Annu. Rev. Ecol. Syst. 1994. 25:495–520

THE ECOLOGICAL CONSEQUENCES OF SHARED NATURAL ENEMIES

R.D. Holt
Museum of Natural History, Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045

J.H. Lawton
NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot SL5 7PY, United Kingdom

KEY WORDS: polyphagous enemies, apparent competition, enemy-free space, predation, indirect food webs, interactions, contingent theory

---

Abstract

When multiple victim species (e.g. prey, host) are attacked by one or more shared enemy species (e.g. predator, pathogen), the potential exists for apparent competition between victim populations. We review ideas on apparent competition (also called "competition for enemy-free space") and sketch illustrative examples. One puzzling aspect of this indirect interaction is the repeated rediscovery of the essential ideas. Apparent competition arises between focal and alternative prey populations because, in the long term, enemy abundance depends on total prey availability; by increasing enemy numbers, alternative prey intensify predation on focal prey. A frequent empirical finding, consistent with theory, is exclusion of victim species from local communities by resident enemies. Theory suggests victim-species coexistence depends on particular conditions. To understand fully the consequences of shared enemies requires a body of contingent theory, specifying the time-scale of the interactions (short- and long-term consequences of sharing enemies generally differ), the structure of the food-web encompassing the interactions, its spatial context, etc. The "core criterion" for a focal victim species to invade a community supporting a resident, polyphagous enemy is $r > aP$ (the invader's intrinsic rate of increase

should exceed attack rate times average enemy abundance). A growing body of data and observations test, and support, this prediction.

A GENERAL PROBLEM: CONTINGENT THEORY IN ECOLOGY

There is a growing recognition in ecology of the need for contingent theory—models tailored to particular systems—developed with strong links to synoptic views of the discipline as a whole (103, 154). This is particularly true for interactions between generalist natural enemies and their victims, a diverse class of interactions transcending taxa, habitats, and biomes. Here, the terms "enemy" and "victim" embrace, respectively: "true" predators, parasitoids, parasites, pathogens, or herbivores; and prey, hosts, or plants. For simplicity we often refer to "predators" and "prey," but unless otherwise stated our arguments apply broadly to all enemy-victim interactions.

What do the following miscellaneous interactions have in common—badgers and hedgehogs (34); sea urchins and the city of Los Angeles (144); rabbits and herbaceous vegetation (176, 177); ants, extrafloral nectaries, and caterpillars (87); Aleuts and sea otters (164); biological pest control by generalist natural enemies (77); and domestic cats and house sparrows (26)? The answer, which may not be obvious at first, is that all involve one (or more) "focal" victim species linked to other prey via a shared, generalist enemy or enemies: The thread tying these examples together is that in each, enemy impact upon particular victim species is profoundly influenced by the availability and productivity of alternative food or victims. Relationships between alternative prey mediated via shared predators are, we believe, a particularly pervasive and important class of indirect interactions (1, 2, 85, 110, 155, 168, 189a). Previous overviews of the role of predation in communities (25, 30, 42, 85, 111, 116, 162) have rarely highlighted the significance for prey species of sharing predators. The problems of coexistence and exclusion for prey species that share predators—due to an indirect interaction denoted by various names, including "apparent competition" (64) and "competition for enemy-free space" (80)—constitute the central focus of this review.

REDISCOVERING THE WHEEL

One of the most puzzling aspects of the phenomenon of shared enemies is the repeated rediscovery of its main ecological and evolutionary consequences by numerous authors, each apparently oblivious of earlier work. It is as if ecologists working on different taxa, in each decade, were continually to rediscover interspecific competition for resources! We have no idea why ecologists in general are so ignorant of the general importance of shared enemies and yet are so familiar with conventional, resource-based interspecific competition.

The essential ideas of enemy-free space and apparent competition are not new. Over 35 years ago, Williamson (185) first showed in a formal model that the consequences of two species sharing a natural enemy are, in general terms, identical to more conventional forms of interspecific competition for limiting resources. Holt (64) coined the term *apparent competition* to emphasize this formal similarity and, with collaborators (64, 66–72), developed a body of theory characterizing this interaction. Recently, Connell (28) and Reader (142) examined evidence for apparent competition between plants via shared herbivores. Jeffries & Lawton (80) listed 20 papers dealing with enemy-free space in general, conceptual terms. They summarize 81 papers, providing examples of ecological and evolutionary consequences, drawn from the marine, freshwater, terrestrial, and paleontological literature, and including organisms from microbes to mammals and phytoplankton to fish. Yet ecologists continue to rediscover one or more aspects of the general problem. Entomologists alone appear to have independently stumbled across the essential ideas at least 20 times (93). There are numerous discoveries of the basic phenomena in the parasite literature (47, 139, 140). Some authors (16, 17, 32, 38, 40, 41, 77, 86, 119, 123, 178) have clearly recognized the importance of alternative prey in defining the impact of polyphagous predators on focal prey in particular systems, without exploring broader implications. Several recent examples of rediscovery are elegant and important (6, 29, 35, 73, 90, 105, 106, 113, 119, 121, 143, 147, 159, 175). They suffer only from not being set in a more general, conceptual framework, and hence they contribute less to testing and developing theory than one might wish.

There are literally hundreds of examples we could use to illuminate how alternative prey for generalist predators influence the distribution and abundance of focal victim species; the papers cited here are illustrative, not exhaustive. To us, these examples tellingly highlight the need for the further development of contingent theories, in the first place tailored to the details of particular systems, then deliberately woven into a broader tapestry of thematically related contingent theories. Some such theories for shared generalist enemies are well-developed (e.g. 1, 2, 33, 50, 55, 58, 62, 64, 66–67, 69–72, 80, 93, 99a, 108, 122a, 153); others await explicit attention from theoreticians.

GENERAL FEATURES OF SHARED PREDATION

A logical series of questions about the effect of a generalist (polyphagous) predator on a focal prey type are: Does the predator cause that prey's local extinction? If not, by how much are prey numbers depressed below the carrying capacity set by other factors? Does predation regulate—or destabilize—the prey population? To answer these questions, one must consider three dimensions to the problem: (i) temporal scale; (ii) food web structure and feedbacks; and (iii) spatial scale. The reader will quickly come to appreciate the need for contingent theory!

Time Scales

The relative generation lengths of enemies and victims influence their linked dynamics (30, 32, 86). Observational time-scales strongly color interpretation (1, 2, 64, 70), and failure to consider time-scales can lead to misleading tests of theory (31). Feedback between predator and prey occurs when the rate of predation over some time-scale depends functionally upon prey abundance. At short time-scales, within a single predator generation, feedbacks are behavioral in nature (114) [e.g. predator satiation, switching, and aggregative responses (30, 57) and prey avoidance behaviors (100, 179)]. These short-term effects can be masked or exaggerated over multiple predator generations—the time-scale pertinent to understanding the role of predation in determining community structure—where the potential for predator numerical responses (30, 57) looms larger. At yet longer time-scales, phenotypic evolution within a given prey species will reflect the phenotypic spectrum characterizing all prey supporting shared predators; niche differentiation among prey may be driven by shared predation (19, 80, 93, 145, 160). Due to space limitation, we say little on evolution here.

SHORT TIME-SCALES Within a single predator generation in a closed community, predator numbers are approximately fixed. The availability of alternative prey influences predator behavior, modulating the predation experienced by a focal prey via the predator's functional response; for instance, alternative prey may lower predation on a focal prey because of predator selectivity or satiation. One important consequence of labile predator behaviors is that generalist predators can contribute to density-dependent regulation of focal prey species (36, 40, 41, 55, 58) and at times can promote the coexistence of competing prey (190).

Such interactions have received considerable attention (29, 44, 48, 74, 143, 187). In short-term experiments with two species of amphibian tadpoles, survival of *Bufo americana* increased in mixed populations with *Rana palustris* when both were exposed to predation by *Anax junius* nymphs (Odonata) or by adult *Notophthalmus viridescens* salamanders. *Rana* survivorship was enhanced by *Bufo* in the presence of *Notophthalmus*, but not with *Anax* (181). Natural fluctuations in prey numbers produce comparable phenomena. On Santa Barbara island, predation by the barn owl (*Tyto alba*) extirpated burrowing owls (*Athene cunicularia*) when alternative prey (small mammals) declined (35), within a single barn owl generation.

These results are predicted by a traditional representation of a predator's short-term (functional) response to multiple prey-species—the generalized Holling "disk" equation (96, 118, 120). In this model, time spent handling one prey item precludes handling another. An increase in alternative prey relaxes predation upon a focal prey; conversely, decreases in alternative prey magnify predation upon focal prey. Thus, short-term interactions between alternative prey mediated by a shared predator can generate "apparent mutualism" (1, 2, 64, 70).

