HIGHER-ORDER PREDATORS AND THE REGULATION OF INSECT HERBIVORE POPULATIONS

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ABSTRACT

Empirical research has not supported the prediction that populations of terrestrial herbivorous arthropods are regulated solely by their natural enemies. Instead, both natural enemies (top-down effects) and resources (bottom-up effects) may play important regulatory roles. This review evaluates the hypothesis that higher-order predators may constrain the top-down control of herbivore populations. Natural enemies of herbivorous arthropods generally are not top predators within terrestrial food webs. Insect pathogens and entomopathogenic nematodes inhabiting the soil may be attacked by diverse micro- and mesofauna. Predatory and parasitic insects are attacked by their own suite of predators, parasitoids, and pathogens. The view of natural enemy ecology that has emerged from laboratory studies, where natural enemies are often isolated from all elements of the biotic community except for their hosts or prey, may be an unreliable guide to field dynamics.

Experimental work suggests that interactions of biological control agents with their own natural enemies can disrupt the effective control of herbivore populations. Disruption has been observed experimentally in interactions of bacteria with bacteriophages, nematodes with nematophagous fungi, parasitoids with predators, parasitoids with hyperparasitoids, and predators with other predators. Higher-order predators have been little studied; manipulative field experiments will be especially valuable in furthering our understanding of their roles in arthropod communities.

INTRODUCTION

A question that has preoccupied ecologists for much of this century is, What factors regulate the density of animal populations? Much of the dialogue

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surrounding this question has been motivated by studies of terrestrial herbivorous arthropods in natural and agricultural settings. A contentious issue that has emerged in considerations of herbivorous arthropods is the relative importance of host plant resources (bottom-up effects) vs natural enemies (top-down effects) (29). This review focuses on the prevalence of top-down control of terrestrial herbivorous arthropods.

Hairston, Smith, and Slobodkin proposed that terrestrial communities are comprised of decomposers plus three trophic levels: plants, herbivores, and predators (the "HSS" model; 74, 155; see also 73, 73a). Under this model each trophic level is functionally distinct; occupants of a given trophic level feed primarily on the next trophic level down. Predators suppress herbivores to low levels, such that herbivore impact on plants is minimal.

In support of their model, Hairston et al argued that plant resources are generally abundant and underexploited (the so-called green world hypothesis). Under the HSS model, biological control agents (predators, parasitoids, and pathogens) are found only at the top of the trophic web and are limited only by the availability of resources (their host or prey populations).

Critics of the HSS model questioned the edibility of defended plants and the ill-defined nature of trophic levels (47, 124). Nevertheless, the HSS model made its way into textbooks of biological control for pathogens and predators of insects (39, 40, 63, 88, 120). An important exception to the adoption of the HSS model occurred for insect parasitoids. Hyperparasitoids were recognized as higher-order predators (i.e. species whose hosts or prey occupy a position in the trophic web that is above the position of herbivores) that might threaten biological control. The exclusion of hyperparasitoids was therefore a primary goal of quarantines implemented during natural enemy importation (39, 40, 88, 146). Early suggestions that higher-order predators might also be important in communities of insect predators (8, 9, 193) went largely unheeded, and higher-order predators of pathogens were simply not considered.

A large body of empirical studies of the dynamics of herbivorous arthropods has been amassed since 1960. Correlational life-table studies (42, 161) and experimental studies (43, 75) have failed to reveal the pattern of consistent top-down control predicted by HSS. Instead, bottom-up and top-down forces appear to be complementary players. This conclusion has promoted a view of herbivore population dynamics in which the search for a single regulating factor has been subordinated to the pluralistic view that multiple factors may make important contributions (12, 52, 89, 101, 157). Alternative models of arthropod natural enemy community structure have also been proposed in which trophic levels are indistinct, higher-order predators and omnivory are widespread, and trophic interactions among natural enemies are potentially important (76, 136–138, 194).

