

THE ECOLOGY AND EVOLUTION OF INTRAGUILD PREDATION: Potential Competitors That Eat Each Other

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INTRODUCTION

Interactions between species are usually categorized as either competition (—), predation/parasitism (+—), mutualism (++), commensalism (+0), or amensalism (—0). Intraguild predation (IGP) is a combination of the first two, that is, the killing and eating of species that use similar, often limiting, resources and are thus potential competitors. Intraguild predation is distinguished from traditional concepts of competition by the immediate energetic gains for one participant (the predator). It differs from classical predation because the act reduces potential exploitation competition. Thus, its impact on population dynamics is more complex than either competition or predation alone (see below).

Our purpose is to document the ubiquity and importance of intraguild predation and to establish a theoretical framework for its analysis. A taxonomically widespread interaction, IGP significantly affects the distribution, abundance, and evolution of many species. One intriguing conclusion is that IGP promotes the occurrence of alternative stable states in many circumstances. Although sometimes recognized by theoreticians and empirically oriented biologists, this is the first synthesis of IGP into a general work.

“Intraguild” predation occurs among members of the same “guild.” Root (119) defined a guild as “a group of species that exploit the same class of environmental resources in a similar way.” We use the term more broadly to include all taxa in a community that use similar resources (food or space) and thus may compete, regardless of differences in tactics of resource acquisition. Synonyms for IGP include predation or predatory interference (16), and predatory aggression (81).

CATEGORIZATION AND TAXONOMIC DISTRIBUTION

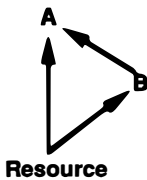
As a simplifying scheme, we cross-classify the bewildering array of IGP configurations in two ways: symmetry (symmetric vs asymmetric) and age structure (relatively unimportant vs important). Asymmetric IGP occurs when one species (*A*, by convention) is always the predator on *B*.

occurs during mutual predation between *A* and *B*. Age structure is important when IGP is influenced by ontogenetic changes in size or vulnerability. In this catalog, we briefly outline examples of IGP for each category. In all cases cited, substantial dietary overlap (i.e. use of common foods) occurs between IG predators and IG prey; in many instances competition was either suspected or demonstrated.

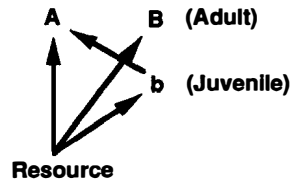
Age Structure Relatively Unimportant, Asymmetrical

OMNIVOROUS INTRAGUILD PREDATION Almost any diet or food web study shows that IGP on smaller predators is ubiquitous. Most predators eat food types in a particular size range regardless of that prey’s trophic levels or feeding history (51, 88, 105, 132). Thus, larger species are frequently omnivorous both on a resource and on smaller (intermediate level) consumers of that resource (see Figure 1a). This “closed loop omnivory” (132) characterizes freshwater (51, 86, 91, 92, 132), marine (20, 27, 83, 85, 101) and terrestrial (12, 88, 105, 145) food webs. In most cases, large *A* eat smaller *B* (Figure 1a). We artificially divide these examples into interactions among taxonomically related vs unrelated guild members.

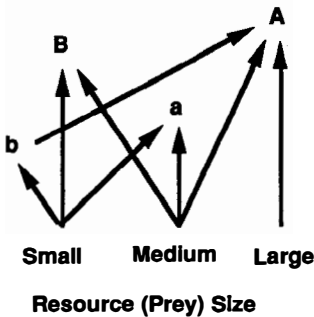
Intraguild predation on smaller, intermediate level predators from unrelated taxa is the norm for consumers that attack general prey classes, e.g. insects, arthropods, plankton, and fish. Nematophagous mites eat fungivorous, microphagous, herbivorous, and predaceous (nematophagous) nematodes (145). The scorpion *Paruroctonus mesaenis* eats more than 50 species of smaller arachnid and insect predators in addition to the prey of these predators (105, 107; see Figure 2). Such omnivory typifies arthropodivores: predators and parasitoids represented, on average, 41% and 52% of the arthropod prey of 15 desert vertebrates and 6 arthropods; other prey were herbivores and detritivores (105). “Insectivorous” birds and lizards regularly eat insect pred-



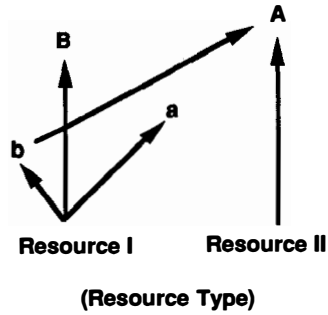
a) Omnivorous IGP on Intermediate-Level Consumer



b) Age-Structure: No Diet Changes



c) Age: Quantitative Diet Changes In The Size of The Same General Resource



d) Age: Qualitative Diet Changes In The Type of Resource

Figure 1 Four simplified configurations of asymmetric IGP. Arrows indicate that one entity (base of arrow) is eaten by a second (point). *A* and *B* are adults; *a* and *b* juveniles. Symmetric IGP (mutual predation) is not shown but can occur in 1b, 1c, or 1d if *B* eats juvenile *a*. See text.

ators and arachnids, e.g. (*Anolis*) lizards on spiders (131 and included refs). Birds eat lizards and the prey of lizards (e.g. *Anolis*; 1, 144, 157; also see 105). Carnivores eat a variety of vertebrates: e.g. desert coyotes eat herbivores (rabbits, rodents, gophers, doves, quails), arthropodivores (snakes, lizards, birds, and mammals), and carnivores (roadrunners, reptiles, and mammals) (as well as scorpions, insects, and fruit) (105). Carnivorous mammals often overlap substantially in diet (30). Many "readily prey on other carnivores" (125), e.g. tigers prey on bears (black, brown, and sloth bears), dogs, wolves, lynx, and badgers (125); leopards prey on lions, cheetahs, wild dogs, and spotted hyenas (also raptors, crocodiles, and pythons; 30, 125, 139) (also see 17, 30, 67, 82, 121, 126, 130).

Hall et al (51, p. 916) summarize that "aquatic predators apparently select prey primarily on the basis of size and . . . thus do not recognize their food as

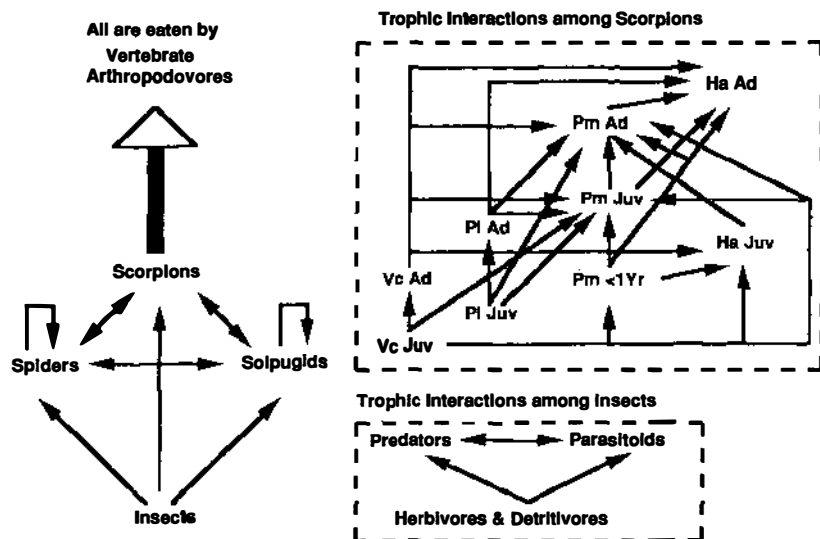


Figure 2 Trophic interactions among a group of desert arthropodivores (from 104, 105, 106, 107). Arrows as in Figure 1; double pointed arrows indicate mutual predation. A vast array of trophic interactions are subsumed in each general category, e.g. "insects." Interactions among insects and scorpions are shown in more detail in dotted boxes. All these arthropods are prey of arthropodivorous vertebrates. Age-structured IGP (with quantitative diet changes) is depicted within the scorpions (Vc - *Vaejovis confusus*, Pl - *Paruroctonus luteolus*; Pm = *P. mesaensis*; Ha = *Hadrurus arizonensis*; Juv = juvenile; Ad = Adult; <1yr = youngest age class). Omnivorous IGP on intermediate level predators occurs when a general group (e.g. insects, spiders) is eaten. Cannibalism within each of five scorpion age classes is not shown.

taxonomic entities nor members of a trophic level." Freshwater examples include fish or amphibians feeding on insects (19, 91, 92) and insects on insects (39, 75, 83, 86, 97, 128). The title "omnivorous zooplankton and planktivorous fish" (22) conveys the notion that fish (and also predaceous zooplankton) eat all trophic categories of zooplankton (28, 51, 70, 132). Omnivorous IGP is also common in marine systems. In planktonic webs, each "trophic level" feeds from most lower levels (as summarized in 101; also see 27, 47, 111, 112), e.g. tertiary carnivores eat secondary and primary carnivores, mixed food consumers (of plants and animals), herbivores, and saprovores. Benthic predators feed on appropriately sized species, e.g. 63% of infaunal predators ate other predators (see 20). Epibenthic IGP by fish, crabs, and birds can influence the abundance of infaunal predators (4). Seastars eat predaceous snails; both eat molluscs (27, 83; a particularly well-known example: *Pisaster* eats *Thais*; both eat *Mytilus* and barnacles). Similar IGP occurs among fish, crabs, seastars, and predaceous snails (84, 85).

