only one study showed such a positive effect on total prey abundance (55), and this only occurred during the fall and winter when bluegill predation on macroinvertebrate prey was relatively low. The mechanism might have been the three-trophic-level effect, a case in which bluegills consumed enough invertebrate predators to allow a large increase in invertebrate prey. In the spring and summer when bluegills feed more actively, they either have no effect on their prey or they reduce total prey abundance (29, 55).

Most of the ideas on indirect effects revolve around the keystone predator effect on species diversity. The usual notion is that if predators prefer the competitive dominant, then the relationship between diversity of prey species and predation intensity should be "hump-shaped"; that is, at low intensities increasing predation prevents competitive exclusion and allows more species to coexist, but at high intensities, predation itself drives prey species extinct. This idea was primarily developed from studies in the marine intertidal, and the suggestion has even been made that the effect only applies to systems with immobile, space-limited organisms (150, 168). Many cases of keystone effects on diversity indeed come from marine intertidal studies (e.g. 98, 133, 134, 135, 138), or studies of herbivory on terrestrial plant communities (e.g. 59, 71). However, in our survey, three cases of keystone predation clearly did not fit the

immobile, space-limited description. Bluegill sunfish can have positive effects
on the diversity of macroinvertebrate prey (55); Thorp & Cothran (184) re-
ported a "hump-shaped" relationship between the density of an invertebrate
predator (odonates) and macroinvertebrate prey diversity; and zooplankton can
have a positive effect on phytoplankton diversity (112).

Other trends   Because we have few clear explanations for the other trends in
the frequency of unexpected effects, we simply provide a brief list:

1. Unexpected effects are far more common in temperate than tropical regions.
   This is probably a premature assessment since so few experimental studies
   have been done in the tropics.
2. Unexpected effects are far more common in freshwater and intertidal sys-
   tems than elsewhere. These are also the systems where indirect effects have
   been noticed and emphasized.
3. Concerning predator trophic level, the ranking of the frequency of un-
   expected effects is primary carnivore > secondary carnivore > herbivore.
   That herbivores have fewer unexpected effects on their prey may reflect less
   clear-cut competitive hierarchies among plants or that herbivores can only
   have positive effects on prey through the keystone effect and not through the
   three-trophic-level effect.
4. Vertebrates have unexpected effects more frequently than do invertebrates.
   This may occur because vertebrates are more often at trophic levels
   high enough to be able to have both keystone and three-trophic-level
   effects.
5. The above trends may be confounded by cross-correlations. Recall that
   manipulations of vertebrates and carnivores are overrepresented in freshwa-
   ter studies. Thus only one causal mechanism may be necessary to explain
   the fact that all three of these categories have frequent indirect effects.

MEDIATING FACTORS   A wealth of theoretical literature exists on factors that
should mediate the effects of predators on prey (see 60, 125, 182 for reviews).
Here, we briefly review some field experiments that bear on two of these
factors: structural heterogeneity and the severity of the environment.

Structural heterogeneity   Structural heterogeneity can, in theory, affect pred-
ator-prey interactions in many different ways. This literature is outside the
scope of this review. We do, however, note two widely discussed mechanisms.
First, heterogeneity can provide spatial refuges, i.e. places where predation risk
is reduced. Although the effect of refuges on predator-prey coexistence can
vary depending on details of the patterns of refuge use (e.g. 113, 125, 160,

171), refuges by definition reduce predator efficiency (at least locally) and should generally reduce the overall effect of predators on prey.

Even in the absence of actual spatial refuges, structural heterogeneity can influence the predator-prey interaction by creating transient refuges. Different mechanisms have been suggested, but the basic idea is that in a structured environment prey can find momentary refuge in patches where predators are temporarily rare or absent (e.g. 30, 50, 67, 125, 145).