Biological control theory is, however, still based primarily on a three–trophic level model of arthropod communities (e.g. 41, 175, but see 40). Why? First, Nicholson's (127) analysis of higher-order predators and parasitoids (hyperparasitoids and predators that attack other predators) predicted influences ranging from enhanced to disrupted biological control, but Nicholson concluded that enhanced herbivore suppression was the most likely outcome. The HSS model has also been bolstered by analyses of ecosystem energetics suggesting that, unlike freshwater or marine ecosystems, terrestrial communities are unable to support more than three trophic levels (73, 73a, 129). Finally, the nonrandom selection of study systems or nonrandom reporting of experimental results by insect ecologists may have promoted the HSS view (2). Scientists devoted to making biological control an accepted alternative to pesticides may have been loathe to promulgate (or even contemplate) a view of insect natural enemies constrained by the action of other consumers. To improve the efficacy of biological control, however, we must understand those factors that impede the top-down regulation of herbivores.

Possible reasons that top-down control of herbivores may not be realized include adverse effects of weather on natural enemies; herbivore defenses or use of structural refuges; lack of synchrony with the herbivore population or absence of key alternate hosts or prey; shortages of non-host resources, such as free water, nectar, honeydew, or pollen; interference from ants associated mutualistically with homopterans; presence of airborne dust; interspecific competition between natural enemies; in agroecosystems, disruptions from pesticide applications or other agronomic practices; and finally, for parasitoids, the action of hyperparasitoids (40, 51, 72, 77, 120, 174).

This review introduces the general hypothesis that higher-order predators can act as an important constraint to the top-down control of terrestrial herbivorous arthropod populations by entomopathogens, entomopathogenic nematodes, parasitoids, and predators. I examine the empirical evidence, including an overview of different groups of higher-order predators and a critical analysis of experiments that have quantified their action. Experimental studies, although few in number, provide substantial support for the hypothesis.

ENTOMOPATHOGENS

Persistence of entomopathogens in the environment is a key influence on their efficacy (64, 96). Studies of persistence have traditionally focused on abiotic factors, including ultraviolet radiation, humidity and water availability, temperature, and pH (13, 64, 96, 113, 118). This focus may be appropriate for pathogens inhabiting exposed plant foliage, where ultraviolet radiation rapidly inactivates most microorganisms and low humidity often precludes germination

and survival of entomopathogenic fungi (13, 64, 96, 113, 118). However, the hosts of many pathogens are found in more protected habitats, such as soil, and many pathogens attacking above-ground hosts survive in the soil in relatively long-lived resting stages (spores of bacteria, protozoa, and fungi; inclusion bodies of viruses) during periods of host absence.

Soil ameliorates the effect of abiotic mortality factors by absorbing solar radiation, maintaining near-100% relative humidities, and buffering temperature fluctuations (13, 64, 113, 118). Thus, biotic factors may emerge as the most important influences on the survival in soil of microbial entomopathogens (13, 64, 65, 109, 188). The effect of biotic agents on the persistence of viruses remains unstudied. The dynamics of pathogen populations in protected reservoirs may be pivotal in shaping entomopathogen epidemiology (13, 19, 82).

Biological control researchers have made major advances in characterizing the competitive and trophic interactions that suppress phytopathogens (7, 27, 100). Work in insect pathology has been largely independent of these advances. However, our still fragmentary understanding of entomopathogen survival in soil suggests that the same interactions that suppress phytopathogens are also important in suppressing entomopathogens.

Fungi

Fungi in soils are subject to parasitism and predation by a diverse micro- and mesofauna, including other fungi (mycoparasites), viruses (mycoviruses), bacteria, actinomycetes, protozoans, mites, nematodes, collembolans, beetles, annelids, and others (7, 27, 44, 100, 122). The impact of these consumers on the persistence of entomopathogenic fungi has been little explored. Mycoparasites of entomopathogens are known (100), but their significance is unknown. Virus-like particles and double-stranded RNAs were isolated from *Metarhizium anisopliae*, but short-term laboratory assays did not reveal an effect on fungal virulence (108).