Various authors have explored a number of theoretical, but realistic, complications in short-term interactions between prey. For instance, the generalized disk equation does not incorporate adaptive foraging behavior by predators, or adaptive escape behavior by prey. If predators switch or forage optimally, apparent mutualism persists and may be reinforced (1, 2a, 50, 65). This and other indirect interactions [e.g. (+,–) called "apparent predation," "indirect antagonism" (74), or "contramensalism" (10)] may arise from shifts in prey behavior, or when predators violate canonical optimal foraging models (1, 65, 70, 74). Moreover, optimal patch use by predators can generate short-term, within-patch apparent competition between alternative prey (21, 70).

LONGER (TRANS-GENERATIONAL) TIME-SCALES Predator abundance in a closed community in the long run is always a dependent variable, and in particular it depends on the availability and productivity of the entire prey base. The rate of predation experienced by a focal prey species can be profoundly influenced by the indirect, cumulative impact of alternative prey, sustaining predator populations at densities higher than allowed by the focal species alone. This dependency is often neglected in field studies of the community effects of polyphagous enemies. Understanding the assembly and persistence of species assemblages, we argue, requires a multi-generational perspective encompassing the full range of potential numerical responses.

Theoretical studies suggest that when predators are largely limited by prey availability (rather than by, say, nest-site availability), alternative prey should experience long-term, negative-negative interactions via shared predation (apparent competition), regardless of short-term contramensalism or apparent mutualisms due to predator satiation, adaptive foraging, or switching (2, 50, 64, 65, 71). These indirect interactions can lead to species exclusions. Ironically, the phenomenon is difficult to demonstrate by observing an established community, because the most severely affected species are absent from the system!

One approach is to compare local assemblages (6, 189). The species composition of *Enallagma* damselflies differs markedly but predictably between permanent lakes, depending upon whether the dominant polyphagous predators are fish (found only in some lakes), or larger Odonata (absent from lakes with fish). Different *Enallagma* species differ in vulnerability to these two predator types and are excluded from lakes with the "wrong" predators (109). (Apparent competition in this example is not just between *Enallagma* spp., but between *Enallagma* and the entire invertebrate prey complexes that support populations of fish or larger odonates). A very different example is provided by comparing fossil and extant marine communities. Certain isolated salt lakes lacking fish are dominated by benthic ophiuroids, and appear to provide a glimpse of Paleozoic marine communities, common in the fossil record, but now largely exterminated by the evolution of predatory fish in the Mesozoic (9).

Exclusion by shared enemies is best demonstrated by experiments, either controlled (3, 34, 82, 119, 121, 151, 152, 159) or more haphazard and accidental (20, 32, 86, 139). Exclusion by shared enemies is also seen dramatically in new, but transient, situations created by invasions, either of novel prey (90, 147, 157, 158), alien enemies (7, 11, 12, 23, 37, 73, 98, 113, 129–131, 150), or both (32, 133, 146). It is not the case that alien predators are somehow different from native predators (35), only that apparent competition to the point of exclusion can be readily observed during an invasion.

Exclusion by shared predators is not inevitable—just as species may compete for food, but coexist. Mechanisms promoting prey coexistence, despite shared predation, have been reviewed in detail elsewhere (64, 66, 69, 71). They include: (i) donor-controlled enemy dynamics; (ii) weak enemy numerical responses (i.e. limitation other than by prey, territoriality for instance); (iii) resource limitation for prey; (iv) resource and habitat partitioning by prey; (v) spatial and temporal refuges for prey; (vi) labile enemy behavior (e.g switching): and (vii) food-web effects (e.g. higher-order predators).

Food-Web Structures and Feedbacks

Sometimes indirect effects resulting from shared predation can be discerned species-by-species, and sometimes only diffusely. Published studies often conform to idealized food webs (Figure 1), although reality will often be more complex, encompassing both more types of prey, and more species of predator, than abstracted by the original author(s).

The simplest cases report a single enemy species and two distinct victim species (Figure 1a) (16, 35, 45, 48, 82, 127, 139, 158). The next most complicated cases (Figure 1b) focus on a single predator species attacking an entire suite of taxa, often with a focal prey (7, 13, 36, 46, 52, 79, 84, 98, 113, 126, 151, 164, 175). A yet more complicated scenario is for two or more distinct generalist predators to be supported by a pair of prey species (14), or by an entire suite of alternative prey, often with one prey selected for particular study (Figure 1c) (40, 41, 44, 55, 88, 91, 92, 101, 172, 178, 188). Finally, the focal prey "type" may be an ensemble of prey species, attacked by a complex of

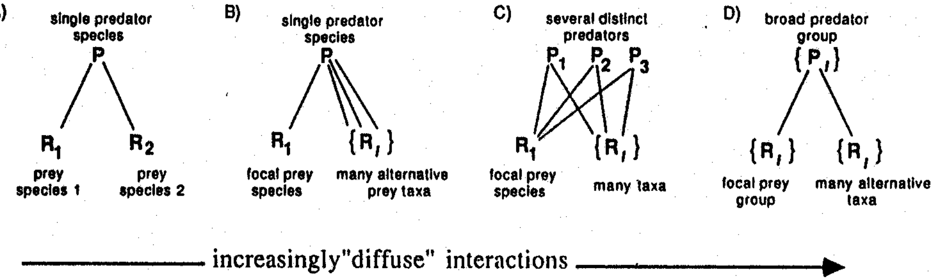

Figure 1 A series of food-web modules, representing increasingly complex and diffuse examples of natural enemies shared by two or more victim species (see text).

predators, treated as a group (Figure 1d) (15, 109). (Other food web effects, such as competition between prey, are discussed below.)

Over and above these relatively simple examples, many cases are difficult to classify, either because essential details are lacking, or because predator-prey interactions vary in complex ways in space and time. For instance, spatially varying assemblages of introduced mammals, sustained by a variety of native and introduced prey, pose major threats to breeding seabirds on sub-antarctic islands (81).

Spatial Scales

The nature of a predator's functional and numerical responses to a focal prey species depends upon the spatial relation of the predator, the focal prey, and alternative prey. In simple cases, the predator may encounter prey (both focal and alternatives) in a fine-grained fashion and have a numerical response to a weighted average of their abundances. This is a useful point of departure for theoretical models (64, 66, 169, 173, 174) and may adequately describe some empirical systems, such as "bottle" experiments (48, 91, 92) and relatively homogeneous field systems with mobile predators. Striped skunks, *Mephitis mephitis,* foraging for invertebrates in grassland, apparently encounter birds' nests at random, but nevertheless impose considerable mortality on several rare and endangered species, a process Vickery et al (175) called "incidental predation."

But often, enemies encounter focal and alternative victims in a coarse-grained fashion, through either time or space (136).

One can usefully distinguish three scenarios:

1. Enemies move from one habitat to another, and encounter different victim types in different habitats. For instance, Arctic foxes move into breeding areas of wading birds from adjacent habitats following lemming population declines and have a major effect on nesting success (172). Impacts on focal

victims depend upon when and how predators move in relation to their prey. In some circumstances, predator movement can cause high mortality to prey in low-productivity patches, because immigration boosts predator numbers above levels sustainable locally by those prey (56, 66, 68, 125, 141). For instance, polar bears, migrating on drift-ice in spring, directly or indirectly caused 60% mortality of brent goose eggs on Svalbard (104). Alternatively, predators may show aggregative responses (30, 57) to different prey in different habitats, generating switching (120) and reduced mortality for species in low density patches. It is less well known that an aggregative response can generate short-term apparent competition between alternative prey within a patch (70), exemplified by kangaroo rat, *Dipodomys merriami,* predation on experimental patches containing two sizes of seeds (21). Evolution of nest-site differences among coexisting bird species is favored by a qualitatively similar mechanism; in a given habitat, predators may be less successful when searching simultaneously for several different nest types than when concentrating on just one (105, 106).

2. Enemies may be stationary, but victims (focal, or other) move between habitats. Asymmetrical spatial flows reduce the potential for classical, density-dependent feedback between enemies and victims in any particular community. Two very different types of interaction are informative. Insectivorous birds are unable to attack below-ground larval stages of periodical cicadas, *Magicicada* spp.; accordingly, birds cannot show sustained numerical responses to cicadas between emergences and are swamped by the overwhelming numbers of adults that emerge synchronously into above-ground habitats (184). [Note that by emerging together (180), the three species of *Magicicada* are short-term apparent mutualists.] In contrast, sustained, predictable flows of food, which enter habitats from elsewhere at a rate independent of resident predators, have quite different effects. Such predators are donor controlled and may build up to large numbers, with major consequences for focal prey. Examples embrace a variety of unconventional flows of alternative foods, enemies, and focal victims: sewage outfalls that sustain sea urchin populations, reducing local communities of attached algae to the point of extinction (144); litterfall that contributes 20–50% to the diet of fallow deer, *Dama dama,* allowing the deer to all but obliterate plants in the forest understorey (12); and food provided by people for domestic cats, with serious consequences for bird and mammalian prey (26, 39; see also 136).

