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There is a long-standing debate in ecology concerning the relative importance of competition and predation in determining community structure. Recently, a novel twist has been added with the growing recognition that potentially competing species are often engaged in predator–prey interactions. This blend of competition and predation is called intraguild predation (IGP). The study of IGP will lead to a reconsideration of many classical topics, such as niche shifts, species exclusion and cascading interactions in food webs. Theoretical models suggest that a variety of alternative stable states are likely in IGP systems, and that intermediate predators should tend to be superior in exploitative competition. Many field studies support these expectations. IGP is also important in applied ecological problems, such as the conservation of endangered species and fisheries management.

Intraguild predation (IGP) is the killing and eating of species that use similar resources and are thus potential competitors. It is a common and often important interaction in a diverse array of communities<sup>1</sup>. IGP occurs among members of the same guild, defined broadly (*sensu* Ref. 2) to include all taxa in a community that use similar resources and thus may compete, regardless of differences in taxonomy or tactics of resource acquisition. IGP cannot be classified simply into existing categories of interspecific interactions. Although combining elements of predation and competition, IGP

is distinct from each. It is distinguished from competition because one participant (the predator) accrues immediate energetic gains. It differs from classical predation because the act reduces potential competition.

Although ubiquitous, IGP has historically been less well integrated into the conceptual framework of ecology than competition and predation considered separately, except in analyses of food-web stability based on Lotka–Volterra models<sup>3</sup>. Competition theory has focused on how similar species divide resources, the mechanisms of coexistence and exclusion, and the characterization of priority effects (alternative stable states). Predation theory has emphasized the factors allowing predators to persist with prey, the degree to which predators suppress prey, and the oscillatory tendencies of predator–prey interactions.

Many studies have analysed systems in which predators and competitors comprise distinct species groups that interact. Theory has elaborated three distinct effects that may occur when predation overlays pre-existing competitive interactions in four-species systems (one resource, two competing consumers and a predator; see Fig. 1a).

(1) Predation on the superior consumer can prevent competitive exclusion and promote coexistence (i.e. the keystone predator effect).

(2) Predation can indirectly increase resource abundance by depressing consumer populations (i.e. the trophic-cascade effect<sup>4–6</sup>). (3) Predation on a productive consumer can allow predators to increase to levels sufficient to exclude the less-productive consumer species (i.e. apparent competition<sup>7</sup>).

IGP is another class of interactions combining predation and competition. In the simplest case, it entails a three-species system where one of the competitors is also a predator and the other is its prey (Fig. 1b). This system provides a rich array of possible outcomes including exclusion, coexistence, priority effects, alternative stable states and increases in resource levels. Pimm and Lawton<sup>8</sup> (who refer to this triangular configuration as 'omnivory') suggested that IGP may be statistically rare in communities because the intermediate predator in such configurations faces a double jeopardy of competition and predation from the top predator, and so is vulnerable to exclusion. Because many examples of IGP exist, it is useful to understand the conditions permitting its persistence in food webs. The impact of IGP on population dynamics is more complex than either competition or predation alone.

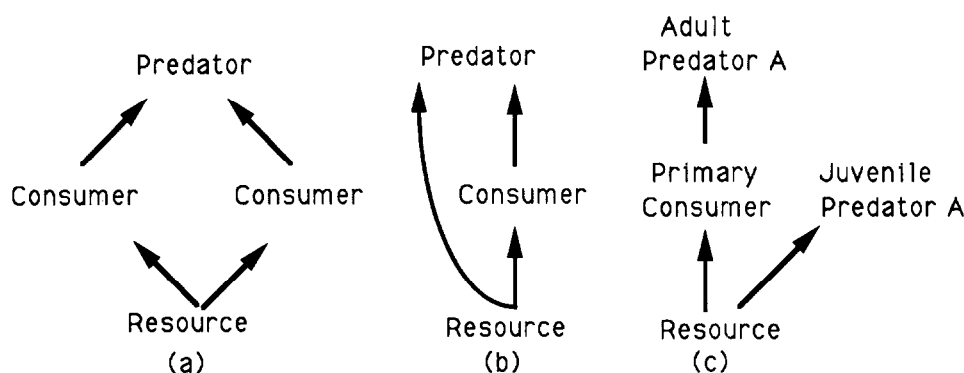
#### Ubiquity of intraguild predation

IGP often occurs among species that eat the same food resources but

## Intraguild Predation: The Dynamics of Complex Trophic Interactions

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**Fig. 1.** Food webs with and without intraguild predation (IGP), illustrating how predation can modify consumer and resource dynamics. (a) A four-species food web without IGP. (b) The switch from a four-species web to a three-species web with IGP when one consumer of the resource also eats the other consumer. (c) IGP in a three-species web with an age-structured species whose juveniles potentially compete with the consumer and whose adults eat the consumer.