IGP among taxonomically similar species occurs sometimes commonly among marine benthic (27, 83, 84, 114) and planktonic predators (J. Purcell,

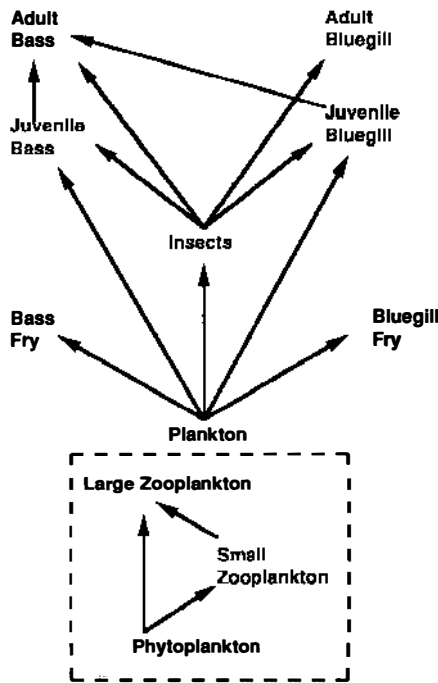


Figure 3 Trophic interactions among lake dwelling plankton, insects, and fish (from 51, 70, 87, 148, 150). Arrows as in Figure 1. Interactions among “plankton” are shown in more detail in dotted box. Age structured IGP (with qualitative changes in diet) is depicted between bluegill and bass but also occurs among plankton. Age-structured (mutual) IGP (with quantitative changes in diet) occurs among “insects” (c.g. belostomatids, corixids, and notonectids) and “plankton” (c.g. cyclopoid copepods). Omnivorous IGP on intermediate level predators occurs when a general group (insects, plankton) is eaten.

personal communication; 33, 47, 56, 96, 112, 158), arachnids (12, 41, 105, 107, 115, 124), insect predators (39, 86, 97, 128), lizards (1), bats (B. Fenton personal communication), raptors (15, 61), and mammalian carnivores (30, 67, 105, 121, 125, 126). Omnivorous IGP is so frequent among spiders, scorpions, and ants that each are often considered their own “worst enemy” (107, 115, 124, 153). Heterospecific spiders formed 1–49% of the diet of 27 spp of spiders we surveyed; 8–22% of the diets of four scorpion species were other scorpions (107). IGP among chaetognathes forms 8% (96) to 13% (33) of the diet. Some of the above examples also involve age structure (see below, Figures 2 and 3).

COINCIDENTAL INTRAGUILD PREDATION Many microorganisms and small metazoa feed on and live within food sources such as carrion, fruit, seeds, soil, or living hosts. IGP occurs when larger consumers eat these same foods

and thus their inhabitants. Janzen (62, p. 691) notes that "one of the most unappreciated classes of interspecific competition is that between microbes and large organisms over three prominent resources: . . . fruits, seeds and newly dead animals." This type of IGP is widespread (see 62), occurring between vertebrates, insects, and microbes both in carrion (105 and included refs) and in fruits and seeds (52, 53, 116, 129). Detritivores and deposit feeders eat microbes, small metazoans, and larvae when they process soil or aquatic sediments (32, 78, 100, 105, 147, 154). IGP may occur by herbivores on small metazoa, larvae, and/or microbes living on or within plants (e.g. 129). Similarly, predators eat pathogens, parasites, and parasitoids when they eat the host. Finally an analog of IGP occurs in some host-parasite interactions when one pathogenic strain infects a host previously infected with another strain which is sometimes eliminated by the invader (55).

MISCELLANEOUS INTRAGUILD PREDATION Ants (13, 81, 120, 143, 153), termites (75), and social carnivores (30, 67, 82, 126) engage in group IGP on resource competitors, often in the same taxa. Groups of marine whelks kill and eat individual lobsters (8, 9). Some massive corals dominate neighboring corals, using extracoelenteric feeding and mesenterial filaments densely armed with nematocysts to eat and digest the tissue of neighbors (71, 138). Very small corals can be completely eliminated in such attacks.

Age Structure Relatively Important, Asymmetrical

NO DIET CHANGES Adult and/or juvenile (larval) *A* and *B* largely eat the same foods, and *A* eats juvenile *B* (see Figure 1b). Examples include many granivores (23, 24, 65, 74, 95, 110 and included refs in each), carrion feeders (142 and included refs), solitary parasitoids (6, 123), facultative hyperparasitoids (31, 37, 129), ectoparasites (29, 114), and herbivorous snails (113). For example, adult and larval granivorous insects (e.g. *Tribolium*, *Rhizopertha*, *Oryzaephilus*, *Gnathocerus*) eat small larvae and/or defenseless stages (eggs and pupae of other granivorous insects). Larvae of some parasitoids kill younger larvae within the same host insect. Facultative hyperparasitoids are diverse and abundant; they feed on (and eventually kill) either the host or other parasitoids of the host. Many blood-sucking arthropods are also facultative IG predators (or parasites) on smaller parasites (e.g. [*Haemogamus*] mites, chiggers, and some Hemiptera eat smaller/larval mites, lice, fleas, ticks, flies and/or their eggs) (29, 114).

QUANTITATIVE DIET CHANGES As they grow, many predators take larger prey: i.e. juveniles eat relatively small prey; adults eat large prey of the same type (104). This leads to age (and size) dependent IGP by *A* on *B* and especially occurs when juvenile *B* are the same general size as the prey normally eaten by adult *A* (104; see Figure 1c). This resembles "omnivorous

IGP" except the prey are intermediate-sized age classes. Such IGP is frequent among generalist predators: e.g. among spiders (105, 107, 115, 124, 141), solpugids (105, 107), scorpions (12, 105, 107), predaceous terrestrial insects (58, 105), lizards (1, 105, 133), marine predators (33, 47, 96, 111, 112, 114a; W. Greve, J. Purcell, personal communication), copepods (5, 36, 132, 158), mysids (132), rotifers (48, 134), predaceous freshwater insects (10, 25, 35, 39, 43, 44, 64, 75, 86, 97, 118), amphibians (50, 89, 90, 135, 136, 146, 156) and fish (2, 42, 63, 72, 109, 137, 150). See Figure 2 for an example involving desert arthropods. For example, five species of (*Diaptomus* and *Cyclops*) copepods eat rotifers (in addition to the nauplii and copepodite stages of each of the other copepods) (5). Large odonate nymphs are especially frequent IG predators on smaller odonates (and other predaceous insects, 10, 25, 35, 64, 86, 118). IGP by larger fish on smaller (and younger) fish is widespread (e.g. in bass 149; trout 72; walleye and sauger, 137; minnows, 42; anchovies and sardines, 2).

QUALITATIVE DIET CHANGES Some taxa dramatically change food types at metamorphosis (e.g. holometabolous insects, many marine invertebrates, amphibians) or by ontogenetic shifts (e.g. fish, some reptiles) (104, 150, 152). Such changes expand a species' trophic niche and establish a size structure conducive to IGP. As a simple example, adult *A* prey on *B*; (but not adult) *A* eat the same foods as *B* [Figure 1d; complexity increases if species undergo multiple diet shifts (150), see Figure 3]. For example, Eurasian perch juveniles and roach both eat zooplankton; adult perch eat roach (99). Similar interactions occur between many fish species, e.g. yellow perch and walleye (38), perch and bass (18), and between bluegill and largemouth bass (150, 149, Figure 3). These complex interactions often include competition and IGP (see below). Some stoneflies shift from herbivores to omnivores to carnivores (eating herbivores) during development (43). *Labidocera* and *Acartia* copepods begin life eating phytoplankton and later shift to zooplankton, including herbivores and the young of other copepods (22, 68, 69, 79). The young of many marine invertebrates are eaten by species with which they could potentially compete (for food and/or space) as adults (154, 155, 100). Coral planula larvae are eaten by corals (45). Barnacles filter and eat larval echinoderms, molluscs, ascidians (and other barnacles) (159). Feeding by filter, suspension, and deposit feeders is a major mortality factor for (post-) larvae colonizing soft bottom communities (see below; 32, 54, 147, 100, 154, 155).

Symmetrical IGP: Mutual Predation and Loops

AGE-STRUCTURED SPECIES Symmetrical IGP occurs when *A* and *B* are mutual predators of one another (as used here, symmetry does not imply equal strength of interaction). Such trophic loops are surprisingly common and

often dynamically important (105; see Community Implications). Ontogenetic reversal of predation is the most frequent form: juvenile *A* are eaten by relatively larger *B*; still larger adult *A* eat *B* (and/or juvenile *B*). Size and development stage are key determinants: Larger individuals from any species can eat smaller individuals from other species; individuals are most vulnerable when small and/or defenseless (e.g. young, eggs, and pupae). In these cases, individual *A* starts life as potential prey of *B* and finishes as *B*'s predator. Looping is most common if asynchronous development produces simultaneously large adults and small juveniles of *A* and *B*.