3. Echoing these spatial processes, there may be a partial or complete temporal (e.g. seasonal) separation of victims, supporting enemies that straddle seasons. The level of predation in one season may depend on the availability of prey in previous seasons. Examples of seasonal flows range from inter-continental migration of birds (with largely unexplored consequences for prey species), and within-continental migration of Odonata (187), to insect hosts

that live in physically separate habitats, coupled by shared, seasonally alternating parasitoids (128, 191). Differences in diel activity can generate asymmetrical relations among alternative prey. For example, Halle (54) reported that a guild of diurnal avian predators attacked the vole *Microtus arvalis* at a considerably higher rate than the mouse *Apodemus sylvaticus*, and suggested that this reflects the partially diurnal habits of *Microtus*.

In brief, a full understanding of the dynamics of coexisting prey and the potential for prey exclusion requires knowledge of both long- and short-term predator responses to alternative prey, anchored in an appropriate spatial, temporal, and community context. Good examples come from simple Arctic and boreal ecosystems, where bird and mammal species show parallel (but frequently asynchronous) cycles in numbers and breeding success, driven by shared predators (22, 55, 88, 101, 172). Understanding these cycles requires knowledge of long-term predator numerical responses, as well as shorter-term aggregative and switching responses from declining prey (e.g. lemmings) to alternative prey (e.g. nesting birds).

VICTIM EXCLUSION IN FEEDBACK AND NONFEEDBACK SYSTEMS

A simple but nonetheless illuminating criterion for exclusion of the focal prey is:

$$0 < r < aP, \qquad 1.$$

where r is the average intrinsic rate of increase of the focal prey (when it is rare enough to ignore intraspecific density-dependence), P is the average abundance of resident predators, and a is the attack rate per predator, per prey when the focal prey is rare (57, 64, 71, 93). If $r > 0$, the prey can cope with the local environment and thus could invade in the absence of predation. Exclusion occurs when $r < aP$.

In some circumstances, r increases with density at low densities (viz., Allee effects), up to an $r_{\max}$ at some density, above which negative density-dependence is felt. Some prey species may be excluded from a community by predation, yet be able to persist if their initial abundance exceeds a certain threshold level. This effect (which is compounded if predators have satiating functional responses, reducing a at higher prey densities) can lead to alternative stable states in prey community composition (64).

Examples of prey exclusion by polyphagous enemies have already been given. Others include exclusion of the water boatman *Corixa expleta* from low-salinity lakes by four species of parasitic water mites (116, 157a); elimination of *Tribolium castaneum* by the shared sporozoan parasite *Adelina tribolii* in mixed cultures with *T. confusum* in Park's (127) classical experiments (in the absence of *Adelina, T. castaneum* out-competes *T. confusum*); and the differential exclusion, or virtual exclusion, of three types of gall-forming nematine sawflies from arroyo willows by a guild of predatory ants (188).

The ambient density of predators, *P*, reflects the cumulative impact of the resident prey community that supports these predators, as well as many other aspects of community structure (see below). By definition, the magnitude of *P* is not governed by feedback with excluded prey! We therefore call predators that exclude prey "despotic."

Different assumptions about the relation between a despotic predator and alternative prey have interestingly different dynamic consequences:

1. Predators may be limited by nontrophic resources such as territories (40) or nest sites (77) (e.g. specially evolved "domatia" on host-plants for predatory ants—78). If so, the productivity of alternative prey may vary widely without influencing the propensity for exclusion of focal prey.
2. The enemy may be food-limited, but in a donor-controlled manner. This describes many systems in which the alternative food supply for the enemy is nonliving (e.g. 12)), such as nectar supplied by plants with extra-floral nectaries, attractive to predatory ants (78). These ants frequently (if not always—87) depress populations of one or more species of phytophagous insects exploiting the host plant, and in extreme cases exclude particular vulnerable species entirely (59, 97). Likewise, sea urchins are sustained at very high densities by Los Angeles sewage effluent and can therefore eliminate local populations of attached algae (144).

   Donor control may also roughly describe systems in which domestic stock sustains infectious diseases (32), and those in which prey have absolute refuges (in space, time, body size, etc) from predation (61). Because heterogeneities of all sorts tend to generate "virtual" refuges from predation, touches of donor control may be common in many environments and may play an important role in maintaining stable, polyphagous, potentially despotic predator populations.

3. A vast literature, based largely on analyses of gut-contents and feces, shows that many vertebrate and invertebrate predators are not only polyphagous, but extremely so (186). In such cases, no particular prey species matters very much in determining *P*, which can often as a first approximation be treated as a constant rather than a dynamical variable responsive to that prey (58, 119). In contrast to case 1. above, predator abundance depends on the productivity of the full prey community. But in comparison with simpler community modules, indirect pairwise interactions between prey species will be difficult to discern (e.g. experimentally).

A Comment on "Ratio-Dependent Predation"

An alternative representation of predator-prey dynamics, ratio-dependent predation, has attracted recent attention; proponents argue that the functional response of a predator to its prey is determined not by prey density, *R*, but by the ratio of prey to predators, *R*/*P* (4, 8, 107).

In a simple ratio-dependent formulation, per capita prey mortality due to predation is independent of the number of predators. Hence if strict ratio-dependence were the rule, much of what we have said is wrong. However, the theory lacks unequivocal experimental support (149) and has been severely criticized for logical flaws (e.g. 2b). The numerous manipulative experiments showing an effect of predator abundance on prey mortality or density suggest that strict ratio-dependence is the exception, not the norm. Moreover, ratio-dependence may inadequately represent how predation affects the capacity of a victim population to increase when it is rare. The latter is what matters for community structure. We therefore accept Equation 1 as the most useful, general, albeit simple, working model for prey exclusion by resident, despotic predators.

REASONS FOR PREY EXCLUSION

The three components of the exclusion criterion (r, a, and P) correspond to (i) inherent physiological and life history properties of the prey in a given environment; (ii) behavioral attributes and environmental context of the predator-prey interaction (e.g. predator hunting efficiency, anti-predator escape strategies, availability of spatial refuges); and (iii) a summation of those factors that control predator numbers, particularly food web effects. We now "unpack" the biological complexities latent in the seemingly simple exclusion criterion; particular instances of exclusion (or coexistence) cannot be fully understood without considering all three components.

Exclusion Because of Low Prey r

If $r < 0$, the focal prey species is excluded from the local environment, irrespective of predation, unless sources provide continuous immigrants into sinks (68, 71, 141). If $r > 0$, but is low relative to mortality imposed by resident enemies, one tends to ascribe exclusion to predation. This is correct, but such exclusion also rests on the prey having a low r.

A prey species may have low r for many reasons, both autecological and synecological. Long generation length and/or low clutch size are obvious contributors. If the prey species is near the edge of its fundamental niche or close to its geographical limits, maximal growth rate may be low (95). For other species, resources may be inherently low in availability or quality, or depressed by interspecific competition.

These observations lead to a series of first-order expectations about prey species most at risk of exclusion from a local community by resident, polyphagous enemies. All else being equal, they are victims near the edge of their distributional ranges, specializing on scarce or low-quality resources, and overlapping in resource requirements with the resident prey community. These predictions appear not to have been tested experimentally [although the establishment of red-legged partridges, *Alectoris rufa,* in Britain in the face of heavy predation by foxes appears to have been favored by high fecundity (138)].

Exclusion Because of a High Attack Rate, a

Attack rates can be decomposed into a series of steps describing the time-course of a predator-prey encounter (63). Average attack rates will be reduced if victims (53a, 93, 161): (i) avoid enemies spatially or temporally; (ii) have behaviors or appearances that reduce detection and recognition; (iii) develop escape abilities; and (iv) resist attack. (Different, detailed considerations are pertinent to plant-herbivore, pathogen-host, and parasite-host interactions, without affecting the basic argument).

One simple conclusion is that if invading prey closely resemble resident prey in niche dimensions that determine vulnerability to predation, the invaders are likely to be excluded by resident enemies (80, 93). Only invaders with less vulnerable phenotypes should be able to enter the community (other things being equal, particularly r). Direct tests of these predictions are also lacking. But many aspects of the biology of coexisting hosts and parasitoids (93) and predators and prey (109, 189) are consistent with them. For example, phytophagous insect species in particular feeding niches are excluded entirely, or almost entirely, from host plants within the hunting ranges of predatory ants (46, 79, 188), seabirds nesting in different sites are differentially vulnerable to mink predation (7), and predation on bird nests increases with overlap in microhabitats exploited for nest placement (105).