differ in body size such that the smaller species or stage class falls within the normal prey size range of the larger. Thus, intermediate-level predators or smaller stage classes eating a general category of prey (e.g. plankton, benthic fauna, nematodes, arthropods, fish) often fall prey to larger predators exploiting the same prey category. Most predators eat prey in a particular size range regardless of the prey's feeding history, i.e. prey categories characterizing a predator's diet often do not comprise a well-defined trophic level<sup>1,8,9</sup>. Such IGP is well-nigh universal in freshwater, marine and terrestrial food webs<sup>1,9-11</sup>. In particular, the existence of age

or stage structure facilitates IGP (e.g. Fig. 1c). The young of many species are vulnerable to species with whom the adults may compete, or which they even eat. For example, IGP by filter, suspension and deposit feeders on the young of other invertebrates with whom they potentially compete (for food and/or space) as adults is a major mortality factor for young recruits in many communities (see below).

#### Community structure

Theoretical models suggest that IGP can lead to exclusion, coexistence or alternative stable states. One way to develop a model of IGP is to start with a model of com-

petition, and introduce additional terms that express the short-term effects of IGP. An example of this approach is presented in Box 1.

Numerous field examples<sup>1</sup> illustrate that predation is often severe enough to reduce local abundance drastically, or even to eliminate populations of competing IG prey. IGP may cause developmental bottlenecks and, in concert with priority events, can produce alternative states in communities<sup>1</sup>. The spatial expression of alternative stable states is patches generated by founder events: whichever species establishes first often dominates via the elimination of later arrivals by IGP on vulnerable stages (e.g. granivorous beetles on eggs and larvae; pre-existing colonies of ants on founding queens). Mutual IGP (adults eating juveniles of competing species), leading to patchily distributed alternative states, characterizes many benthic and planktonic communities<sup>1</sup>. Thus, established populations of filter-, suspension- and deposit-feeding benthic organisms often form 'meiofaunal bottlenecks' that limit local recruitment.

#### Niche shifts

Similar patterns of niche and resource use among guild members can be produced by IGP and resource competition. IG prey often segregate from IG predators. Such segregation may result from an evolutionary response or from short-term behavioral avoidance, or it may simply reflect mortality from IGP. Such shifts are widespread, usually with the IG prey occupying times and habitats that are relatively less productive or beyond the physiological tolerance of IG predators. Well-studied examples include experimental demonstrations of such shifts in scorpions<sup>12</sup>, fish<sup>13</sup> and salamanders<sup>14</sup>. A difficult empirical task in such systems is to gauge the relative impact of predation and competition in generating the observed patterns.

#### Indirect effects on prey resources

IGP exerts strong indirect effects in many systems by excluding or decreasing populations of superior resource competitors, thus increasing the supply of the shared

#### Box 1. A model of the effect of intraguild predation (IGP) on competition

As an example, consider how IGP influences competition for a single limiting resource. Models of exploitative competition<sup>32</sup> assume that the per capita growth rate for species *i* can be expressed as an increasing function  $f_i(R)$  of  $R$ , the abundance of a limiting resource. Each competitor's population will decline below a critical value of  $R$ ; above this value, the population will grow. With IGP, the growth rate of the IG predator (denoted as species 1) and the growth rate of the IG prey (species 2) are respectively:

$$dN_1/dt = N_1 (f_1(R) + g(y(N_2))) \text{ and } dN_2/dt = N_2 (f_2(R) - y(N_2)N_1)$$

where  $N_1$  and  $N_2$  are the densities of the IG predator and the IG prey,  $y(N_2)$  is the functional response of the predator to its prey, i.e. per capita predator consumption, and  $g(y(N_2))$  is the benefit that the predator gains from this consumption ( $g > 0$ ). (The model is completed by an equation for the limiting resource, which is not needed for the following points.)

This model illustrates several general features of IGP systems. First, for both species to coexist at a stable equilibrium, the IG predator must be inferior at exploiting the resource. Given that the IG predator is in equilibrium, it must be the case that  $f_1(R) = -g(y(N_2)) < 0$ ; for the IG prey to be in equilibrium, one must have  $f_2(R) = y(N_2)N_1 > 0$ . Hence,  $f_1(R) < 0 < f_2(R)$ : the IG predator would decline were it to be supported by just the resource, whereas the IG prey would increase were it not for predation. The above inequality operationally defines superiority in resource exploitation by the IG prey. If the IG predator is superior at exploiting the resource, the IG prey tends to be excluded even in the absence of predation, and with predation the IG prey is excluded by each of the two sets of harmful effects. An immediate implication of this result is that in a stable IGP system, top-predator removal should ultimately depress resource abundance. The above model structure also readily leads to alternative stable states, in which either species at equilibrium with the resource can exclude the other species; this is particularly likely if IGP is strongly asymmetrical, so that the cost inflicted on the prey greatly outweighs the benefit enjoyed by the predator. These predictions – intermediate predator superior at resource exploitation; resource depression following top-predator removal; and multiple stable states – characterize a much broader array of IGP models<sup>1</sup>.