Age-dependent mutual IGP is widespread among terrestrial and aquatic guilds. It is frequent among granivores (24, 95, 65), spiders (105, 140, 141), scorpions (107), arthropod predators (12, 105, 106), parasitoids (6, 123) and hyperparasitoids (31, 37, 105). Loops were observed between 7 of 12 species-pair combinations among four spiders (140, 141) and 9 of 12 among four scorpions (107). Desert scorpions, spiders, and solpugids each eat juveniles and smaller species from each of these taxa; age-dependent loops were observed among 10 pairs of species (106, 107; see Figure 2). Bradley (12) analyzed trophic relations among 8 desert arthropodivores: 6 pairs engaged in mutual IGP (18 cases of closed loop omnivory were also observed). Mutual IGP occasionally occurs among terrestrial vertebrate carnivores. For example, gophers and rattlesnakes prey on eggs and nestlings of burrowing owls; adult owls prey on these snakes (105). Leopards are mutual predators with lions, spotted hyenas, tigers, large raptorial birds, crocodiles, and pythons (30, 125, 126, 139).

Mutual IGP on larvae is a normal by-product of feeding in benthic marine communities (27, 32, 100, 114, 147, 154, 155). Adult killifish eat adult and juvenile grass shrimp, adult shrimp eat young killifish (66). It is frequent in planktonic communities (22, 47, 79, 68, 96 and included refs in each; W. Greve, J. Purcell personal communication). *Noctiluca* dinoflagellates, copepods, and more than 90 spp of jellyfish and ctenophores eat fish eggs or larvae; older fish prey on many of these same species (26, 47, 87, 101, 112). Dayton (27, p. 192) comments, "Copepods are important predators on the larvae of fish that, should they survive, become important predators on copepods. Indeed it is reasonable to imagine that small plankters such as copepods, euphausiids, chaetognaths, etc, are important predators on even very large carnivores such as tuna. A terrestrial analogy would involve the spectre of say, tigers or wolves releasing thousands of tiny tiger-lets or wolflets, which were largely consumed by spiders, lizards, birds, shrews, etc."

Mutual predation is also common in plankton communities. Sprules & Bowerman (132) found an average of 1.5 (range: 0–10) cases per zooplankton assemblage of 515 lakes. They conclude (p. 424) that "reciprocal predation is

common in plankton communities” because “asynchronous seasonal development leads to . . . simultaneous existence of large adults and small juveniles.” *Mysis relicta* (73, 132) and copepods (*Diaptomus*, and cyclopoids; 5, 132, 70) readily eat the young of every copepod species. Predation on each other’s young-of-the-year is common (150), e.g. between walleye and sauger (137). Mutual IGP also occurs among rotifers (48), insects (39, 86, 128), and amphibians (89, 90).

GROUPS Mutual intraguild predation is frequent among social insects and social carnivores. Ants engage in two types of mutual predation (76, 81, 120, 122, 143, 153). Founding queens of any species are frequently killed by workers from almost any coexisting species, e.g. *Eciton* army ants prey on more than 100 species of ants; these species eat *Eciton* queens (76). Wars also occur between entire colonies. Among ants of similar body size, wars are usually won by larger colonies, regardless of species. Group size is also important among social carnivores, e.g. individual lions prey on individual hyenas; groups of hyenas on single lions; groups of lions prey on groups of hyenas (30, 67, 126). Leopards and packs of wild dogs can kill and eat solitary lions; two or more lions eat and kill leopards and wild dogs (30, 126, 139). Similar mutual IGP occurs between leopards and spotted hyenas (30, 126, 139); jackals and cheetahs (14, 30); and wolves and bears (82). Mutual IGP also occurs among feeding groups of marine whelks and solitary lobsters (8, 9).

MISCELLANEOUS Mutual IGP can occur independent of age structure or social behavior. Black widow spiders (*Latrodectus*) catch three species of desert scorpions by using web silk to pull them up off the ground; black widows travelling on the ground are captured by these same scorpion species (105, 106, Figure 2). IGP by means of digestive dominance between corals is sometimes mutual (71, 138). Finally, loops can occur without IGP if mutual predators do not share resources. Thus, some aphids eat the eggs of their coccinellid predators (7). Barnacles filter and eat zooplankton including larval echinoderms (159); adult echinoderms are predators on barnacles (83). In a “widespread” interaction, vertebrates eat their ectoparasitic fauna (29).

GENERAL CHARACTERISTICS

Relative body size and degree of trophic specialization are the two most important factors influencing the frequency and direction of IGP. Most IGP occurs in systems with size-structured populations by generalist predators that are usually larger than their intraguild prey. Many of these IG predators are also cannibalistic on smaller conspecifics (see 39, 75, 103, 114a). Because

size is critical, historical effects and factors that influence the rate and duration of growth are of paramount importance (see below).

IGP sometimes increases with decreased abundance of nonguild prey, e.g. among scorpions (107), raptorial spiders (140), ants (81), blowfly larvae (142), granivores (23), planaria (11), copepods (79, 56, 158), and social carnivores (30, 67, 126). Increased IGP may be passive (i.e. it increases simply because the ratio of guild:nonguild prey is higher), or may involve active behavioral shifts. Hungry predators may expand their diet to include guild members. Alternatively, hungry consumers may move more and so contact IG predators more frequently. IGP sometimes increases with increasing density of IG prey. Density dependent IGP appears to operate among granivores (23, 65, 74), copepods (22, 69), amphibians (135), and fish (99). The relationship between IGP and the relative abundance of guild and nonguild prey needs more study.

Finally, IGP is sometimes directed preferentially towards the predator's closest potential competitors (i.e. those with greatest resource overlap). This may result from direct selection to attack these prey (see Evolution) or may simply be a by-product of the fact that encounter rates typically increase with similarity of niche use. Whatever the reason, this phenomenon appears to be widespread in terrestrial arthropods (13, 81, 107, 115, 120, 140, 143, 153), granivores (65, 95; but see 23), terrestrial carnivores (30, 67, 126), and freshwater (69, 79, 158) and marine (96, 114a, 155, 159) invertebrates.

IMPLICATIONS FOR INDIVIDUALS

Below we outline how intraguild predation influences individual fitness, and the evolution and expression of behavioral, morphological, and life history characteristics of interacting species. IGP may act directly, e.g. due to differential mortality on more vulnerable genotypes; or indirectly, e.g. by inducing a niche shift in IG prey that subsequently results in adaptation to the altered niche. In many ways, these effects are special cases of adaptations associated with classical predation except they occur among guild members.

Behavioral, Morphological and Chemical Modifications

IG prey often exhibit escape behaviors from IG predators (e.g. 36, 83, 107, 129, 133). Further, maternal behavior may reduce IGP on eggs and young, e.g. many parasitoids and hyperparasitoids actively avoid ovipositing on hosts containing potential IG predators (6, 37, 31, 123). Some crab spiders leave shrubs from which they forage to oviposit in other shrubs that harbor relatively few IG predators (140). Marine invertebrates that brood their young suffer less IGP on larvae than do species that broadcast larvae (32, 154; but see 147). Species that brood are more likely to dominate soft-bottom communities

when interference and IGP are strong. The behavior of young may also reduce IGP, e.g. larval sand dollars settle in response to a chemical produced by adults, thus reducing susceptibility to IGP from abundant tanaidacean crustaceans that are excluded from sand dollar beds (54). Young killifish reduce IGP by staying in refuges high in the intertidal, beyond the range of most IG predators (66). IGP may be implicated in a wide variety of behaviors not included here, e.g. the evolution of slave-making in ants (13; also see 34, 114a).

The morphology of some predators explicitly increases successful IGP. Early instars of some parasitoids have specialized sickle-shaped mandibles that are ill-adapted to feeding on soft host tissue, but well suited for IGP and cannibalism (6, 123). Later, the mandibles become smaller and unsclerotized, and then are better suited to absorbing the host's tissue. Similarly, highly modified, "cannibalistic" morphs of *Scaphiopus* tadpoles are poor grazers and sediment feeders, but good predators on other tadpoles (108). Finally, IGP via digestive dominance is best developed in corals with a greater concentration of nematocysts (138). The morphology of some IG prey reduces susceptibility to IGP (e.g. 34, 134). Toxins can represent another defense. For example, *Notophthalmus* salamanders develop toxins as adults and thus escape IGP from larger *Ambystoma* (89). Toxins of microbes within carrion, fruit, and seeds inhibit coincidental IGP by larger animals (62, 117).

Life History Characteristics

Brood size, growth rates, life span, reproductive phenology, and other life history traits often influence the strength and direction of IGP interactions. IGP can be important in the evolution of life cycles, e.g. among praying mantids (58), spiders (140, 141), scorpions (107) and freshwater zooplankton (5, 132). For example, asynchronous life cycles among two mutual odonate predators (*Tetragoneuria* has a two-year life cycle, and *Celithemis* has only one) allow large *Celithemis* to eat hatchling *Tetragoneuria* in early summer, but both age classes of *Tetragoneuria* to eat *Celithemis* later in summer (10, 86). These phenological differences decrease diet overlap and competition, but facilitate IGP. Further empirical work is needed to assess the relative importance of competition and IGP in determining the evolution and expression of life history traits (see Population Implications for the influence on growth and survivorship).