Persistence of entomopathogenic fungi can be reduced substantially in nonsterile vs sterile soil (109, 133). For the many entomopathogenic fungi that are facultatively saprophytic, this antagonism may reflect a combination of exploitative competition (a bottom-up effect), interference competition (e.g. the production of antibiotics, a lateral effect, sensu 75), and predation or parasitism (a top-down effect). Simple comparisons of nonsterile vs sterile soil cannot distinguish these possibilities.

Beauveria bassiana persistence was slightly reduced in nonsterile vs sterile agricultural soil (109). A common fungus in this soil, *Penicillium urticae*, was found to produce patulin, a metabolite that inhibited germination and growth of *B. bassiana* conidia (109, 153). Predation also contributes to *B. bassiana* mortality in nonsterile soil (55). Blastospores incubated in soils in laboratory

microcosms were completely inactivated within 3 weeks. Electron microscopy revealed that blastospores were invaded by diverse bacteria, resulting in autolysis of the blastospores. Bacteria penetrated spores enzymatically, making perforations 0.1–0.5 mm in diameter. Larger perforations (2–4 mm) generated by amoebae were also observed, along with physical damage resulting from feeding by mites or collembolans. Formulating the blastospores in a coating of clay substantially retarded the process of biodegradation.

In summary, for *B. bassiana* at least, both interference competition and predation appear to influence persistence in soil. Additional work is needed to assess the importance of higher-order predators in the ecology of entomopathogenic fungi.

Protozoa

Intracellular protozoan (i.e. microsporidian) parasites of insects are widespread and may be transmitted vertically or horizontally through the production of spores. In laboratory microcosms, spores of *Nosema locustae* experienced no mortality in sterile sand but 99% mortality after 1 week in nonsterile soil (65). Spores on soil slides were attacked by actinomycetes and rod- and coccoid-shaped bacteria (65, 66); however, it was unclear if these bacteria preyed on living spores or simply digested spores that had been killed by some other agent.

Bacteria

Like soil fungi, soil bacteria have many natural enemies, including viruses (bacteriophages), other bacteria, protozoans, nematodes, mites, collembolans and other microarthropods, and enchytraeids (7, 27, 44, 122). Although entomopathogenic bacteria often survive longer in sterilized than in nonsterilized soil, few studies have determined the relative importance of predation, exploitative competition (relevant for the many entomopathogenic bacteria that are not obligate pathogens; 107), and interference competition (antibiosis) in explaining this result (64, 107).

Despite considerable interest in the field persistence of *Bacillus thuringiensis*, our understanding of its natural enemies is limited (3). When incubated in sterilized rather than nonsterilized soil, *B. thuringiensis* spores, parasporal crystals, and toxicity to insects persist longer, and viable bacteria reach densities that are two to three orders of magnitude greater (187–191). Water extracts of the soil analyzed by West et al (189–191) did not inhibit *B. thuringiensis*, suggesting that antibiotics were not the cause of the sterilization effect. Furthermore, no bacteriophages were detected in these soils (187, 188, 192).

Few observations of predation on *B. thuringiensis* have been made. West (187) used radioisotope labeling to demonstrate that *B. thuringiensis* parasporal crystal protein is decomposed by microorganisms in nonsterile soil.

Petras & Casida (134) reported nematodes ingesting *B. thuringiensis* spores, but it is unclear if the spores were digested and thereby deactivated. Using immunofluorescence techniques, West et al (192) showed that an actinomycete bacterium consumed heat-killed vegetative cells of *B. thuringiensis*, but no natural enemies were detected for live vegetative cells or spores. Protozoans consume *B. thuringiensis* in soil (31), but protozoan densities were stable or decreased when *B. thuringiensis* was added to soil, suggesting that *B. thuringiensis* toxins may poison potential protozoan predators (31, 134).

Addison (3) has hypothesized that *B. thuringiensis* toxins may have evolved as defenses against bacterivorous organisms (see also 115). Other potential predators of *B. thuringiensis*, including other bacteria, actinomycetes, fungi, and nematodes, showed numerical responses when *B. thuringiensis* was added to soil (134), but it is unclear if this response reflects their consumption of *B. thuringiensis*. In short, soil sterilization effects still cannot be definitively ascribed to either competition (188) or predation.