Exclusion Because of High Predator Abundance, P

Obviously, a given invading prey is likely to be excluded if highly productive resident prey or nonliving food resources sustain a large population of resident predators (P). But the problem is more interesting than that. The invasion criterion for prey species i, $r_i > a_iP$, can be restated as:

$$r_i/a_i = P^*, \qquad 2.$$

where P^* is the greatest density of predators prey i can tolerate and still persist. If prey species i occurs alone with the predator, then P^* defines the maximum abundance of the predator sustainable by that prey. This leads to a simple criterion for dominance under shared predation: the species with the largest value for P^* tends to exclude alternative prey. This simple P^* rule characterizes the outcome of apparent competition in a diverse array of models, including classical Lotka-Volterra models (64, 66, 122a), host-parasitoid models (71), and some models with mixed exploitative and apparent competition (69). Microcosm studies (91, 122) have validated this criterion, but its efficacy in explaining dominance in field situations (e.g. 158) has not yet been tested experimentally. This "rule-of-thumb" for dominance may break down if key assumptions are violated, for instance, because of complex functional responses, or because predators themselves are attacked by higher-order enemies. Nonetheless, the P^*-rule provides a useful yardstick for gauging the likely importance of such complications.

When Prey Are Not Excluded

If the focal prey can invade (i.e. $r > aP$), many of the above considerations still pertain, but with the significant difference that various feedbacks may arise.

A focal prey may persist at an equilibrium density well below carrying capacity, because alternative prey support generalist enemies at high densities. Such a prey is unlikely to have a large effect on the remainder of its community. A particularly well-documented example is provided by Potts's (137) work on grey partridges, *Perdix perdix,* in which breeding densities are depressed by a complex of predators (e.g. foxes and crows) without significantly influencing predator numbers. Alternatively, invading focal prey can build up to high levels, allowing an increase in enemy numbers that depress and potentially threaten populations of resident, alternative victims. Two cases of invading phytophagous insects, a leafhopper *Erythroneura variabilis* in California (71, 158) and a gall wasp *Andricus quercuscalicis* in Britain (157), provide good examples. In the first case, increases in populations of a shared parasitoid, *Anargus epos,* appear to have caused marked reductions in resident *E. elegantula;* in the second, increases in gall inquilines potentially threaten native gall-formers.

Suppression, rather than exclusion, of focal prey populations by shared pathogens is also documented (32). Populations of another British gamebird, red grouse (*Lagopus lagopus*), are suppressed by louping-ill virus, maintained at high levels by alternative domesticated and wild hosts, including sheep, goats, hares, and deer. Models indicate that grouse alone cannot sustain the virus (32, 75, 76).

COMPLICATIONS OF COMMUNITY STRUCTURE

In natural communities, simple food-web modules are typically embedded in more complex webs, including higher-order predators, omnivory/intraguild predation (31, 132, 134), and predation upon competing prey (27, 69). It would take us too far afield to characterize in detail all these community-level complications, but it is useful to briefly consider a few.

Higher-Order Predators

By dampening or eliminating the long-term numerical response of intermediate predators to their prey (124), higher-order predators can weaken apparent competition between focal prey and alternative prey (64). Removal of higher-order predators allows intermediate predators to increase, often with devastating consequences for prey species lower in the trophic chain (24, 85, 164)—a phenomenon termed "mesopredator release" by Soulé et al (165). Prey species impacted by polyphagous predators undergoing mesopredator release are victims of apparent competition.

Analyzing the net impact of a guild of predators upon a focal prey becomes more complicated—and in interesting ways—given omnivory or intraguild predation. In the simplest case, higher-level predators not only attack intermediate predators (in this instance, the focal prey), they also share their resources (132, 134, 135). The combined problems of predation from, and interspecific competition with, higher-level predators make the persistence of intermediate predators more difficult (35, 134, 135, 156, 166, 167). In contrast, if focal prey experience predation from a predator guild, intraguild predation within that guild can relax the total impact of predation on the focal prey (34, 134). Again, we know of no experimental tests of these predictions.

Competition Among Prey

The traditional focus in community ecology has been on how predation modifies preexisting competitive interactions, permitting competitively incompatible species to coexist. This emphasis pervades both empirical (e.g. 99, 126) and theoretical (e.g. 27, 89, 102, 173, 190) studies. "Keystone species" were originally defined as predators with major impacts on competitively dominant prey (115, 126, 164). We by no means discount the potential importance of predation as a factor diversifying communities with strong competitive interactions. However, the notion that polyphagous predators characteristically promote prey coexistence [*Pisaster* providing the classical example—126)] is neither the simplest nor most general case. A single-minded emphasis on this effect may be a sociological factor predisposing ecologists to "rediscovering the wheel" of negative indirect interactions via shared predation.

If resident prey compete with focal prey, adding direct competition further hampers the persistence of focal prey. If resident prey compete among themselves, the number of predators supportable by those prey tends to be reduced, enhancing coexistence. Thus, the effect of prey competition upon focal prey exclusion depends on whether such competition acts among the alternative prey, or between them and the focal prey. Predation can also sharpen competitive interactions (53). For instance, if refuges are limited in supply, interspecific competition between victims may be intensified (61, 67, 74, 117).

Adding direct competition to predator-prey systems opens up a Pandora's box of dynamic possibilities, such as limit cycles and chaotic dynamics (49, 173, 174), essentially because of long feedback loops (predator A knocks down competitor B, which allows competitor C to increase, which cannot support predator A, which declines, allowing competitor B to increase again, and so on). The simple criterion for exclusion of focal prey (Equation 1) is rigorously true for constant P; more complicated criteria for invasion are needed for variable P (71). Simple criteria such as $r > aP$, however, help one gauge the significance of more refined criteria—yet another example of the conceptual utility of contingent theory.

In Community Ecology, It Gets Worse Before It Gets Better

The above remarks provide just a taste of the complexities inherent in almost any multi-species food web. A basic, humbling message emerging from theoretical studies of complex webs is that with many potential routes for indirect interactions between any species pair, it may be difficult to predict the effect of one species upon another (64, 189a, but see 110, 155).

Although it is important to recognize such complexities, it is equally important not to despair of simple explanations for broad ecological patterns. Contingent models of shared predators with pronounced numerical responses reveal that alternative prey can exclude or reduce the abundance of a focal prey. Without pretending to explain any particular example in all its details, this message rings loud and clear in many case studies.

SOME CASE HISTORIES

A few studies go beyond qualitative agreement with the predictions of contingent theory to more rigorous, quantitative tests.

Protist Assemblages

"Bottle experiments" (83) offer powerful opportunities to test the contingent theories of apparent competition. Lawler (91), for instance, grew two species of bacterivorous protists, *Chilomonas,* a flagellate (denoted C below), and *Tetrahymena* (T), a small ciliate, with a predatory protist, *Euplotes* (E), a larger ciliate, in assorted combinations. She demonstrated that in one predator–one prey treatments (E-C and E-T), E persisted for 40–60 generations with either C or T. Moreover, the two prey species coexisted in the absence of predation. She further noticed (personal communication) that compared with prey abundances in the absence of predation, E depressed T by around 50%, whereas C was depressed nearly two orders of magnitude; moreover, equilibrial abundance of E in the E-C treatment was much less than in the E-T treatments. These results suggest the predator has a much higher attack rate on C than on T, i.e. $a_C >> a_T$, permitting over-exploitation of C.

Lawler further noted that T became very abundant in microcosms within two days after introduction into single-species cultures, while C did not become abundant until the fourth day, suggesting that $r_T >> r_C$. Hence, $r_T/a_T > r_C/a_C$. Theoretically, the prey that supports the highest predator density (i.e. highest r/a, see above) should displace alternative prey. In other words, T should displace C in the face of shared predation by E.

This is exactly what happened. In experimental treatments beginning with E-C-T, C disappeared rapidly as E grew beyond the average abundance supported in the E-C treatments. This experiment appears to be the first demonstration of apparent competition in a controlled laboratory microcosm. It is completely consistent with the a priori theoretical expectations for prey dominance under apparent competition.

"Bottle experiments" have also been carried out by Nakajima & Kurihara (122). They used a continuous dialysis system with a bacterium (*Escherichia coli*) supporting a protozoan (*Tetrahymena thermophila*), to show that mutant bacterial clones with higher growth rates or lower attack rates successfully supplant resident clones by enhancing the predator's equilibrium density (generating increased predation upon the ancestral clones).

Habitat Partitioning

Habitat segregation between alternative prey is one potential outcome of shared predation (66). Schmitt (152) documented an example in a subtidal reef community and experimentally corroborated the role of shared predation.