Coincidental IGP may be important in the evolution of complex life cycles in parasites. Selection would favor parasites that resist digestion within the gut of the consumer of the parasite's host; eventually the parasite may fully adapt to life within the consumer, thus making the consumer a final or intermediate host.

Effects on Individual Fitness

A number of important fitness benefits potentially accrue to the intraguild predator. Predation on guild members, as on nonguild species, typically yields nutritional and energetic gains that translate to increased growth, reproduction, and survival. These gains may be especially important for IG predators that feed primarily on plants (see 103 and included refs). While animals are more than 50% protein (7–14% N by weight), plant tissue is mostly carbohydrates, with only 0.03–7% N. In prairie soils, 23% of microarthropods that eat fungi and algae also eat the nematodes that feed on these plants. Consumption of nematodes is essential to the survival of some arthropods and may greatly increase egg production (145). IGP can also reduce N deficiencies in frugivorous and granivorous birds (52). IGP by “granivores” on ants and insects (up to 40% of the summer diet of *Dipodomys kangaroo* rats) can significantly reduce the number of seeds needed to fulfill energy requirements (116). IGP may also provide an important source of seasonal water (e.g. for Gambel’s quail from eating harvester ants, 46).

Guild members are often important prey for nonherbivores (see earlier). IG prey comprise 25% of the energy budget of some copepods (68, 69), 18–51% of some large chaetognaths (33, 96), and 4.9–10% of some scorpions (107). Wars among species of *Formica* ants can yield more than 10,000 ants returned to the burrow for food, during periods of low prey abundance (81). Many fish that eat zooplankton also depend on other (zooplanktivorous) fish as prey. Some species (e.g. pike, some perch, zander) are unable to sustain normal growth in the absence of fish prey, even when zooplankton are abundant (109). In the absence of yellow perch, walleyes continue to feed on zooplankton, but at the cost of retarded growth (38). Pearre (96), modelling IGP and cannibalism in chaetognaths, concluded that feeding on other chaetognaths may be necessary for the existence of large species. In ectoparasitic mites, a mixed diet of blood and other parasites yielded higher reproductive rates than a pure hematophagous diet (114).

Enhanced growth has obvious benefits in ephemeral habitats. IGP can promote faster growth and earlier metamorphosis of amphibian larvae, facilitating escape from ponds (108, 152). An analogous situation occurs for blowfly larvae in carrion (142).

RELEASE FROM COMPETITION AND/OR PREDATION IG predators can benefit from reduced competition, especially under conditions of local resource competition. IGP often frees resources directly used by the IG predator and sometimes produces overdispersion among interacting species. Many marine invertebrates clear the area around their burrows by eating (settling juvenile) guild members (3, 4, 32, 100, 154), often those with whom they are closely related taxonomically (and presumably, ecologically; 155). Similar in-

teractions exist among ants (13, 76, 81, 120, 153), Isoptera (75), some arthropod predators (104, 107), and social carnivores (30, 67, 126). Digestive dominance by corals can clear local areas of faster growing corals (71, 138). Decreased resource competition accrues via IGP among large carnivores (30, 67, 126), solitary parasitoids (6, 123), blowflies (142), and plankton (36). Release from local competition is expected to be a common phenomena among species with spatially structured populations (see Evolution). Finally, release from predation may be an important consequence of IGP: When mutual predation is possible, IGP can eliminate individuals that could otherwise prey on the IG predator or its relatives (see Categorization).

POPULATION LEVEL IMPLICATIONS

Empirical Observations on Population Dynamics

IGP may influence population size, stability, and resilience of the IG predator, the IG prey, and nonguild species in the community. We use empirical examples to illustrate some possible outcomes of IGP; later we show how these outcomes emerge from theoretical models.

POPULATION REDUCTION In some cases, the predation component of IGP is severe enough to reduce drastically, or even eliminate, local populations of IG prey (also see Community Implications). For example among terrestrial taxa, IGP can exclude species of carrion insects (142), granivores (24, 65), and ants (120, 143). Parasitoids often eliminate other parasitoids within shared hosts (6, 31, 37, 123). It can be a major mortality factor that limits populations below their carrying capacities, e.g. in scorpions (107), spiders (115, 124) and social insects (13, 75, 76, 153). In field experiments, the populations of two smaller scorpion species increased 150% and 600% (relative to controls)—and spider abundance doubled—when the large IG predator scorpion, *P. mesaensis*, was removed (106, 107). IGP was the key factor; a robust analysis produced no evidence of exploitation competition.

Spiders are 10 times more abundant on Caribbean islands without lizards (131 and included refs). On islands with both taxa, lizard removals resulted in a 3–20 times increase in spider abundance, mostly due to predatory rather than competitive release. Lions cause over half the total deaths of spotted hyenas (67). Red foxes are the most important predator on Arctic foxes (17). Mortality in cheetah kittens may reach 95%, with over half often due to IGP by other carnivores, especially lions and hyenas (14, 30 and included refs; J. Henschel, personal communication). Such IGP may be a major factor limiting cheetah populations. For example, maintenance of large populations of other carnivores (e.g. lions, hyenas, leopards, wild dogs) on African game reserves and parks (e.g. in Nairobi Park and South Africa) greatly depresses cheetah

populations (these carnivores also steal food from cheetahs). In Namibia, where populations of these other carnivores were drastically reduced by hunting, cheetahs are now so abundant that they often are considered "vermin" by ranchers because they eat domestic animals.

Reductions/local extinctions are also observed in the marine environment (2, 3, 22, 27, 32, 47, 54, 56, 66, 68, 79, 112, 113, 147, 154, 159). Peterson (100) reviewed many marine benthic studies and concluded that IGP by adults on colonizing larvae was a major factor in keeping densities below carrying capacity in soft-sediment benthic communities. Ambrose (3, 4) suggests that IGP by epibenthic predators is a general factor that limits populations of benthic predators. In freshwater environments, IGP by *Notophthalmus* newts on eggs of *Ambystoma* salamanders excluded *Ambystoma* from a pond in some years (89, 90). Bluegill and largemouth bass abundances are often inversely related (149; competition and IGP are both important, 149). IGP can cause significant population reductions in freshwater zooplankton and insects (22, 25, 39, 51, 60, 64, 73, 80, 118, 134).

INTERACTION BETWEEN COMPETITION AND IGP An interesting documentation of the joint effects of competition and predation on population dynamics comes from the introduction of red shiners into a Canadian lake with a resident population of rainbow trout (72, 150). Adult trout eat shiners, and so they benefited from the introduction. Young trout, however, became less successful (i.e. had less food in their stomachs and slower growth rates) due to competition with shiners. The overall effect was to decrease the trout population. Similarly, when threadfin shad were introduced as food for largemouth bass, the introduction increased piscivorous (adult) largemouth bass (due to IGP), but decreased the growth and survival of less piscivorous (smaller) bass (presumably due to competition with the shad; 150). Bass also show predatory and competitive interactions with bluegills (Figure 3; 149, 150 and included refs). Bluegill can outcompete young bass for plankton and reduce recruitment of bass to larger, piscivorous size classes. Developmental bottlenecks may be common when, as in this example, the IG prey is a more efficient competitor. Predation by adult bass may, in turn, reduce bluegill populations. In like manner, recruitment of perch to piscivorous size classes may be limited by competition with roach (99 and included refs).

Mysis relicta has been introduced into many lakes in North America and Scandinavia to increase fish production by providing a new forage item for intermediate-sized salmonids (73). However, *Mysis* predation on zooplankton often alters the trophic structure of the lake to the detriment of target fish species. The complex effects include competition between *Mysis* and young fish; Superior exploitation by *Mysis* depletes shared prey.

Several experimental studies explicitly examined the contribution of the

predatory vs the competitive component of interactions among terrestrial taxa. The predatory component was judged more important to population dynamics in each of the following cases: lizards and spiders (131 and included refs), scorpions and spiders (106), among raptorial spiders (140), among web building spiders (115), among scorpions (107), and among salamanders (50). Both the predatory (1, 144) and the competitive (157) components of the interaction between “insectivorous” birds (IG predator) and lizards were considered paramount. Both components contribute to the population dynamics of blowflies (142) and parasitoids (31, 37). *Lucilia* and *Chrysomia* larvae primarily fed on decaying meat (142). IGP by *C. albiceps* is the main factor limiting populations of cooccurring dipteran larvae. Competition limits population growth of these Diptera when *C. albiceps* is absent.

EFFECTS ON INTRA- AND INTER-SPECIFIC COMPETITION IG predators may paradoxically increase the abundance of their IG prey, given a sufficient compensatory response by that prey to decreased intraspecific competition (S. Cortwright, personal communication; also see 152). In contrast, the presence of an IG predator may increase intraspecific competition among IG prey for refuges. For example, juvenile *Anolis aeneus* move to refuges to avoid IGP by adult *A. richardii*; intense competition for limited space in refuges reduces juvenile populations and places a bottleneck on adult recruitment (133). Similarly, the use of the vegetated littoral zone as a refuge from IGP by small bluegills may increase intraspecific competition (149 and included refs).