Bacteriophages are specialized viruses that can cause their bacterial hosts to lyse and die. Bacteriophages have been isolated from many entomopathogenic bacteria (71, 93, 107, 128) and can cause the collapse of commercial production of these bacteria (71, 128). In the laboratory, interactions of bacteriophages and bacteria within the insect host can decrease bacterium-induced host mortality. Bacteriophage fed to the New Zealand grass grub, *Costelytra zealandica*, reduced mortality generated by the bacterium *Serratia entomophila* (128). Intrahemocoelic injections of *B. thuringiensis* and its bacteriophage produced a slower course of host mortality than an injection of the bacterium alone (142). Final levels of mortality were unchanged, however, apparently because of the propagation of *B. thuringiensis* resistant to the bacteriophage. Because laboratory colonies of bacteriophage and bacteria may have limited genetic variability, laboratory studies may not be predictive of phage-bacterium interactions in nature.

Laboratory microcosm studies conducted by Hussein et al (93; see also 95) are noteworthy because they employed field-collected water samples harboring natural densities of bacteriophage. Nine of twelve sampled field sites had at least one bacteriophage attacking *B. thuringiensis* or *Bacillus sphaericus*, and up to seven distinct phage isolates parasitizing a single bacterial host species were identified from a single field site. Laboratory assays were conducted by adding either *B. thuringiensis* or *B. sphaericus* to field water samples, introducing mosquito larvae, and assessing mortality after 3 days. My analysis of data presented in Reference 93 reveals a significant inverse relationship between the number of phage isolates attacking each bacterium per site and the mortality generated by the bacteria (for *B. thuringiensis*, $r^2 = 0.54, n = 12, P = 0.006$; for *B. sphaericus*, $r^2 = 0.71, n = 12, P = 0.0006$). Mortality rates declined

from 90–100% in sites without phage to 50–60% in sites with the greatest numbers of phage.

A field experiment conducted by Hussein et al (94) suggested that bacteriophage populations may increase in response to field applications of entomopathogenic bacteria, rendering subsequent applications of bacteria ineffective. Two mosquito habitats that initially harbored phage at densities too low to be detected were treated with both *B. thuringiensis* and *B. sphaericus*. Within 3–7 days, phage of *B. sphaericus* were detected at both sites; however, phage attacking *B. thuringiensis* were not detected over the course of the 21-day experiment. Water samples were taken at weekly intervals and placed in laboratory assay units with mosquito larvae and either *B. thuringiensis* or *B. sphaericus*. Water from the field sites became highly suppressive to *B. sphaericus* (efficacy declined from 95–100% to 8–18%) over 3 weeks post-application, but only very slightly suppressive to *B. thuringiensis*. Because *B. thuringiensis* is ubiquitous in soil worldwide (115) and is even common on foliage (156), natural populations of bacteriophages may also be widespread, with potentially important implications for *B. thuringiensis* recycling, persistence, and efficacy.

Finally, bacteriophages have also been isolated from *Xenorhabdus* spp. bacteria, the symbionts of entomopathogenic nematodes. These phage, along with antibiotics and bacteriocins, mediate competitive interactions between *Xenorhabdus* spp. and other bacteria that infect the insect host (14). It is unknown if the phage play a broader role in the population dynamics of *Xenorhabdus* spp. and the efficacy of entomopathogenic nematodes.

ENTOMOPATHOGENIC NEMATODES

Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae are obligate pathogens of insects found in or on the soil. The only free-living stage is the third-stage infective juvenile (102). Infective juveniles can live in the absence of hosts for long periods in the laboratory, but persistence in the field is generally much shorter (10). In laboratory microcosm studies, nematode persistence is often enhanced by sterilizing the soil, suggesting that soil organisms are antagonists of nematodes (106, 163, 170). Variable persistence in the field may contribute to the erratic performance of nematode biological control agents and thus may be an impediment to their wider use (10).