Our survey includes a number of studies that address the influence of spatial structure or heterogeneity on prey responses to predators. Two similar studies directly manipulated structure. Both (29, 55) examined the influence of structure (real or artificial macrophytes) on the effects of bluegill sunfish on macroinvertebrate prey. In both studies, prey biomass increased with increasing levels of structure. Gilinsky (55) also documented an increase in species richness in more highly structured environments. The mechanism was probably that structure reduced predator foraging rate. Laboratory studies have shown that fish forage less efficiently in structurally complex environments (e.g. 26, 162, 197). Interestingly, Crowder & Cooper (29) showed that bluegill growth rate was highest at intermediate rather than low levels of structure. Presumably the increased prey density at intermediate levels of structure more than compensated for the decrease in feeding efficiency.

Three other studies that did not experimentally manipulate refuges nonetheless showed that refuges enhance prey persistence. Quammen (149) investigated the effects of fish and shorebirds on mudflat invertebrates. She found that because sand interfered with shorebird feeding, shorebirds did not affect total prey abundance at sites with high sand concentration. Menge & Lubchenco (116) and Lubchenco (100) observed that many sessile organisms in the rocky intertidal system only persisted in crevices. A more complete review of field studies of refuges can be found in McNair (113).

Several experimental studies showed that prey increased their use of refuges in the presence of predators (27, 49, 170, 201). Although none of these studies directly compared predation rates in the presence and absence of refuges, refuges probably enhanced the coexistence of predators and prey (see also 171).

In summary, we can say that although the existing theoretical literature addresses numerous ways in which spatial structure and heterogeneity can affect predator-prey interactions, field studies to date have primarily addressed the simplest mechanism: that spatial refuges are actively used by prey and that these refuges enhance prey persistence by reducing predator efficiency. In addition, although most of the theory addresses the stability of the interaction, virtually no field studies include analyses at this level.

Environmental stress   It has often been suggested that the importance of predation decreases with increasing environmental stress (e.g. 22, 63, 117,

204). This generalization assumes that stress reduces average predation rates per prey more than it reduces average growth rates of the prey population. If stress inhibits prey growth more than it inhibits predation, then predation should actually be more important in stressful environments.

Our survey yielded some studies that showed a negative relationship between stress and predator importance (55, 94, 114, 116, 176) and other studies in which the relationship was positive (31, 80, 96, 186). In some cases, the type of stress studied involved relatively abrupt disturbances, such as storms and habitat destruction (114, 176); in other cases the stress was relatively continuous, such as extreme temperatures or moisture levels (55, 94, 96, 186). Some studies compared different sites (80, 94, 96, 114, 116, 176), while others compared different seasons at the same site (31, 55).

Despite the low sample size and broad range of study situations, we noticed two patterns that may prove general. In rocky intertidal studies of invertebrate predators, wave shock decreases (101, 114, 116), whereas desiccation stress increases, the importance of predation (31, 101, 186). Apparently wave shock affects motile predators more than the generally sessile prey, whereas desiccation has a greater effect on prey than on predators. (In these examples, prey were often plants that are relatively incapable of behaviorally regulating their exposure to desiccation.)

In a given environment, vertebrate predators may be less affected by stress than are invertebrate predators. In the intertidal system, as mentioned above, wave shock decreases the importance of invertebrate predation, but it may increase the importance of vertebrate predation (80). However, Keller (80) emphasized that this effect is not consistent and may even result from a caging artifact. More interestingly, Louda (94, 96) suggested that for two congeneric plants in the same general locations, insect predation decreased whereas vertebrate predation increased in importance in more stressful environments.

In conclusion, environmental stress can either increase or decrease the importance of predation. The outcome depends on the relative effects of stress on predation rates and on prey growth rate. To a large extent this depends on the efficacy of each group's adaptations to the particular type of stress. Both a larger survey of comparative data and some experimental manipulations of stress should help to identify general patterns and contribute to theoretical development on this question.

PREDATION VERSUS COMPETITION

Although predators usually have important effects, the key controversy concerns the relative importance of predation and competition, rather than the importance of predation per se. We approach this issue from two directions. First, we statistically compare the frequency and magnitude of effects in surveys of predation and competition experiments. These surveys, however,

include different techniques, different locations, different systems, etc. Our second approach is to review 17 studies that have examined both predation and competition via experiments. We complete this section with some suggestions on protocols for evaluating the relative effects of these two factors.