Many facets of population dynamics have not yet been addressed in empirical studies of IGP. For instance, its role in population regulation (vs population limitation) is unclear. In like manner, predator-prey systems often exhibit a propensity for damped or sustained oscillations, and so IGP systems may show pronounced population fluctuations. Consider the common scenario in which the IG predator as resources decline expands its diet to include the IG prey. By expanding its diet, the predator reduces its rate of decline, thus tending to stabilize its population. By contrast, the IG prey suffers greater mortality when resources are more limiting, and so its population will tend to be destabilized (leaving aside compensatory responses). A full understanding of the population level consequences of IGP requires us to place it into a larger community context.

Population Models

The classical theory of competition aims at understanding how species coexistence is constrained by similarity in resource use, and how resource use generates density-dependent interactions within and among species (see 59 for review). The classical theory of predator-prey interactions attempts to eluci-

date the factors permitting the long-term persistence of effective predators and their prey, with particular attention on the possibility of sustained, coupled cycles (93). Most theory examining the combined effects of predation and competition has assumed that predators are taxonomically distinct from the guild of competing prey on which they feed. Some salient conclusions of the work on mixed competition-predation systems are: (a) predation may enhance coexistence if it differentially impinges on prey that are superior exploiters, but otherwise predation may preclude coexistence, particularly if the predator is a generalist whose numbers are governed by the availability of multiple prey species (57); (b) along increasing gradients in productivity, the impact of predation tends to become more pronounced. All these themes arise, with twists and modifications, in models of intraguild predation.

In contrast with competition and predation, which enjoy rich, integrated bodies of theory, theoretical work on IGP is scattered and diffuse. Levins (77), using loop analysis, and Rosenzweig (121), with an isocline model, observed that IGP could allow coexistence of competing predators, but neither elaborated. General food web models almost always include some IGP, usually in the form of omnivory on intermediate-level predators (102). Here we show how the conclusions of some familiar models of competition and predation are modified by including IGP. For each IGP type (see Figure 1a–d) one could construct explicit models to examine the consequences for species coexistence and population stability. We first focus on the simple but central case of “omnivorous” IGP on intermediate-level predators without age-structure effects (see Figure 1a).

Consider the standard Lotka-Volterra model of competition, in which linear density-dependence describes the effects of competition within and between species. As is familiar from textbook accounts, this model generates linear zero-growth isoclines in a phase plane defined by species densities, and it can describe unilateral dominance by either species, competitive coexistence, or a priority effect, with the winner determined by initial densities. The simplest assumptions about IGP are that each encounter between a predator and prey produces a fixed expected benefit for the predator, and a fixed expected cost for the prey, and that encounters occur at random. These assumptions require that the feeding interaction be described by a linear functional response, that the predatory behavior be fixed (in particular, not a function of absolute or relative prey abundances), and that the relative spatial distributions not change as population densities change. Figure 4 depicts how this simple kind of IGP shifts the zero isoclines for each of the outcomes of the original Lotka-Volterra model. Let species *A* be the IG predator on *B*. If *A* is the competitive dominant without IGP, incorporating IGP only increases its dominance (Figure 4a). If the two species coexist without IGP, adding IGP increases the density of *A*, and decreases the density of *B*, possibly to the

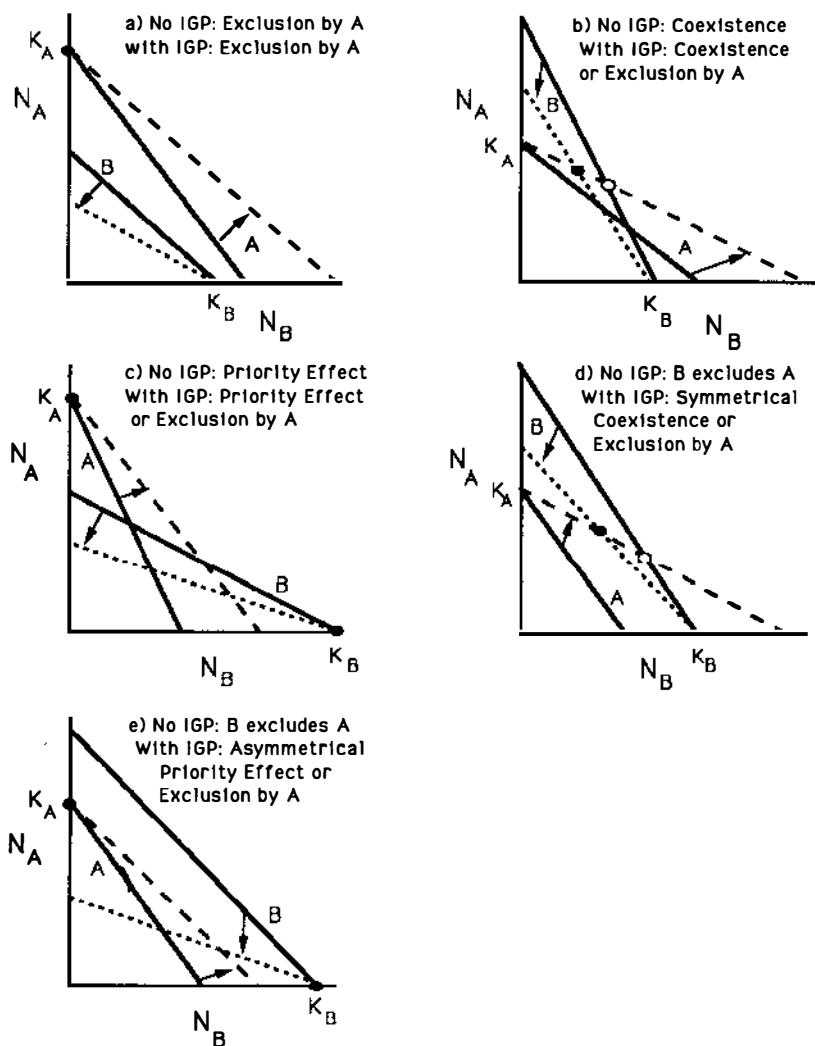


Figure 4 Isoclines of the Lotka-Volterra competition model, with modifications induced by IGP. Solid lines: isoclines without IGP. Dashed lines: isoclines of the predator (species A), including beneficial effect of IGP. Dotted lines: isoclines of prey (species B), including extra mortality imposed by the IG predator. The model is $dN_A/dt = N_A r (1 - N_A/K - \alpha N_B/K) + a N_A N_B$ $dN_B/dt = N_B r' (1 - N_B/K' - \alpha' N_A/K') - a' N_A N_B$, where r_i and K_i are the respective intrinsic growth rates and carrying capacities of species i , α and α' are competition coefficients (effect of j on i), a is the benefit provided A by IGP, and a' is the extra mortality suffered by B due to IGP. Carrying capacities are not altered by IGP. (a) Without IGP, A unilaterally excludes B; its competitive advantage is enhanced by IGP (b) With no IGP, the competitors coexist. IGP increases A and decreases B; if IGP is great enough, this may lead to the exclusion of B by the combined effects of predation and competition. (c) Without IGP, there is a priority effect. With IGP, there may still be a priority effect, or unilateral dominance by A. (d) Without IGP, B excludes A. With IGP effects roughly equal in magnitude, coexistence may be produced by IGP. (e) Without IGP, B excludes A. With strong, asymmetrical IGP, a priority effect is observed.

point of exclusion (by a combination of competition and IGP) (Figure 4b). If without IGP there is a priority effect, with IGP there is still a priority effect (*A* unilaterally wins, Figure 4c). The richest array of effects arise where *B* is intrinsically the competitive dominant. If IGP has a strong positive effect on *A*, as well as a negative effect on *B*, it may permit coexistence of both species (with a reduced density in *B*) (Figure 4d). By contrast, if the beneficial effect of IGP on *A* is small, but the negative effect on *B* is large, IGP may create a priority effect, where either species can exclude the other (Figure 4d). Because *B* is dominant competitively, and *A* does not gain much from eating *B*, it will be difficult for *A* to increase when rare. However, a strong negative effect of predation by *A* on *B*,

competition, may prevent invasion by *B* when it in turn is rare. Without a substantial positive effect on *A*, the top-level predator, IGP is unlikely to create unilateral dominance for *A*.