This community has two distinct habitats: high-relief reefs, with surface texture providing refuges from predation; and cobble reefs, offering few refuges. A guild of mobile predators (e.g. lobster, octopus, whelk) attacks two functional groups of molluscan prey, sessile bivalves (the most common being *Chama arcana*) and mobile herbivorous snails (three species) (a "many-to-many" scenario; see Figure 1). Even though bivalves are preferred prey, they are common on high-relief reefs, where predators are also common but gastropods rare. Conversely, on cobble reefs gastropods are relatively common, but bivalves rare. The two functional prey groups use distinct resources and do not compete directly.

Experimental augmentation of bivalves in the cobble reef increased predators four-fold via aggregative numerical responses; this increased gastropod mortality and sharply reduced gastropod abundance. A correlative study using transplanted *Chama* on the cobble reef revealed that local predator abundance (and *Chama* mortality) tracked local gastropod abundance. Schmitt argued (personal communication) that even the low abundance of predators maintained by resident gastropods on the cobble reefs suffices to eliminate sessile bivalves there; reciprocally, the high abundance of predators maintained on high-relief reefs by partially protected bivalve populations keeps gastropods rare. Schmitt concluded that this habitat segregation reflects shared predation. Further field experiments are needed to validate this hypothesis fully.

One further example will suffice, incorporating several processes. Bergerud (16, 17) argued that on Newfoundland, large lynx populations (high P) are maintained by productive snowshoe hare populations in boreal habitats. Resulting intense lynx predation limits arctic hares to tundra—a habitat not occupied by snowshoe hares. Arctic and snowshoe hares introduced onto islands without predators coexist; in one case, later introducing lynx forced the arctic hare to extinction (112). Arctic hares have intrinsically low r's (60), particularly when restricted to boreal forest foodstuffs (14), making it unlikely that $r > aP$ in this habitat. Other predators, particularly red foxes, may be as important mortality agents for arctic hares as lynx (AT Bergerud, personal communication), implicating other alternative prey, such as voles, as determinants of arctic hare distribution. A final twist is that snowshoe hares are differentially highly vulnerable to avian predators in tundra habitats (14), which may in part explain the confinement of snowshoe hares to boreal forest.

APPLIED IMPLICATIONS OF SHARED PREDATION

Indirect interactions via shared predators are significant in many applied ecological problems. We touch on three.

Wildlife Disease Epidemiology

A well-known phenomenon in wildlife disease epidemiology is that certain hosts provide "reservoirs" for infectious disease agents, which can severely depress focal host populations (32, 116, 153). White-tailed deer sustain and can withstand a meningeal worm fatal to caribou. Hence, "caribou cannot be introduced to ranges where white-tailed deer have a high frequency of meningeal worm infections" (18, see also 72, 75, 76, 133, 146).

Biological Control

Aspects of apparent competition are important in biological pest control (71, 94). Howarth (73) summarizes several examples where polyphagous parasitoids, released as biological control agents, appear to have caused the local or regional extinction of the pest or of native, nontarget hosts. In the Florida Keys, the endemic cactus *Opuntia spinosissima* is threatened with imminent extinction by an introduced biocontrol agent, *Cactoblastis cactorum,* whose population is sustained by the target weed, an introduced cactus, *O. stricta* (163). Conversely, released biocontrol agents may fail to establish because of attack by indigenous, polyphagous enemies (51, 71, 90).

Biocontrol practitioners have long recognized the significance of several of the phenomena highlighted in this review as means of increasing predation and parasitism on economically important focal prey. These include the use of "supplementary resources" (e.g. pollen, nectar, and honeydew—management that boosts alternative "prey" numbers) to maintain high populations of potential control agents (43, 45, 77, 82, 178), and provisioning alternative nesting, feeding, or over-wintering sites to boost predator numbers, either within a crop, or to promote predator flows from a reservoir (77, 171).

Landscape Effects and Conservation

Alternative prey are significant causes in the declines of many endangered populations. Examples involving alien prey or predators were noted above. But native predators can also be important (175). Many forest landbirds are decreasing precipitously in forest fragments in the United States because of high parasitism by cowbirds and nest losses from avian and mammalian predators (108, 148, 182, 183). Large enemy populations are maintained by food outside forest fragments, including anthropogenic sources. Mesopredator release poses a significant conservation threat to prey populations via apparent competition in many parts of the world (137, 159, 165, 170).

Human impacts on landscapes may be exacerbated by polyphagous herbivores. In eastern and central United States, white-tailed deer have increased greatly due to forest clearing and deliberate game management, creating early to mid-successional vegetation. Deer move into mature forest stands, where their selective herbivory profoundly alters community composition (5). For instance, young age classes of hemlock, yew, and white cedar can be abundant within exclosures, yet absent outside.

FUTURE DIRECTIONS

Part of our original intent in sculpting this review was to provide a table, akin to that in Sih et al (162), cross-classifying a wide range of empirical studies of shared predation according to various criteria, then comparing the patterns in the table to basic theoretical expectations. We abandoned this goal, because only rarely do authors report all the pertinent information needed to relate empirical studies to theory. Ideally, the following desiderata would be provided:

1. Habitat
2. Number of enemy species, with Latin family and specific names (it is appalling how rarely the latter are provided outside the entomological literature)
3. Number of victim species, with Latin names
4. Knowledge of resource-based competition among victims
5. Nature of data (controlled experiment; quasi-experiment; observational)
6. Spatial scale (e.g. quadrat sizes)

7. Spatial context (open/closed to enemy/victim dispersal; landscape configuration)
8. Temporal scale of study (relative to enemy and victim generations)
9. Enemy response to focal victim populations (e.g. aggregative or reproductive response)
10. Impact on victims (e.g. none; apparent mutualism; victim exclusion).

This may appear a daunting list, but much can be gauged with reasonable accuracy from basic natural history. Given the burgeoning state of the ecological literature, it is imperative that ecologists provide enough information to link their published work with related empirical studies, and with general theory, and in particular to identify those contingent theories that have explanatory power in particular systems.

The case studies and theory summarized in this review convince us that indirect inhibitory interactions arising from shared enemies are a powerful, dominant theme in natural communities, and a significant component in many applied ecological problems. We have identified a number of theoretical predictions that have yet to be tested, and shared predation scenarios that have yet to be examined theoretically. Much remains to be done.

ACKNOWLEDGMENTS

We thank Claire Challis, Wendy Wastell, Brenda Kaye, and Jennifer Wilson for assistance in manuscript preparation, and Peter Abrams and Billy Schweiger for perceptive comments on the manuscript. Preparation was supported from the core grant to the NERC Centre for Population Biology, and by grants from the US National Science Foundation and the British Ecological Society to RD Holt. JH Lawton thanks the Konza Prairie for allowing him to share ticks with bison; RD Holt thanks his lucky stars for walks in enemy-free space. We thank numerous colleagues for preprints and advice. Apologies to the authors of many excellent papers we had no room to cite.

Literature Cited

1. Abrams P. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. See Ref. 85, pp. 38–54
2. Abrams PA. 1987. On classifying interactions between populations. *Oecologia* 73:272–81

2a. Abrams PA. 1993. Indirect effects arising from optimal foraging. In *Mutualism and Community Organization*, ed. H Kawanabe, JE Cohen, K Iwasaki, pp. 255–79. Oxford: Oxford Univ. Press

2b. Abrams PA. 1994. The fallacies of "ratio dependent predation." *Ecology*. In press

3. Addicott JF. 1974. Predation and prey

community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. *Ecology* 55:475–92