A Statistical Survey

Both predation and competition have significant effects on prey individuals, populations, and communities in the great majority of the studies examined: predation: 95.6% (this study); competition: 90.0% (167). To do more detailed analyses, we reevaluated a subsample of the studies of competition. We did this both because our methods differed somewhat from those of Connell (24) and Schoener (167), and in particular because they did not attempt to evaluate the relative magnitude of the effects. We took the 72 studies cited by Connell (24) and reanalyzed them using the methods described earlier (simply replacing data for "predator" with "competitor removed").

Table 4 shows the distribution of response types addressed by studies of predation and competition. It is interesting that although many studies purport to examine the effects of competition on prey communities, only 14 of the 164 studies cited by Schoener (167) actually looked for the effects of competitor manipulations on a community parameter. In contrast, of 139 predation experiments, 19 address effects on species diversity and 30 on total prey abundance. The other end of the scale is also interesting. Competition studies address effects on individual-level parameters (growth, fitness, feeding rate, behavior) far more often than do predation studies. This may purely reflect a difference in investigator viewpoints or it may be a hint that predator manipulations have more far-reaching effects on their communities. The latter idea, of course, cannot currently be tested because competition studies have rarely addressed community parameters.

Using our 1412 predation comparisons and 594 competition comparisons drawn from studies in 24, we evaluated the relative frequency and magnitude of effects caused by predator and competitor manipulations. Table 10 shows that predators have both more frequent and stronger effects than do competitors. This is almost entirely explained by the fact that this survey suggests that herbivory is more important than competition for terrestrial plants. Only two other trends show predation to be more important than competition: (a) in the intertidal system, predators have larger (but not more frequent) effects than do competitors; and (b) in lakes, predators have more frequent (but not larger) effects than do competitors.

Experimental Studies of Both Predation and Competition

Though many of the investigations reviewed considered both predation and competition, only 17 of the 139 experimental analyses of predation incorporated density manipulations of both predators and potentially competing

Table 10 Contrast of predation versus competition experiments for the proportion of comparisons yielding any significant effects, large significant effects, or unexpected significant effects (%)

Grouping	Effect			Large			Unexpected		
	Predator		Competition	Predator		Competition	Predator		Competition
All comparisons	59.9 (1412)[b]	>[c]	38.4 (594)	72.1 (717)	>	42.1 (178)	24.7 (770)	>	26.2 (225)
Organism[a]									
Plants	65.4	>	32.8	80.1	>	23.7	17.2	<	31.9
Herbivores	57.5		49.3	64.0	<	81.0	31.3		21.4
Carnivores	47.4		42.9	73.3		56.3	20.7		17.9
System									
Intertidal	66.1		60.8	79.1		45.9	24.7		15.6
Other marine	48.6		55.0	80.1		94.7	9.9		0.0
Lentic	70.5	>	48.7	66.2		76.2	39.1	>	21.6
Terrestrial	55.8	>	30.4	69.6	>	23.8	16.9	<	36.4

[a]Refers either to the type of prey studied or the type of competitor manipulated.
[b]Numbers in parentheses are sample sizes.
[c]< or > indicate significant differences at the 0.05 level.

prey within the same study (34, 35, 40, 71, 75, 80, 99, 100, 103, 114, 129, 134, 141a, 175, 178, 203, 205—see Tables 2 and 10). Possible reasons for the rarity of such studies include their difficulty of execution and perhaps the fact that the stridency of the competition vs predation controversy has only recently become conspicuous in the literature. In the remainder of this section, we characterize the few competition-predation studies that have been carried out, briefly summarize their results and implications, and suggest some guidelines for the design of future experiments.