Many ecologists criticize the Lotka-Volterra model. Schoener (127) proposed alternative models for competition that may be more reasonable descriptors of exploitative competition, at least when a fixed supply of resources is divided among a set of competitors. These models often lead to strongly nonlinear isoclines. Figure 5 illustrates how IGP modifies the outcome of competition for a single resource, assuming that *A* is inferior at exploiting the resource, and that the simple model of IGP outlined above holds. If *A* is superior at exploitation, it unilaterally excludes *B*. In contrast with the linear Lotka-Volterra model, this model can generate strongly hyperbolic isoclines for *A*, which can combine predator-like and competition-like features. Consider the case shown in Figure 5a. The isocline of *B* has a negative slope; an increase in the density of *A* always depresses the growth rate of *B* (due to both competition and predation). By contrast, *A* experiences a mixture of negative (competitive) and positive (predatory) interactions with *B*. The underlying model of exploitative competition is highly nonlinear, with stronger per capita effects at low densities. When *B*, the superior exploiter, is at low densities, it can strongly affect resource availability for *A* but can provide little direct benefit via predation. Thus, at these low densities, *A* exhibits an isocline with negative slope, reflecting this predominance of competition. However, at higher densities the direct beneficial effect via predation predominates, and a second part of the isocline of *A* shows a positive slope. This example shows how IGP can allow coexistence when the benefits to the predator and costs to the prey are roughly equal in magnitude. Near equilibrium, the populations are effectively a predator-prey system, which show damped oscillations back to equilibrium following a small perturbation. The overall effect of *A* on *B*, however, is competitive.

By contrast, figure 5(b-e) shows systems in which the negative effect imposed on *B* greatly exceeds the positive effect enjoyed by *A*, arranged along

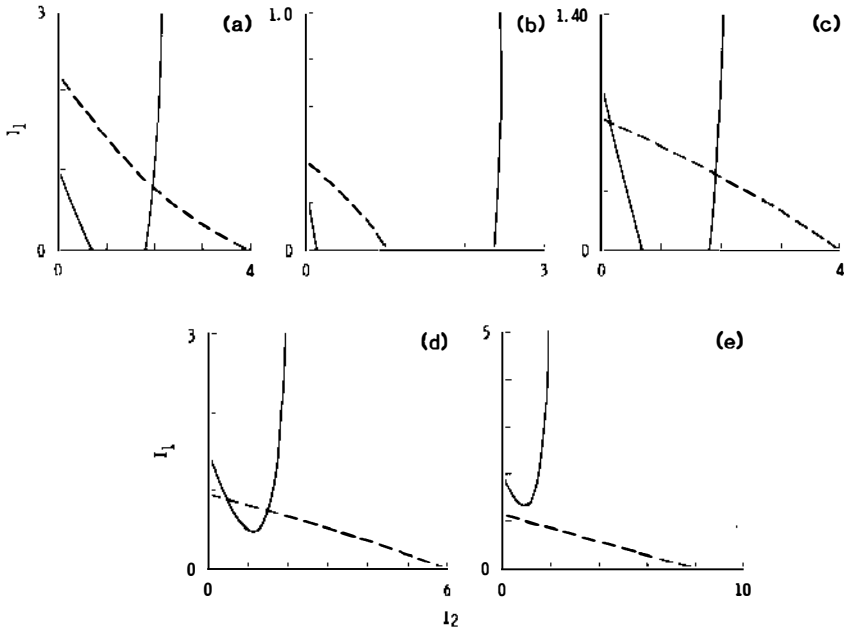


Figure 5 Isoclines of exploitative competition model with IGP. This model stems from Schoener (127), and assumes that a fixed input I of resources is divided among competitors. A acquires a fraction $eN_A / (eN_A + e'N_B)$ of the available resources, and the remainder is consumed by species B. The model is $dN_A/dt = N_A e b I / (eN_A + e'N_B) - mN_A + aN_A N_B$, $dN_B/dt = N_B e' b' I / (eN_A + e'N_B) - m'N_B - a'N_A N_B$ where a_j measures the rate of resource acquisition of species i , b_i converts resources acquired into consumer births, m_i is a rate of density-independent mortality, and a and a' measure the IGP coupling between A and B. The isoclines of this model are hyperbolas. The isocline of B always has a negative slope. The isocline of A may have a negative slope at low densities of B, but bends to show a positive slope at high densities. In all the examples shown $e = 1$, $e' = 2$, $b = 1$, $b' = 2$, $m = 1$, $m' = .5$, $a = .5$. In the absence of IGP, the equilibrium densities of A and B are respectively 1 and 4, and A is competitively excluded. (a) $I = 1$, $a' = .6$. The magnitude of IGP effects are comparable for A and B. The isocline of A consists of two disjunct pieces: one near the origin, with a negative slope (as in a typical competition isocline), and one further away, with a positive slope (as in a typical predator isocline). For combinations of densities between these two lines, A has a negative growth rate. Outside the isocline for B, B has a negative growth rate; inside it, B has a positive growth rate. There is a unique equilibrium given by the intersection of the two isoclines. Near this equilibrium, the interaction is essentially a predator-prey interaction, showing damped oscillations following perturbation. Yet globally, B depresses the abundance of A. For (b) through (e), $a' = 6$ (strong asymmetry in IGP effects). The figures are arranged in order of increasing resource input I (a measure of environmental productivity): (b) .25; (c) 1; (d) 1.5; (e) 2.0. (b) shows unilateral dominance by B. (c) and (d) show alternative stable states: the system persists either with A alone, and B competitively excluded, or A and B persisting in a predator-prey combination. In (e), B is excluded.

a gradient in environmental productivity. At low productivities, *B* predominates; the low carrying capacity of *B* prevents the IGP advantage enjoyed by *A* from surmounting its intrinsic competitive disadvantage. At higher productivities, enough of *B* are present to allow *A* to increase when rare, and the two species can settle into a kind of predator-prey equilibrium. However, when *A* is present initially, the high mortality it imposes on *B* prevents invasion. Thus, the system may exist in two alternative stable states: one, an equilibrium comprised just of *A* at its carrying capacity, and the other, a predator-prey equilibrium with both species present, but *A* at lower densities than allowed by its carrying capacity. At yet higher productivities, *A* is unilateral dominant over *B*.

This model suggests that IGP can generate alternative stable states in which one of the states has both species present. This is not usually seen in exploitative competition models. These results mesh nicely with the general conclusions of predation and competition theory sketched above: for coexistence, the species that is differentially subject to predation must be one that is superior at resource exploitation; along gradients in productivity, predation (in this case, IGP) becomes relatively more important compared to resource exploitation.

It is useful to consider a final model of IGP without age-structure. The above two models assume either unspecified mechanisms for competition (the Lotka-Volterra model), or a particular form of exploitative competition (the model of Figure 5). In many systems, IGP and cannibalism both occur (see Characteristics). If we assume that cannibalism is the only density-dependent factor operating on the top-level predator, and that both species tend to grow exponentially without IGP or cannibalism, we arrive at the following simple model: $dN_A/dt = N_A(r - aN_A + bN_B)$, $dN_B/dt = N_B(r' - b'N_A)$. The value for *a* reflects the rate at which conspecific *A* meet, and the negative average cost of one being eaten by the other. (If the sign of this term were not negative, averaged over both winners and losers, *A* would grow in an ever increasing orgy of self-benefaction.) For *B* to persist, it must be the case that $r'/b' > r/a$. For species with roughly equal intrinsic growth rates, *B* persists only if $a > b'$; the rate of damage imposed by *A* on itself due to cannibalism must exceed the cost resulting from IGP imposed on *B*.

Many examples of IGP involve age-structure effects. Space limits the development of a fully articulated formal model of IGP with age structure. As a heuristic device for thinking about age structure effects, we present a conceptual "value model" suggesting that IGP can exert significant effects on stable point(s) in the community, guild composition, and species coexistence. *A* and *B* are mutual predators via ontogenetic reversals: adult *A* eats adult and juvenile *B*; adult *B* eats juvenile *A*. Imagine that the number of *A* and *B* that escape to adulthood is controlled by valves whose flow rates are determined

by interactions with the other species. High rates of IGP by adult *B* on juvenile *A* represent a low flow rate for *A*, i.e. few *A* pass thru the valve to become adults. Although adult *A* are dominant as individuals (in the sense that they can prey on all *B*), they may not be numerically dominant and thus cannot substantially reduce the population of *B* via IGP. Under these conditions, coexistence might be maintained, or species *B* might even exclude *A*. Coexistence might occur if juvenile *A* were competitively inferior to *B* and passed thru a "developmental bottleneck" limiting recruitment (see Empirical Observations). High flow rates for *A* would establish a positive feedback increasing *A* to the detriment of *B*: as adult *A* eats *B*, *B*'s population declines, and more juvenile *A* survive to become adult predators of *B*. The exact outcome between *A* and *B* is a function of such variables as flow rate, initial densities, and the relative intensities of IGP and competition by each *A* and *B*.

The verbal and formal models elevate historical events to a particularly important position in determining the eventual stable point(s) or composition of a guild. The outcome can be determined by the priority of colonization or by stochastic perturbations (e.g. storms, harvesting, pollution; see Community Implications) that disproportionately affect one species. Unlike classical competition models, however, with IGP one of the alternative states may have both species present at a stable equilibrium. Below we outline numerous instances of alternative stable states. We also show that the typical IG prey (i.e. intermediate-level predators) is usually superior to the top-level IG predator at exploiting shared resources. This observation is what the above models predict.

COMMUNITY LEVEL IMPLICATIONS

IGP can exert significant direct and indirect effects on community structure. Here we show that IGP acting alone or in conjunction with historical effects, competition, and/or interference can dramatically influence guild structure, community diversity, stability, and food web structure. As predicted by the models, IGP can lead to exclusion, coexistence, and alternative stable states.