4. Akçakaya HR. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecol. Monogr.* 62:119–42
5. Alverson WS, Waller DM, Solheim SL. 1988. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2: 348–58
6. Anderson DJ. 1991. Apparent predator-limited distribution of Galápagos red-footed boobies *Sula sula*. *Ibis* 133:26–29
7. Andersson Å. 1992. Development of waterbird populations in the Bullerö archipelago off Stockholm after colonization by mink (Swedish, English summary). *Ornis Svecica* 2:107–18
8. Arditi R, Perrin N, Saiah H. 1991. Functional responses and heterogeneities: an experimental test with cladocerans. *Oikos* 60:69–75
9. Aronson RB, Sues H-D. 1987. The paleoecological significance of an anachronistic ophiuroid community. See Ref. 85, pp. 355–66
10. Arthur W, Mitchell P. 1989. A revised scheme for the classification of population interactions. *Oikos* 56:141–43
11. Atkinson IAE. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In *Conservation of Island Birds*, ed. PJ Moors, pp. 35–81. *ICBP Tech. Publ. No. 3*
12. Atkinson IAE., Cameron EK. 1993. Human influences on the terrestrial biota and biotic communities of New Zealand. *Trends Ecol. Evol.* 8:447–51
13. Baillie S, Gooch S, Birkhead T. 1993. The effect of magpie predation on songbird populations. In *Britain's Birds in 1990–91: the Conservation and Monitoring Review*, ed. J Andrews, SP Carter, pp. 68–73. Thetford: Br. Trust for Ornithol., Joint Nature Conserv. Com.
14. Barta RM, Keith LB, Fitzgerald SM. 1989. Demography of sympatric arctic and snowshoe hare populations: an experimental assessment of interspecific competition. *Can. J. Zool.* 67:2762–75
15. Belovsky GE, Slade JB. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos* 68: 193–201
16. Bergerud AT. 1967. The distribution and abundance of arctic hares in Newfoundland. *Can. Field Nat.* 81:242–48
17. Bergerud AT. 1983. Prey switching in a simple ecosystem. *Sci. Am.* 249:130–41
18. Bergerud AT, Mercer WE. 1989. Caribou introductions in eastern North America. *Wildl. Soc. Bull.* 17:111–20
19. Bernays E, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886–92
20. Black RW II, Hairston NG Jr. 1988. Predation driven changes in community structure. *Oecologia* 77:468–79
21. Brown JS, Mitchell WA. 1989. Diet selection on depletable resources. *Oikos* 54:33–43
22. Bulmer MG. 1975. Phase relations in the ten-year cycle. *J. Anim. Ecol.* 44: 609–12
23. Burdon JJ. 1993. The role of parasites in plant populations and communities. In *Biodiversity and Ecosystem Function*, ed. E-D Schulze, HA Mooney, pp. 165–79. Berlin: Springer-Verlag
24. Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, et al. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–76
25. Case TJ, Bolger DT. 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. *Evol. Ecol.* 5:272–90
26. Churcher PB, Lawton JH. 1987. Predation by domestic cats in an English village. *J. Zool.* 212:439–55
27. Comins HN, Hassell MP. 1976. Predation in multi-prey communities. *J. Theor. Biol.* 62:93–114
28. Connell JH. 1990. Apparent versus "real" competition in plants. In *Perspectives on Plant Competition*, ed. JB Grace, D Tilman, pp. 445–74. New York: Academic
29. Copeland RS, Craig GB Jr. 1992. Interspecific competition, parasitism, and predation affect development of *Aedes hendersoni* and *A. triseriatus* (Diptera: Culicidae) in artificial treeholes. *Ann. Entomol. Soc. Am.* 85:154–63
30. Crawley MJ, ed. 1992. *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*. Oxford: Blackwell Sci. 576 pp.
31. Diehl S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68:151–57
32. Dobson AP, Hudson PJ. 1986. Parasites, disease and the structure of ecological communities. *Trends Ecol. Evol.* 1:11–15
33. Dobson AP, May RM. 1991. Parasites, cuckoos, and avian population dynamics. See Ref. 129a, pp. 391–412
34. Doncaster CP. 1992. Testing the role of intraguild predation in regulating hedge-

hog populations. *Proc. R. Soc. Lond. B* 249:113–17

35. Drost CA, McCluskey RC. 1992. Extirpation of alternative prey during a small rodent crash. *Oecologia* 92:301–4
36. Dunn E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46:633–52
37. Ebenhard T. 1988. Introduced birds and mammals and their ecological effects. *Swed. Wild. Res. - Viltrevy* 13(4):5–107
38. Elton C. 1927. *Animal Ecology*. London: Sidgwick & Jackson. 204 pp.
39. Elton CS. 1951. The use of cats in farm rat control. *Br. J. Anim. Behav.* 1:151–55
40. Erlinge S. 1987. Predation and noncyclicity in a microtine population in southern Sweden. *Oikos* 50:347–52
41. Erlinge S, Göransson G, Högstedt G, Jansson G, Liberg O, et al. 1984. Can vertebrate predators regulate their prey? *Am. Nat.* 123:125–33
42. Estes JA. 1994. Top-level carnivores and ecosystem effects: questions and approaches. In *Linking Species and Ecosystems*, ed. CG Jones, JH Lawton. New York: Chapman & Hall. In press
43. Evans EW. 1994. Indirect interactions among phytophagous insects: aphids, honeydew, and natural enemies. In *Individuals, Populations, and Patterns in Ecology*, ed. S Leather, N Mills, A Watt. Andover: Intercept. In press
44. Fauth JE, Resetarits WJ Jr. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. *Ecology* 72:827–38
45. Flaherty DL. 1969. Ecosystem trophic complexity and Willamette mite, *Eotetranychus willamettei* Ewing (Acarina: Tetranychidae), densities. *Ecology* 50:911–15
46. Fowler SV, MacGarvin M. 1985. The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *J. Anim. Ecol.* 54:847–55
47. Freeland WJ. 1983. Parasites and the coexistence of animal host species. *Am. Nat.* 121:223–36
48. Gilbert JJ, MacIsaac HJ. 1989. The susceptibility of *Keratella cochlearis* to interference from small cladocerans. *Freshwater Biol.* 22:333–39
49. Gilpin ME. 1979. Spiral chaos in a predator-prey model. *Am. Nat.* 113:306–8
50. Gleeson SK, Wilson DS. 1986. Equilibrium diet: optimal foraging and prey coexistence. *Oikos* 46:139–44
51. Goeden RD, Louda SM. 1976. Biotic interference with insects imported for weed control. *Annu. Rev. Entomol.* 21: 325–42
52. Gooch S, Baillie SR, Birkhead TR. 1991. Magpie *Pica pica* and songbird populations. Retrospective investigation of trends in population density and breeding success. *J. Appl. Ecol.* 28: 1068–86
53. Grosholz ED. 1992. Interaction of intraspecific, interspecific, and apparent competition with host-pathogen population dynamics. *Ecology* 73:507–14

53a. Gross P. 1993. Insect behavioral and morphological defenses against parasitoids. *Annu. Rev. Entomol.* 38:251–73

54. Halle S. 1988. Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*). *Oecologia* 75: 451–55
55. Hanski I, Hansson L, Henttonen H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60:353–67
56. Hansson L. 1989. Predation in heterogeneous landscapes: how to evaluate total impact? *Oikos* 54:117–19
57. Hassell MP. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton, NJ: Princeton Univ. Press. 237 pp.
58. Hassell MP, May RM. 1986. Generalist and specialist natural enemies in insect predator-prey interactions. *J. Anim. Ecol.* 55:923–40
59. Heads PA, Lawton JH. 1984. Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. *J. Anim. Ecol.* 53:1015–31
60. Hearn BJ, Keith LB, Rongstad OJ. 1987. Demography and ecology of the arctic hare (*Lepus arcticus*) in southwestern Newfoundland. *Can. J. Zool.* 65:852–61
61. Hixon MA, Menge BA. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoret. Pop. Biol.* 39:178–200
62. Hochberg ME, Clarke RT, Elmes GW, Thomas JA. 1994. Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. *J. Anim. Ecol.* 63:375–91
63. Holling CS. 1965. The functional response of predators to prey densities and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:5–60
64. Holt RD. 1977. Predation, apparent competition, and the structure of prey