Experiments in 10 of the relevant 17 studies were performed in rocky intertidal systems (34, 35, 75, 80, 99, 100, 103, 114, 134, 178), usually with echinoderm or gastropod predators or herbivores, and with molluscs or algae as the manipulated competitors. Most of these used cage enclosures or exclosures; in others, at least some exclusions were initiated and maintained by hand removal (35, 75, 134, 178). Their results generally ascribe important influences to both competition and predation, though 3 seem to attribute somewhat more importance to competition (99, 100, 114), and 1 (80) somewhat more to predation. A relatively thorough investigation of two subtidal bivalves (141a) revealed that predation by gastropods and crabs is more important than interspecific competition between the bivalves but indicated that *intra*specific competition is particularly strong.

Of the 17 studies, 5 examined lentic freshwater systems—3 with plankton manipulated in large containers (40, 130, 175), and 2 with larval amphibians in enclosures (203) or in replicated tanks (205). Again, the consensus seems to be that both competition and predation were important (but see 40). In the extensive amphibian experiments (203, 205), predation and both inter- and intraspecific competition were quite important and interacted in complex ways.

A single terrestrial study, of ant and rodent seed-predators and annual desert plants (71), detected strong effects of competition (though all plants were manipulated together) and especially of predation (both by ants and by rodents).

Thus in these few examples featuring manipulation of both predator and competitor, both appear consistently and comparably important, as measured by the responses of one or more of the interacting populations. But many of the most interesting and significant questions to be asked about predation and competition become tractable only with carefully tailored experimental designs. We illustrate this below by considering some general questions and some designs of increasing complexity.

The minimal design for evaluating the relative importance of predation and competition requires three combinations—normal predators/normal competitors; no (or low) predators/normal competitors; and normal predators/no competitors. All 17 of the studies discussed in this section included these treatment levels. This design does not address interactions between predation and competition, however; that requires a fourth treatment level—no predators/

no competitors. Only 6 of the 17 studies included the full four-treatment-level factorial design (i.e. 34, 71, 80, 99, 203, 205). In at least 3 (34, 71, 205), the interactions were strong and central to a full understanding of the dynamics.

Inclusion of all 4 density combinations also allows for testing more complex hypotheses, such as that predation may often overwhelm any detectable response to competition in the absence of predators, or that predation can prove indirectly beneficial to competing prey. A few of the predation-competition field studies were both designed and presented to test such hypotheses (see Table 11). A majority of these studies detected indirectly beneficial predation (well-represented in the overall data set, too—see Table 9); examples consistent with other hypotheses are also noted in Table 11.

A still more informative design measures the responses of *both* (or all) competitors to the appropriate combinations of competitor and predator populations. Consider for example a predator species *(P)* and two competitor species distinguished by being dominant *(C)* and subordinate *(c)* in the predator's absence, grouped into six combinations: *C, c, Cc, CP, cP,* and *CcP*. With this approach, some additional generalizations about the influence of

Table 11 Some experimental manipulations of both predators and competitors

Species-combination ranking for a target competitor[a]				Interpretation	Examples
C_T	$>C_TC_M$	$>C_TP$	$>C_TC_MP$	Pred.[c] > comp. > 0	
C_T	$>C_TP$	$>C_TC_M$	$>C_TC_MP$	Comp. > pred. > 0	Sousa 1979[d]
					Lubchenco 1980
C_T	$=C_TC_M$	$>C_TP$	$=C_TC_MP$	Pred. > 0 = comp.	Keller 1983
					Dodson 1974[e]
C_T	$=C_TP$	$>C_TC_M$	$=C_TC_MP$	Comp. > 0 = pred.	
C_T	$>C_TC_M$	$>C_TP$	$=C_TC_MP$	Pred. swamps comp.	Wilbur et al 1983
C_T	$>C_TP$	$>C_TC_M$	$=C_TC_MP$	Comp. swamps pred.	
C_TC_MP	$>C_TC_M$;	C_T	$>C_TC_M$[b]	Indirectly beneficial pred.[b]	Neill 1984[f]
					Jara & Moreno 1984[f]
					Dodson 1974[g]
					Inouye et al 1980[e]
					Sousa 1979[e]
C_TC_MP	$>C_TP$;	C_T	C_TP[d]	Indirectly beneficial comp.[b]	Dodson 1974[g]

[a] Relative benefits to a particular competitor species (the "target competitor") of four species combinations: C_T includes only the target competitor species; C_TC_M includes both the target competitor and the other competitor species (the "manipulated competitor"); C_TP includes the target competitor and the predator species; and C_TC_MP includes all three species.