Guild Structure

It is widely believed that interactions between guild members over both ecological and evolutionary time strongly influence numerous characteristics of virtually all species. What has been underappreciated is that predation, as well as competition, between guild members can shape these traits. IGP and competition can produce similar patterns among interacting species. However, because IGP causes death, selective pressure caused by IGP may be much greater than that of competition alone. Below we review how IGP may have influenced distribution, resource use, and ecomorphology of guild members.

NICHE SHIFTS Species that suffer intraguild predation often exhibit different patterns in space and/or time than do their IG predators. Such patterns may be an evolutionary response, a short-term behavioral response to avoid IGP, or simply a reflection of mortality due to IGP. It is often difficult to assess the relative importance of competition vs predation in determining niche shifts, but predation is likely to be the key factor when shifts cause one species to inhabit areas or times that significantly lower per capita energy gain. The bluegill-largemouth bass interaction is well studied (87, 149, 150 and included refs). Young bluegill live in the littoral zone. Although the pelagic zone is more profitable, the risk of predation is 40–80 times higher. Bluegill move into the pelagic upon attaining a size that confers a sufficiently reduced risk. IGP also induces habitat shifts in minnows: juvenile *Rinichthys* move into safer areas in the presence of adult *Semotilus*, an IG predator (42). In terrestrial arthropods, IGP influences the displacement of some scorpion species away from productive sandy areas (107), raptorial spiders away from some host plants (141), and ants away from favorable nesting and foraging sites (41, 76, 81, 120, 143). Frugivorous birds feed mainly on ripe fruit; many frugivorous insects actively avoid IGP by these birds by feeding on unripe fruit (52). In estuarine copepods, IGP by *Sulcanus* and *Acartia* restricts the distribution of *Gladioferens* to areas of low salinity (56).

IGP appears to have influenced the evolution of size and resource use in a guild of *Desmognathus* salamanders (50 and included refs). Experiments suggest that guild patterns are more consistent with predictions based on IGP than on competition. Removal of the smallest species, *D. ochrophaeus*, decreased abundance of two larger *Desmognathus*, as would be expected if *D. ochrophaeus* were an important prey, and opposite the effect predicted if it were a competitor. It is hypothesized that IGP by larger, more aquatic salamanders has forced smaller species to less productive, more terrestrial environments.

IGP is suggested to be the determinant factor behind the temporal separation of some African carnivores (30), scorpions (107), and diurnal hawks and nocturnal owls (15, 61). In these and the above examples, IG prey primarily are restricted to places or times not occupied by their IG predators. These times and habitats may be relatively less productive (49, 50, 87, 107, 149); or beyond the physiological tolerance or morphological adaptations of IG predators (49, 50, 52, 56, 66, 81, 107, 120, 113, 133, 143). Often the fundamental niche of the IG predator is included within the fundamental niche of the IG prey; the broader niche of the IG prey may allow it to persist in the face of IGP.

HISTORICAL EFFECTS AND ALTERNATIVE STATES Historical events can determine which species becomes numerically dominant among granivores

(24, 95), parasitoids (123, 6), ants (143, 120), amphibians (89, 90, 151), and marine taxa from the plankton (47), hard substrate (8, 9, 114a, 159) and soft substrate (32, 54, 100, 147, 154). For example, priority determines the winner between the granivores *Rhizopertha* and *Sitotroga*: The established species dominates by killing and/or preying on vulnerable stages of the second introduced species (24). At high initial densities of *Tribolium*, *Gnathocerus* was always exterminated via IGP; however, if the initial densities of *Tribolium* were low, IGP by large populations of *Gnathocerus* eliminated *Tribolium* (95). Similarly, preexisting colonies of *Myrmica*, *Formica*, and *Lasius* ants prevent colonization of other species on Baltic islands (120, 143). This priority effect is maintained by IGP on founding queens and incipient small colonies. IGP by some island species (e.g. *Lasius niger*) totally excludes other species (e.g. *F. truncorum*) that, on the mainland, regularly eliminate the island species by IGP.

Priority effects combined with IGP and interference determine the composition of many soft-bottom marine communities (32, 54, 100, 147, 154). Established populations of filter, suspension, and deposit feeding benthic organisms represent a "meiofaunal bottleneck" that limits successful recruitment of larvae and juveniles, especially those produced by other assemblages. As a result, extreme patchiness often occurs. For example, *Macoma* clams are rare in most areas of the Baltic because high densities of *Pontoporeia* amphipods eat all settling juveniles (32). *Macoma* becomes the biomass dominant in areas of heavy pollution where amphipods do not survive well. Some areas support dense (equally aged) populations of both species; it is hypothesized that all recruitment occurred at a time when *Pontoporeia* populations were depressed.

Mutual IGP causing developmental bottlenecks produces local patchiness and alternative planktonic communities in the North Sea (47, W. Greve, personal communication). *Calanus* copepods and *Pleurobrachia* ctenophores both eat small zooplankton. Adult *Calanus* significantly decreased populations of *Pleurobrachia* by eating young *Pleurobrachia*. Adult *Pleurobrachia* eat juvenile *Calanus* and thus limit *Calanus* populations. Dominance within patches is determined by which species is the first to establish. Further, if adult *Calanus* decrease, *Pleurobrachia* populations bloom and vice versa. Another ctenophore predator (*Beroe*) also reduces *Pleurobrachia* sufficiently to allow *Calanus* blooms. *Notophthalmus* newts and *Ambystoma* salamanders each prey on the eggs and (for *Ambystoma*) larvae of the other (89, 90). IGP by *Ambystoma* was sufficient to exclude *Notophthalmus* from certain ponds in some years.

Barkai (personal communication; 8, 9) provides a fascinating example of how IGP has produced alternate stable states in the absence of age-structure effects. In the subtidal off two islands in the south Atlantic, both *Burnopena*

whelks and *Jasus* lobsters are predators on the same species of mussels and snails. Lobsters form 70% of the total benthic biomass on Malgas island but are totally absent on Marcus island. Whelks are abundant on Marcus; Marcus populations are 19% those of Malgas. Heavy IGP by Malgas lobster on whelks produces this difference. Introduction of lobsters to Marcus resulted in total failure because lobsters cannot colonize: large numbers of whelk (groups of >300) attack and kill individual lobsters within 15 min (all flesh is eaten in <60 min). Lobsters were present on Marcus in historical times; evidently a severe storm or overharvesting reduced lobster densities to a point that they could no longer control whelk numbers, and the community switched.

INDIRECT EFFECTS IGP directed at superior resource competitors can produce similar effects on community structure as does regular predation. IGP was shown to exclude or decrease populations of the better exploiter in many systems (4, 5, 18, 27, 28, 31, 36, 37, 38, 41, 66, 70, 80, 83, 94, 110, 120, 130, 131, 142). In many of these cases, the supply of the common resource increases because the abundance of the IG prey is reduced. For example, both predaceous anthocorid bugs and parasitoid braconid wasps eat pyralid moths (110). Anthocorid IGP on wasps reduces wasp populations and indirectly causes a 180% increase in moth populations (over levels that occur with wasps only). Similarly, anole IGP on spiders causes a 30–40% increase in the abundance and biomass of arthropod prey eaten by spiders and anoles (131 and included refs). Killifish IGP eating grass shrimp causes a significant increase in one of six prey taxa (66). IGP by *Odonaster* seastars appears to control the population of *Acondontaster* seastars, thus allowing increases in the populations of five sponge species eaten by both stars (see 27, 83).

IGP on intermediate level marine predators is so pervasive that Ambrose (4) proposed a general model: IGP by marine epibenthic predators controls the abundance of infaunal predators that, in turn, controls the abundance (and diversity) of other infauna. Thus, high populations of these predators exert a positive effect on the density and diversity of (nonpredaceous) infauna. A similar model in lakes, the “size efficiency hypothesis” (21, 28, 51, 70), states that predation by large predators (fish, salamanders) on smaller (intermediate-level) predaceous zooplankton decreases their populations, thus allowing increases in the populations of zooplankton prey (some of which are eaten by fish and salamanders). Such indirect effects may be a common product of IGP on smaller intermediate-level predators. In theory, these indirect effects can stabilize nonguild resource populations during times of declining resource abundance: If the IG predator expands its diet to include (more efficient) IG prey, mortality on resource populations is indirectly reduced, thus tending to stabilize these populations.

In many of the above systems, “keystone IGP” increases the diversity of

nonguild and/or IG prey. For example, spider diversity increases in the presence of anoles (131 and included refs). IGP among ants can eliminate or reduce populations of dominant ant species (41, 120); this produces less competition for nesting sites and foraging space and allows increases in normally subordinate ant species. Species of competitively inferior, "successional" ants were 50% more diverse and twice as dense in local areas raided by *Eciton* army ants (41). IGP through its effects on the diversity and abundance of prey contributes to the structure of entire communities (for complex examples partially involving IGP see 51, 80). For example, a relatively simple community exists on Malgas island: Lobsters control mussels and barnacles (the two dominant space competitors) and urchins (herbivores) thus allowing the establishment of a rich algal community (8, 9). On Marcus, lobsters are absent and algae are rare; algae are eaten by abundant urchins and outcompeted (for space) by mussels and barnacles.