communities. *Theoret. Pop. Biol.* 12: 197–229

65. Holt RD. 1983. Optimal foraging and the form of the predator isocline. *Am. Nat.* 122:521–41
66. Holt RD. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124:377–406
67. Holt RD. 1987. Prey communities in patchy environments. *Oikos* 50:276–90
68. Holt RD. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives,* ed. RE Ricklefs, D Schluter, pp. 77–88. Chicago: Univ. Chicago Press
69. Holt RD, Grover J, Tilman D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.* 144:741–71
70. Holt RD, Kotler BP. 1987. Short-term apparent competition. *Am. Nat.* 130: 412–30
71. Holt RD, Lawton JH. 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. *Am. Nat.* 142:623–45
72. Holt RD, Pickering J. 1985. Infectious disease and species coexistence: a model of Lotka-Volterra form. *Am. Nat.* 126:196–211
73. Howarth FG. 1991. Environmental impacts of classical biological control. *Annu. Rev. Entomol.* 36:485–509
74. Huang C, Sih A. 1990. Experimental studies on behaviorally mediated, indirect interactions through a shared predator. *Ecology* 71:1515–22
75. Hudson P. 1992. *Grouse in Space and Time: The Population Biology of a Managed Gamebird.* Fordingbridge, UK: Game Conservancy. 224 pp.
76. Hudson PJ, Dobson AP. 1991. Control of parasites in natural populations: nematode and virus infections of red grouse. See Ref. 129a, pp. 413–32
77. Huffaker CB, Messenger PS, eds. 1976. *Theory and Practice of Biological Control.* New York: Academic
78. Huxley CR, Cutler DF, eds. 1991. *Ant-Plant Interactions.* Oxford: Oxford Univ. Press. 601 pp.
79. Ito F, Higashi S. 1991. Variance of ant effects on the different life forms of moth caterpillars. *J. Anim. Ecol.* 60:327–34
80. Jeffries MJ, Lawton JH. 1984. Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.* 23:269–86
81. Jouventin P, Weimerskirch H. 1991. Changes in the population size and demography of southern seabirds: management implications. See Ref. 129a, pp. 297–314
82. Karban R, Hougen-Eitzman D, English-Loeb G. 1994. Predator-mediated apparent competition between two herbivores that feed on grapevines. *Oecologia.* 97: 508–11
83. Kareiva P. 1989. Renewing the dialogue between theory and experiments in population ecology. In *Perspectives in Ecological Theory,* ed. J Roughgarden, RM May, SA Levin, pp. 68–88. Princeton, NJ: Princeton Univ. Press
84. Kenward RE, Parish T, Robertson PA. 1992. Are tree species mixtures too good for grey squirrels? In *The Ecology of Mixed-Species Stands of Trees,* ed. MGR Cannell, DC Malcolm, PA Robertson, pp. 243–53. Oxford: Blackwell Sci.
85. Kerfoot WC, Sih A, eds. 1987. *Predation: Direct and Indirect Impacts on Aquatic Communities.* Hanover, NH: Univ. Press New Engl.
86. Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* 32:674–82
87. Koptur S. 1991. Extrafloral nectaries of herbs and trees: modelling the interaction with ants and parasitoids. In *Ant-Plant Interactions,* ed. CR Huxley, DF Cutler, pp. 213–30. Oxford: Oxford Univ. Press
88. Korpimäki E, Huhtala K, Sulkava S. 1990. Does the year-to-year variation in the diet of eagle and Ural owls support the alternative prey hypothesis? *Oikos* 58:47–54
89. Kretzschmar MR, Nisbet RM, McCauley E. 1993. A predator-prey model for zooplankton growing on competing algal populations. *Theoret. Pop. Biol.* 44:32–66
90. Lake PS, O'Dowd DJ. 1991. Red crabs in rain forest, Christmas Island: biotic resistance to invasion by an exotic snail. *Oikos* 62:25–29
91. Lawler SP. 1993. Direct and indirect effects in microcosm communities of protists. *Oecologia* 93:184–90
92. Lawler SP. 1993. Species richness, species composition and population dynamics of protists in experimental microcosms. *J. Anim. Ecol.* 62:711–19
93. Lawton JH. 1986. The effect of parasitoids on phytophagous insect communities. In *Insect Parasitoids. 13th Symposium of the Royal Entomological Society, London,* ed. J Waage, D Greathead, pp. 265–87. London: Academic
94. Lawton JH. 1990. Biological control of plants: a review of generalisations, rules

and principles using insects as agents. In *Alternatives to Chemical Control of Weeds: Proceedings of an Int. Conf., Rotorua, New Zealand*, ed. C Bassett, LJ Whitehouse, JA Zabkiewicz, pp. 3–17. Rotorua: Ministry of For., For. Res. Inst. Bull. 155

95. Lawton JH. 1993. Range, population abundance and conservation. *Trends Ecol. Evol.* 8:409–13
96. Lawton JH, Beddington JR, Bonser R. 1974. Switching in invertebrate predators. In *Ecological Stability*, ed. MB Usher, MH Williamson, pp. 141–58. London: Chapman & Hall
97. Lawton JH, Heads PA. 1984. Bracken, ants and extrafloral nectaries I. The components of the system. *J. Anim. Ecol.* 53:995–1014
98. Lawton JH, Woodroffe GL. 1991. Habitat and the distribution of water voles: why are there gaps in a species' range? *J. Anim. Ecol.* 60:79–91
99. Leibold MA. 1991. Trophic interactions and habitat segregation between competing *Daphnia* species. *Oecologia* 86: 510–20

99a. Leibold MA. 1994. A graphical model of keystone predators in food webs: effects of productivity on abundance, incidence, and diversity patterns in communities. MS.

100. Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–40
101. Lindstrom E, Angelstam P, Widen P, Andren H. 1987. Do predators synchronize vole and grouse fluctuations? *Oikos* 48:121–24
102. Louda SM, Keeler KH, Holt RD. 1990. Herbivore influences on plant performance and competitive interactions. In *Perspectives on Plant Competition*, ed. JB Grace, D Tilman, pp. 415–44. New York: Academic
103. MacArthur RH. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row. 269 pp.
104. Madsen J, Bregnballe T, Mehlum F. 1989. Study of the breeding ecology and behaviour of the Svalbard population of light-bellied brent goose *Branta bernicla hrota*. *Polar Res.* 7:1–21
105. Martin TE. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proc. Natl. Acad. Sci. USA* 85:2196–99
106. Martin TE. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evol. Ecol.* 2: 37–50
107. Matson P, Berryman A. 1992. Ratio-dependent predator-prey theory. *Ecology* 73:1529–66
108. May RM, Robinson SK. 1985. Population dynamics of avian brood parasites. *Am. Nat.* 126:475–94
109. McPeek MA. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71:83–98
110. Menge BA. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.* In press
111. Menge BA, Sutherland JP. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130:730–57
112. Mercer WE, Hearn BJ, Findlay C. 1981. Arctic hare populations in insular Newfoundland. In *Proc. World Lagomorph Conf.*, ed. K. Myers, CD MacInnes, pp. 450–68
113. Miller DJ. 1989. Introduction and extinction of fish in the African Great Lakes. *Trends Ecol. Evol.* 4:56–59
114. Miller TE, Kerfoot WC. 1987. Redefining indirect effects. See Ref. 85, pp. 33–37
115. Mills LSM, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43: 219–24
116. Minchella DJ, Scott ME. 1991. Parasitism: a cryptic determinant of animal community structure. *Trends Ecol. Evol.* 6:250–54
117. Mittlebach GG, Chesson PL. 1987. Predation risk: indirect effects on fish populations. See Ref. 85, pp. 315–32
118. Murdoch WW. 1973. The functional response of predators. *J. Appl. Ecol.* 10:335–42
119. Murdoch WW, Bence J. 1987. General predators and unstable prey populations. See Ref. 85, pp. 17–30
120. Murdoch WW, Oaten A. 1975. Predation and population stability. *Adv. Ecol. Res.* 9:1–25
121. Naeem S. 1988. Predator-prey interactions and community structure: chironomids, mosquitoes and copepods in *Heliconia imbricata* (Musaceae). *Oecologia* 77:202–9
122. Nakajima T, Kurihara Y. 1994. Evolutionary changes of ecological traits of bacterial populations through predator-mediated competition. I. Experimental analysis. *Oikos*. In press

122a. Nakajima T, Kurihara Y. 1994. Evolutionary changes of ecological traits of bacterial populations through predator-mediated competition. II. Theoretical considerations. *Oikos*. In press

123. Newton I. 1991. Concluding remarks. See Ref. 129a, pp. 637–54

124. Oksanen L, Fretwell SD, Arruda J, Niemalä P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240–62

125. Oksanen T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. *Evol. Ecol.* 4:220–34

126. Paine RT. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65–75

127. Park T. 1948. Experimental studies on interspecific competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecol. Monogr.* 18:267–307

128. Parnell JR. 1964. The parasite complex of two seed beetles *Bruchius ater* (Marsham) (Coleoptera: Bruchidae) and *Apion fuscirostre* Fabricius (Coleoptera: Curculionidae). *Trans. R. Entomol. Soc., London* 116:73–88

129. Pech RP, Sinclair ARE, Newsome AE. 1994. Predation models for primary and secondary prey species. *Aust. Wildlife Res.* In press

129a. Perrins, CM, Lebreton J-D, Hirons GJM, eds. 1991. *Bird Population Studies: Relevance to Conservation and Management.* Oxford: Oxford Univ. Press

130. Pimm SL. 1987. The snake that ate Guam. *Trends Ecol. Evol.* 2:293–95

131. Pimm SL. 1991. *The Balance of Nature?* Chicago: Univ. Chicago Press. 434 pp.

132. Pimm SL, Lawton JH. 1978. On feeding on more than one trophic level. *Nature* 275:542–44

133. Plowright W. 1982. The effects of rinderpest and rinderpest control in east Africa. *Symp. Zool. Soc. Lond.* 50:1–28

134. Polis GA, Holt RD. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7:151–55

135. Polis GA, Myers CA, Holt RD. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330

136. Polis GA, Holt RD, Menge BA, Winemiller K. 1995. Time, space, and life history: influences on food webs. In *Food Webs*: Integration of Patterns and Dynamics, ed. GA Polis, K Winemiller. London: Chapman & Hall. In press