[b] Unlike the others, these two rankings are not mutually exclusive (e.g. see the results of Dodson 1974).

[c] *Pred.* is predator; *comp.* is competitor.

[d] Most results.

[e] Some results

[f] No C_T treatment level; results were $C_TP > C_TC_MP > C_TC_M$.

[g] No C_T treatment level; the trend for one species was $C_TC_MP > C_TC_M = C_TP$.

predation on competition can be directly tested. Two of many possibilities include the following.

1. *Predation reduces or prevents interspecific competition* (e.g. see 101 and references therein). Let i (j) represent the response (e.g. density) of species i to treatment-level j. For example, c (cP) indicates the response by subordinate competitors to the treatment level containing subordinate competitors and predators but no dominant competitors. Then this hypothesis makes the following predictions:

(a) $c(Cc) < c(c)$—subordinate competitors are inhibited by dominants in the absence of predators.
(b) $c(Cc)/c(c) < c(CcP)/c(cP)$—introducing the dominant is less inhibitory to the subordinate in the presence of predators than in their absence.
(c) if $C(Cc) < C(C)$, then $C(ec)/C(C) < C(CcP)/C(CP)$—if subordinates inhibit dominants in the absence of predators, then this inhibition also should be reduced in their presence.

2. *Predation tilts the balance between competitors.* (This implies that the dominant and subordinate competitors exchange roles in the presence of the predator, though they are referred to here according to their relative success in the predator's absence.) From this hypothesis arise the following predictions:

(a) $c(Cc) < c(c)$—as in 1(a), subordinate competitors are inhibited by dominants, in the absence of predators.
(b) $C(CcP) < C(CP)$—in the presence of predators, the former subordinate species inhibits the former dominant.
(c) $c(Cc)/c(c) < C(Cc)/C(C)$—with predators absent, introducing the other competitor inhibits the subordinate more than the dominant.
(d) $C(CcP)/C(CP) < c(CcP)/c(cP)$—with predators present, introducing the other competitor inhibits the former dominant more than the former subordinate.

Note that hypotheses 1 and 2, though making specific predictions based on rather different conceptions of how predation and competition may interact, are not mutually exclusive.

Only three studies from our data set (80, 203, 205) present sufficient information from the minimal six treatment levels to test hypotheses 1 and 2 and their relatives. One of these studies (205) agrees closely with hypothesis 1; none is consistent with hypothesis 2. Both of these hypotheses deserve further experimental scrutiny.

Strangely neglected in many investigations, including 11 of the 17 predation-competition studies, *intra*specific competition could be of critical importance in understanding the dynamics of interacting populations (as in all five of the investigations in which it was analyzed separately—80, 141a, 175, 203, 205).

In particular, the potential for coexistence of competitors in the presence or absence of the predator may depend in part on the intensity of intraspecific relative to interspecific competition. Further expansion of the design to eight treatment levels (C, c, CC, cc, Cc, CP, cP, and CcP) permits this and related hypotheses to be evaluated.

So far, we have not stressed the particularly rich possibilities for interactions between (and within) size-structured animal populations. It is especially appropriate to mention this in the context of effects and interactions of predation and competition, because relative size (reflecting both fundamental differences between taxa and differences in degree of development or feeding history) may often determine capabilities and susceptibilities to predation and competition. Animals of similar taxa may tend to compete more intensively when of similar sizes, but they may tend to prey on each other (mainly, the large eating the small) when of different sizes (e.g. 203). Such size-structure effects apparently extend broadly across systems and taxa—for example, freshwater fish (119) and insects (6), marine bivalves (141), and terrestrial insects (180). See (200) for a review.