Finally, the ubiquity of IGP questions the generality of many proposed food web patterns (e.g. in 102; see 105). (a) Many web models assume that looping is either "unreasonable" or "very rare" (102). Mutual predation and cannibalism are "looping" trophic interactions. If nodes of a web are defined as species, loops are in fact rather common, as shown here and elsewhere (39, 75, 103). Looping also violates the common assumption that body size relations of predators and prey order species along a cascade or hierarchy, such that a given species can prey on only those below it and can be preyed on only by those species above it. (b) IGP, especially on intermediate level predators, is one of several factors that greatly increases omnivory. (c) The ubiquity of looping and omnivory make the "trophic level" concept nonoperational as applied to any particular species. For example, if *A* eats *B* but *B* eats *A*, is *B* on the first, third, or (after another loop) fifth trophic level? Assigned trophic levels may poorly reflect complexity of nature.

THE EVOLUTION OF IGP

The evolution of any interspecific interaction has to be understood from the perspective of each of the participants. In the past two decades, a large body of evolutionary and ecological theory on diet choice (optimal foraging theory) and a smaller but growing body of theory on escape tactics of prey have arisen. Does any aspect of IGP exhibit evolutionary consequences not already embodied in this extant theory? IGP accrues all the selective advantages for the IG predator as does predation on nonguild members (see Individual Fitness). However, two unique benefits may exist in populations under certain widespread conditions (see below). IGP directly enhances individual fitness when local resources are freed by the elimination of a competitor (104). Second, in cases of mutual predation, the IG predator may increase its fitness

by removing a potential predator on itself and/or its offspring. IGP in spatially unstructured populations does not increase relative fitness because all members receive benefits (104).

Is the reduction in competition of direct selective significance, or is IGP more accurately viewed as an action of predation, with decreased competition as a side effect? This question is addressed explicitly by many authors (13, 30, 32, 39, 75, 81, 104, 107, 114a, 120, 124, 134, 153). In most cases, IGP appears to be a simple act of predation directed at nutritionally profitable prey that happen to use similar resources as the predator; i.e. IGP is an act of predation, and decreased competition is epiphenomenal. However, in some cases, the evolutionary explanation of IGP may be more complex, and the reasons it occurs may vary, depending on context, even for the same pair of interacting species. For example, lions and hyenas may kill one another in disputes over territory and carcasses, or hunt each other as prey (30, 67, 126 and included refs). Thus, IGP is sometimes extreme aggressive interference directed at close competitors as a form of, e.g., "territorial aggression" (81); in defending a specific foraging area or resource, victims are killed but not always fully eaten. At other times, IGP is "predatory aggression" that often increases during periods of hunger; victims are fully eaten. Context-dependent IGP also occurs among ants (13, 81, 120, 153) and spiders (124).

Optimal foraging theory can help distinguish the selective basis (predation or competition) of IGP. IGP is likely to have a competitive basis when consuming the prey is suboptimal according to the criteria of standard optimal diet models. For instance, the energetic costs of IGP may exceed its benefits, as when prey are killed but not (fully) eaten. In this context, the evolution of IGP is an example of the evolution of interference competition (15, 16, 104 and included refs). Direct dominance over potential competitors appears to be a major factor in the evolution of some IGP (13, 30, 32, 39, 75, 81, 104, 114a, 120, 134, 153). A theoretical progression has been proposed (13, 16, 104, 153), starting with exploitation competition for limiting resources, followed by aggression to monopolize local resources—eventually producing IGP as a particularly effective way to eliminate competitors.

However, trade-offs are involved (16, 104). Individuals that successfully interfere with or eat competitors may experience costs in terms of resource exploitation and reproductive rates. Interference costs time and energy that could otherwise be devoted to harvesting resources. Moreover, the morphological, physiological, and behavioral modifications necessary for IGP may reduce the ability to harvest resources efficiently. The increase in size that allows IGP may make the predator less efficient on those smaller resources. Thus, we expect species successful at IGP often to be relatively inefficient at harvesting jointly exploited resources. This occurs in such diverse taxa as corals (71, 138), chaetognaths (96), freshwater zooplankton (36, 70, 73, 79),

blowflies (142), parasitoids (31, 37), and fish (88, 98, 109, 149). We found no cases where a species superior at IGP was better at exploitation competition. (However, many IG predators aggressively monopolize higher quality resources.)

Despite these costs, intraguild predation should evolve more readily than nonpredatory interference (104). Without IGP, interference towards competitors can evolve only if local resources are monopolized. Without local resource competition, IGP may increase individual fitness, whereas non-predatory interference decreases relative fitness (104). Under these conditions, nonpredatory interference cannot evolve at the level of the individual to reduce exploitative competition; such resource-related interference is altruistic (or spiteful) and can only evolve via group/kin selection. By contrast, IGP can evolve in both spatially unstructured and structured populations. This may explain partially why IGP is so widespread.

CONCLUSIONS

To place IGP into a broader context, consider the simple food webs of Figure 6, which schematically embody many of the central notions of community ecology. Exploitation competition (Figure 6a), an indirect interaction arising from the shared dependency of two consumer species on a limiting resource, leads to a problem of how species coexist; all else being equal, the species better at exploiting the common resource excludes the other. In apparent competition (57; Figure 6b), predation may exclude one prey species because an alternative, more productive prey is present, sustaining the predator at high density. In classical, mixed (nonguild) predation-competition systems (Figure 6c), coexistence requires one species to be superior at resource utilization, the other at withstanding predation (a kind of niche differentiation). In a three-link chain (Figure 6d), the impact of the primary consumer on its resource depends on the effectiveness of the top-level consumer. IGP incorporates elements of all these other trophic structures: (a) a propensity to exclusion, either because of competition for a limited resource (as in Figure 6a), or because the predator can be sustained by a productive, alternative prey (as in Figure 6b); (b) a possibility of coexistence, if the species more vulnerable to predation is superior at resource exploitation (as in Figure 6c); and (c) an increase in underlying resource levels because of the IG predator's effect on the IG prey (paralleling Figure 6d). IGP systems are particularly prone to exhibiting alternative stable states.

The significance of any particular IGP interaction will vary with its overall community context (Figure 6e). Exclusive resources for the IG predator make the status of the IG prey more precarious. By contrast, exclusive resources for the IG prey, or other predators that attack just the IG predator, dilute the

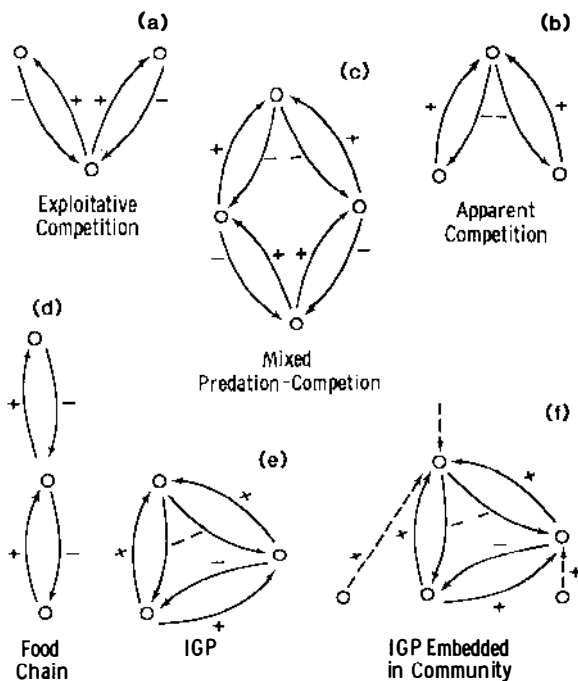


Figure 6 The relationship between IGP and other interspecific interactions. (a) Exploitative competition. (b) Apparent competition. (c) Mixed predation-competition. (d) Three-link food chain. (e) Intraguild predation. (f) Intraguild predation in a complex community, including (dotted lines): exclusive resources for species A and B; higher-level predators attacking just A.

impact of the IGP interaction. Many studies outlined above show that IGP can sometimes be a dominant factor in determining distribution and abundance; alternatively, the overriding effects of extraneous factors may often reduce its importance.

Thus, interactions in natural communities are complex. Both the empirical studies and models show that IGP can affect the biology of interacting populations in ways that cannot be typologically classified in terms of simple + or -. The combined effects of competition and predation often produce concurrent differences in the dynamics, growth, survivorship, and resource use within age classes of interacting populations.

Future research on IGP could proceed in a number of directions. IGP, as the cooccurrence of competition and predation between two species, must be incorporated more explicitly into empirical studies and models of populations and food webs. Age structure is critical to most types of IGP and likewise must be considered. Experiments are needed to disentangle the roles of IGP

and resource competition in determining realized guild structure. An open question for both theoretical and empirical work is to examine the possibility of cyclic and other complex dynamical behaviors in IGP systems. The existence of alternative stable states is particularly intriguing. Finally, an evolutionary understanding of IGP requires a better grasp of its ecological context and the spatial structure of populations. Our review shows that intraguild predation is a ubiquitous and often powerful interaction central to the structure and functioning of many natural communities; closer attention to it will enrich our understanding of population and community ecology.

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