137. Potts GR. 1986. *The Partridge: Pesticides, Predation and Conservation.* London: Collins. 274 pp.

138. Potts GR. 1993. Red-legged partridge. In *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*, ed. DW Gibbons, JB Reid, RA Chapman, pp. 134–35. London: Poyser, TAD

139. Price PW, Westoby M, Rice B. 1988. Parasite-mediated competition; some predictions and tests. *Am. Nat.* 131:544–55

140. Price PW, Westoby M, Rice B, Atsatt PR, Fritz RS, et al. 1986. Parasite mediation in ecological interactions. *Annu. Rev. Ecol. Syst.* 17:487–505

141. Pulliam HR. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132: 652–61

142. Reader RJ. 1992. Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology* 73:373–76

143. Resetarits WJ Jr. 1991. Ecological interactions among predators in experimental stream communities. *Ecology* 72: 1782–93

144. Ricklefs RE. 1979. *Ecology*. New York: Chiron Press

145. Ricklefs RE, O'Rourke K. 1975. Aspect diversity in moths: a temperate-tropical comparison. *Evolution* 29:313–24

146. van Ripper C III, van Ripper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327–44

147. Robinson JV, Wellborn GA. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea:* fish predation effects. *Oecologia* 77: 445–52

148. Robinson SK. 1992. Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape. In *Ecology and Conservation in Neotropical Migrant Landbirds*, ed. JM Hagen III, DW Johnston, pp. 408–18. Washington, DC: Smithsonian Inst. Press

149. Ruxton GD, Gurney WS C. 1992. The interpretation of tests for ratio-dependence. *Oikos* 65:334–35

150. Savidge JA. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–68

151. Schlumprecht H. 1989. Dispersal of the thistle gallfly *Urophora cardui* and its endoparasitoid *Eurytoma serratulae* (Hymenoptera: Eurytomidae). *Ecol. Entomol.* 14:341–48

152. Schmitt RJ. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology* 68:1887–97

153. Schmitz OJ, Nudds TD. 1994. Parasite-mediated competition in deer and moose: how strong is the effect of me-

ningeal worm on moose? *Ecological Appl.* 4:91–103

154. Schoener TW. 1986. Overview: Kinds of ecological communities—ecology becomes pluralistic. In *Community Ecology*, ed. J. Diamond, TJ Case, pp. 467–79. New York: Harper & Row

155. Schoener TW. 1993. On the relative importance of direct versus indirect effects in ecological communities. In *Mutualism and Community Organization*, ed. H Kawanaba, J Cohen, pp. 365–408. Oxford: Oxford Univ. Press

156. Schoener TW, Spiller DA. 1987. Effects of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science* 236:949–52

157. Schönrogge K, Stone GN, Crawley MJ. 1994. Spatial and temporal variation in guild structure: Parasitoids and inquilines of *Andricus quercuscalicis* Burgsd. (Hymenoptera: Cynipidae) in its native and alien ranges. *Oikos*. In press

157a. Scudder GGE. 1983. A review of factors governing the distribution of two closely related corixids in the saline lakes of British Columbia. *Hydrobiologia* 105: 143–54

158. Settle WH, Wilson LT. 1990. Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology* 71: 1461–70

159. Sieving KE. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* 73:2310–28

160. Sih A. 1985. Evolution, predator avoidance, and unsuccessful predation. *Am. Nat.* 125:153–57

161. Sih A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. See Ref. 85, pp. 203–24

162. Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K. 1985. Predation, competition and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:269- 311

163. Simberloff D. 1992. Conservation of pristine habitats and unintended effects of biological control. In *Selection Criteria and Ecological Consequences of Importing Natural Enemies*, ed. WC Kauffman, JR Nechols, pp. 103–17. Landham, MD: Entomol. Soc. Am.

164. Simenstad CA, Estes JA, Kenyon KW. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* 200: 403–11

165. Soulé ME, Bolger DT, Alberts AC, Wright J, Sorice M, et al. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2:75–92

166. Spiller DA, Schoener TW. 1988. An experimental study of the effect of lizards on web-spider communities. *Ecol. Monogr.* 58:57–77

167. Spiller DA, Schoener TW. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83:150–61

168. Strauss SY. 1991. Indirect effects in community ecology: their definition, study and importance. *Trends Ecol. Evol.* 6:206–10

169. Takehuchi Y, Adachi N. 1983. Existence and bifurcation of stable equilibrium in two-prey, one-predator communities. *Bull. Math. Biol.* 45:877–900

170. Terborgh J, Winter B. 1980. Some causes of extinction. In *Conservation Biology: An Evolutionary-Ecological Perspective*, ed. ME Soulé, BA Wilcox, pp. 119–33. Sunderland, Mass: Sinauer

171. Thomas MB, Wratten SD, Sotherton NW. 1991. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *J. Appl. Ecol.* 28: 906–17

172. Underhill LG, Prys-Jones RP, Syroechkovski EE Jr, Groen NM, Karpov V, et al. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeast Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277–92

173. Vance RR. 1978. Predation and resource partitioning in one predator-two prey model communities. *Am. Nat.* 112:797-813

174. Vandermeer J. 1991. Contributions to the global analysis of 3-D Lotka-Volterra equations: dynamic boundedness and indirect interactions in the case of one predator and two prey. *J. Theor. Biol.* 148:545–61

175. Vickery PD, Hunter ML Jr, Wells JV. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63:281–88

176. Watt AS. 1981. A comparison of grazed and ungrazed Grassland A in East Anglian Breckland. *J. Ecol.* 69:499–508

177. Watt AS. 1981. Further observations on the effects of excluding rabbits from Grassland A in East Anglian Breckland: The pattern of change and factors affecting it (1936–1973). *J. Ecol.* 69:509–36

178. Way MJ, Khoo KC. 1992. Role of ants in pest management. *Annu. Rev. Entomol.* 37:479–503

179. Werner EE. 1992. Individual behavior and higher-order species interactions. *Am. Nat. (Supplement)* 140:5–32

180. White J. 1980. Resource partitioning by ovipositing cicadas. *Am. Nat.* 115:1–28

181. Wilbur HM, Fauth JE. 1990. Experimental aquatic food webs: interactions between two predators and two prey. *Am. Nat.* 135:176–204

182. Wilcove DS. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–14

183. Wilcove DS, McLellan CH, Dobson AP. 1986. Habitat fragmentation in the temperate zone. In *Conservation Biology. The Science of Scarcity and Diversity*, ed. ME Soulé, pp. 37–56. Sunderland, Mass: Sinauer

184. Williams KS, Smith KG, Stephen FM. 1993. Emergence of 13-yr periodical cicada (Cicadidae: Magicicada): phenology, mortality, and predator satiation. *Ecology* 74:1143–52

185. Williamson MH. 1957. An elementary theory of interspecific competition. *Nature* 180:422–25

186. Wise DH. 1993. *Spiders in Ecological Webs.* Cambridge: Cambridge Univ. Press. 328 pp.

187. Wissinger S, McGrady J. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology* 74:207–18

188. Woodman RL, Price PW. 1992. Differential larval predation by ants can influence willow sawfly community structure. *Ecology* 73:1028–37

189. Woodward BD. 1983. Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. *Ecology* 64:1549–55

189a. Wootton JT. 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* In press

190. Yodzis P. 1986. Competition, mortality, and community structure. In *Community Ecology*, ed. J Diamond, TJ Case, pp. 480–91. New York: Harper & Row

191. Zwölfer H. 1961. A comparative analysis of the parasite complexes of the European fir budworm, *Choristoneura murinana* (Hub.) and the North American spruce budworm *C. fumiferana* (Clem.). *CIBC Tech. Bull.* 1:1–162

NOTE ADDED IN PROOF

We have become aware of two excellent examples of apparent competition between plants due to shared herbivory, both highlighting spatial consequences: MA Parker & RB Root, 1981. Insect herbivores limit habitat distribution of a native composite, *Machearanthera canescens Ecology* 62:1390–92; CD Thomas, 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia* 70:113–17. A broad overview of herbivore effects on plant communities is provided by N Huntly, 1991. Herbivores and the dynamics of communities and ecosystems *Annu. Rev. Ecol. Syst.* 22:477–503. Finally, poaching on African buffalo (a grazer) in the Serengeti has depressed lion numbers, leading to marked increase in impala (a browser)—an inadvertent experiment indicating the existence of apparent competition via shared lion predation: ARE Sinclair, 1995. Population limitation of resident herbivores. In *Serengeti II: Research, Management and Conservation of an Ecosystem*, ed. ARE Sinclair and P Arcese. Chicago: Univ. Chicago Press. In press. We would welcome being told of additional pertinent examples.