In light of the need for additional experimental studies that simultaneously analyze competition and predation (especially in nonintertidal systems) and of the lessons to be learned from investigations to date, what factors deserve consideration in the design of such experiments?

1. Factorial designs permit the detection and analysis of interactions between factors such as different predators or intra- vs interspecific competition. They also produce large (and often unmanageably large) numbers of treatment combinations. Juggling this trade-off sensibly is central to any design and must ultimately rest on biological insight and preliminary data.
2. When cages are necessary to maintain density manipulations, cage controls (that mimic the physical effects of cages without the enclosure or exclosure effect) can help to isolate cage effects from treatment effects. Unfortunately, this straightforward design concept is not consistently implemented.
3. Studies based on easily manipulated organisms may require no caging (or its analogues) and will expend less effort on controls, which thus permits more emphasis on treatments or replication.
4. A truly quantitative assessment of the importance of predation and competition requires experiments initiated (and replicated) with similar designs in different places at different times of year (see 101).
5. Though several densities of each manipulated population may be highly desirable for clarifying details of the density-dependence of various interactions, the effort may often be better spent on replication or on adding more treatments (e.g. combinations of populations) to the design.

In summary, the few experimental field studies involving manipulations of both predators and competitors have mostly been carried out in rocky intertidal systems; they suggest that both predation and interspecific competition are generally (and about equally) important. Future studies should be designed to detect intraspecific competition and interactions between predation and competition.

Predation, Competition, and Indirect Effects

Most empirical and theoretical studies on the effects of predators and competitors emphasize direct effects. The direct effect of predation is prey mortality. The "direct" effect of competition is usually thought to come through reductions in resource availability either by exploitation (using resources up) or interference (restricting access to resources). However, predation and competition can also have two types of indirect effects on prey communities. We refer to these as multispecies-related and life-style–related indirect effects.

Multispecies indirect effects occur when changes in a third species mediate the effect of one species on a second species (or analogous higher-order interactions). Examples include the "unexpected" and indirectly beneficial effects of predation (see Tables 2, 9, and 11). We termed the mechanisms presumed to be involved the *keystone predator* effect and the *three-trophic-level* effect. In both cases, the overall effects of predators on prey are heavily influenced by the predator's effects on either a competitive-dominant or a middle-level predator. By this definition, exploitative competition for living resources is also an indirect effect: one competitor affects the other by reducing the availability of a third species, the limiting resource. Few studies have experimentally addressed indirect interactions (but see our section on Experimental Studies of Both Predation and Competition, above).

A second type of indirect effect concerns prey life-styles. Both predation and competition can profoundly affect the morphology, physiology, chemistry, or behavior of prey. Prey behaviors that may be affected include habitat use, time of activity, foraging mode, diet (or analogous "behaviors" for plants), mating system, and life history. Prey life-styles in turn determine prey encounter rates with predators, competitors, and food. The two types of indirect effects are not mutually exclusive. For example, a secondary carnivore can affect the degree to which a herbivore's life-style is influenced by a primary carnivore.

Many of the traits listed above are elements of an organism's niche. Although most existing niche theory assumes that niches are primarily determined by competition, antipredator needs probably also have crucial effects on niche characters (see 77, 172 for reviews). To date, many experimental studies have looked at the effects of competition on niches, whereas relatively few have examined the effects of predation (Table 4). Similarly, a vast theory exists for the effects of competition on niche-related coexistence (e.g. 19, 197, 109). In

contrast, ecologists have only begun to develop theory that attempts to explain the coexistence of prey in terms of predator-influenced niches ("enemy-free space," e.g. 77, 147, 163). In most cases, probably both competitive (resource-related) and antipredator needs affect niche characters (e.g. 38, 49, 91, 148, 154, 170, 201). This suggests that niche theory should incorporate both needs. Further theory and data on the interacting nonlethal effects of predation and competition on the life-styles of organisms, and thus indirectly on prey community structure, should prove insightful.

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