resource<sup>1</sup>. This is so pervasive in marine benthic communities that Ambrose<sup>15</sup> proposed a general model: IGP by epibenthic predators controls the abundance of infaunal predators that, in turn, control the abundance (and diversity) of other infauna. Thus, epibenthic IG predators exert a positive effect on the (nonpredaceous) infauna that they eat. Such indirect effects may characterize IGP on smaller intermediate-level predators in many systems<sup>1</sup>.

#### IGP and indeterminacy of field experiments

Direct and indirect effects of IGP can complicate the interpretation of experiments. Although predators typically suppress their prey, if the predator is an IG predator on a more efficient IG prey, it may actually relax the predation load on their shared prey, thus increasing the shared prey's abundance (e.g. the epibenthic predators cited above). Thus, an IGP consumer species may indirectly facilitate its prey while concurrently exploiting it via direct consumption. Moreover, the removal of an IG prey can produce unexpected results. For example, Hairston<sup>14</sup> removed the salamander *Desmognathus ocoephaeus* to relax food competition with its congeners. Competition theory would predict that two other, larger *Desmognathus* species should have increased in abundance; in fact, these two species actually decreased in abundance, as expected were *D. ocoephaeus* an important prey. The caveat is clear: experiments can produce counterintuitive results, depending on the relative strengths of the direct and indirect effects of IGP<sup>1,16</sup>.

#### IGP, trophic cascades and the regulation of community structure

IGP is important in the evaluation of vying trophic-level hypotheses – for example, Hairston, Smith and Slobodkin<sup>17,18</sup> (HSS) versus Menge and Sutherland (Ref. 19 and see Ref. 20) – and trophic cascades<sup>4–6</sup>. These hypotheses involve webs that have between three and five links (e.g. plant → herbivore → intermediate-level predator → top predator; Fig. 2). In the HSS and trophic-cascade scenarios, a change in one trophic level affects other levels via tight

linkage between species on adjacent levels. For instance, an increase in a top predator decreases intermediate-level predator numbers, which, in turn, allows herbivore abundance to increase, ultimately decreasing plants. This scenario depends on the absence of strong IGP links (i.e. top predators that also eat herbivores; Fig. 2). If this link is strong (as is often the case<sup>1</sup>), changes in the top predator will not cascade or may even act in an opposite direction to that predicted by HSS (e.g. increasing top predators in a four-link system may decrease herbivore abundances, so that plants increase).

As the importance of IGP increases, community structure changes from that envisioned by HSS and the trophic-cascade models (in which predation and competition alternate in importance as one descends a food chain) to that predicted by Menge and Sutherland<sup>19,20</sup>, in which predation monotonically increases in importance at progressively lower trophic levels. Spiller and Schoener<sup>21,22</sup> make this point with respect to communities on small islands in the Bahamas. Thus, the specific geometry of strong links in webs and, in particular, the incidence of 'triangular' structures determine whether trophic cascades occur. Much evidence (e.g. Refs 5, 9, 10, 12, 15, 19–22) shows that either or both links (top to intermediate predators; top predator to herbivore) can be strong (in terms of dynamics and energetics). Thus, IGP systems do not always collapse to shorter webs where top IG predators obtain most of their energy from herbivores, as suggested by Oksanen<sup>6</sup> in his interpretation of the HSS paradigm.

#### Implications for conservation and management Fisheries

An understanding of IGP is central to the biology of many economically important and endangered species. For example, the dynamical complexity of IGP has caused repeated disasters in fisheries when exotics are added as prey for existing species. For instance, the introduction of shiners (*Richardsonius balteatus*) into a Canadian lake as food for resident trout (*Salmo gairdneri*) had this effect<sup>23</sup>. Piscivorous adult

trout benefited greatly; young trout, however, grew less due to resource competition with shiners. Eventually the entire trout population declined.

The interplay between the predatory and competitive components of IGP is well studied for bass (*Micropterus salmoides*) and bluegills (*Lepomis gibbosus*)<sup>13</sup>. Bluegills can outcompete young bass for plankton and reduce bass recruitment to larger, piscivorous sizes. Developmental bottlenecks may be particularly common when, as in this example, the IG prey is the more efficient competitor. Predation by adult bass may, in turn, reduce bluegill populations. Similarly, recruitment of perch (*Perca fluviatilis*) to piscivorous size classes may be limited by competition with roach (*Rutilus rutilus*)<sup>24</sup>.

The opossum shrimp, *Mysis relicta*, is a 'prey' species whose introduction into more than 100 lakes was often disastrous for several species of salmonid fishes<sup>25,26</sup>. Adult salmonids consume and benefit from *Mysis*; however, *Mysis* outcompetes planktivorous juvenile salmonids by depleting the

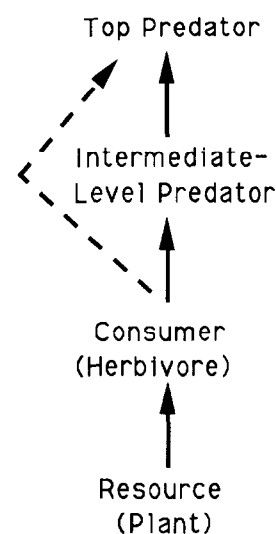


Fig. 2. The geometry of a cascading trophic interaction with and without intraguild predation (IGP). Trophic cascades are only possible if the IGP link (here, the dashed line between top predator and herbivore) is not strong compared to the link between the top and intermediate-level predators. Empirical studies indicate that, depending on the specific system, either link can be relatively stronger. As the strength of the IG link increases, community structure shifts from the 'green world' envisioned by Hairston, Smith and Slobodkin (Refs 17, 18 and see Ref. 6) to that predicted by Menge and Sutherland (Ref. 19 and see Ref. 20).

zooplankton eaten by both species. The subsequent crashes in stocks of target salmonids may ramify extensively up the food chain, causing precipitous declines in the populations of birds and mammals.

Alternatively, the stocking of many 'piscivorous' game fish has proved unsuccessful because juveniles of the introduced fish are outcompeted by resident fish species, which in turn are the required prey of the adult game fish; such competition forms an effective bottleneck into adult stages. Since this age-biased competition is largely seasonal, managers must know when to stock to avoid intense competition with planktivorous prey<sup>27</sup>.

In the south Atlantic, *Jasus* lobsters are abundant on Malgas island but are totally absent on Marcus island<sup>28</sup>. By contrast, several species of whelks (genus *Burno-pena*) are abundant on Marcus but rare on Malgas. Heavy IGP by Malgas lobsters on whelks produces this difference. Both are competitors, eating the same species of molluscs. The management goal was to establish harvestable populations of lobster on Marcus. IGP by whelks on lobsters made this impossible: lobster introductions to Marcus failed because whelk groups (of more than 300 individuals) immediately attack, kill and eat any colonizing lobster. Mutual IGP can produce alternative stable states, even in the absence of age-structure effects, a possibility that must be considered by resource managers.

#### The rarity of cheetahs

IGP combined with current management policies is apparently a significant factor decimating cheetah populations. IGP by other large carnivores is often the major mortality factor on kittens and may limit cheetah populations<sup>29</sup>. Management for large populations of these other carnivores (especially lions and hyenas, which also steal food from cheetahs) in reserves (as in Kenya and South Africa) greatly depresses cheetah numbers. In Namibia, where other carnivores were nearly extirpated by hunting, cheetahs are now so abundant that they are considered 'vermin' by ranchers because they eat domestic animals.

#### Biological control

That IGP is often directed at the most efficient resource exploiters in a guild causes us to rethink the use of multispecies assemblages in the biological control of pests. As discussed earlier, adding a consumer that is an IG predator may ultimately increase the target pest species because of the reduced effectiveness of the IG prey. For example, both predaceous bugs and parasitoid wasps eat pest moths<sup>30</sup>, but bug IGP on wasps reduces wasp populations, and indirectly causes a substantial increase in moth populations (over levels that occur with wasps only). Thus it is important to (re)structure introduced guilds of biological control agents (e.g. parasitoids, spiders) to exclude important IG predators so as to increase the overall effectiveness of the guild in controlling the pest species<sup>31</sup>.

#### Conclusion and future directions

Given the ubiquity of IGP in natural communities, this interaction deserves concerted attention from theoretical and empirical ecologists. On the theoretical front, it would be desirable to ascertain the potential for dynamical complexity (e.g. limit cycles, chaos) to arise because the triangular IGP loop leads to time-lags in density-dependent feedbacks, and to examine the coupling of populations operating at different time scales (IGP often involves organisms differing greatly in body size and thus generation length). On the empirical front, it would be useful to have a greater repertoire of examples, buttressed by field experiments, in which one could gauge the relative contribution of predation and competition in determining the impact of each species on the other.

It would also be exceptionally interesting to find counterexamples to the theoretical prediction that IG prey are superior to IG predators in competing for resources. We suspect that such cases will almost always feature nonshared resources that are exclusive to the prey. And finally, when viewed in the context of foraging theory, it would be valuable to ascertain the circumstances in which the competitive interaction between the predator and the prey influences

the foraging decisions made by the former.

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