Many microarthropods found in the soil are omnivorous, creating extremely complex trophic webs (44, 122). In laboratory trials employing bioassay dishes without soil or alternate prey, *Steinernema* and *Heterorhabditis* spp. nematodes were consumed by collembolans, tardigrades, mites, and other nematodes (50, 67, 103), and this nematode mortality translated directly into reduced ability to kill a laboratory host, the wax moth, *Galleria mellonella* (50, 67). However, in

laboratory microcosms incorporating plugs of turf, the nematophagous collembolan *Folsomia candida* did not diminish the ability of *Steinernema glaseri* to kill grubs of the Japanese beetle, *Popillia japonica*. This result highlights the difficulty of extending results from laboratory assay units that lack structural refuges to the complex soil environment. *F. candida* forages primarily on the soil surface and may have minimal impact on a subterranean-foraging nematode such as *S. glaseri*. Surface-foraging nematodes, such as *Steinernema carpocapsae* and *Steinernema scapterisci*, may be more at risk from collembolans such as *F. candida* (26, 67).

The best-studied natural enemies of entomopathogenic nematodes are the nematophagous fungi, including the nematode-trapping fungi, which employ mechanical traps or adhesive structures to ensnare nematodes, and the endoparasitic fungi, which produce conidia that adhere to passing nematodes (70). Nematophagous fungi growing on agar culture plates or in sterilized sand infect and kill many species of entomopathogenic nematodes (169). Some nematodes, however, show partial or complete immunity because of their retention of the protective second-stage cuticle (168, 169) or apparently because they lack key carbohydrate residues on the cuticle that are bound by lectins on the fungal adhesive structures (70, 135).

Fungi suppressed entomopathogenic nematodes in microcosm studies employing raw soil or sterilized soil to which fungi were added experimentally (170). Fowler & Garcia (61) found nematophagous fungi growing on the cuticle of field-collected mole crickets, *Scapteriscus borellii*, in populations subject to infection by natural populations of *Steinernema feltiae*. Assays in petri dishes showed that the fungi protected crickets from infection, which suggests that the relationship between these two species is mutualistic.

Ongoing work on the dynamics of *Hepialus californicus*, a caterpillar that feeds on the roots of a perennial lupine, *Lupinus arboreus*, in a coastal shrubland, promises to provide the first assessment of factors suppressing field populations of an entomopathogenic nematode. *H. californicus* causes mass die-offs of *L. arboreus* in areas where densities of the nematode *Heterorhabditis hepialus* are low (162, 164). The nematode causes heavy mortality of caterpillars in other areas where lupine survival is higher. Because *H. californicus* is univoltine and because there are no alternate hosts, infective juveniles of *H. hepialus* must survive in the soil for 7–10 months between periods of host availability. Infective juveniles experience mortality in soil collected from the lupine rhizosphere, and mortality rates are higher in areas where lupine mortality is greater (163). Sterilization of the soil eliminates this effect.

Jaffee et al (97) have isolated 12 species of nematophagous fungi, which in agar plate assays and in soil microcosms using realistic fungal densities caused substantial mortality of *H. hepialus* (106). *H. hepialus* comprises only a small fraction of the total soil nematode community exploited by nematophagous

fungi (bacteriophagous, fungivorous, and phytophagous species are much more abundant). Thus, if nematophagous fungi are suppressing *H. hepialus*, higher fungal densities would be predicted in areas where lupine die-offs occurred. Initial studies, however, have not demonstrated such correlations (97). Furthermore, the numerically dominant nematophagous fungus, *Arthrobotrys oligospora*, is also a mycoparasite and suppresses other nematophagous fungi in microcosms (105). Additional field experimentation is underway in this exciting system.

PARASITOIDS

Parasitoids may be infected by viruses, bacteria, fungi, protozoa, and nematodes (24, 148, 166, 184). Although laboratory and field studies have documented potentially high rates of infection and both sublethal and lethal effects, no manipulative field experiments examining the consequences for herbivore suppression have been reported.

Hyperparasitism

Insect ecologists traditionally have recognized only one group of higher-order predators as a potentially important constraint to top-down control of herbivores: the hyperparasitoids. The role of obligate hyperparasitoids has not been resolved, however, largely because of the paucity of manipulative experiments. The ecological roles of facultative hyperparasitoids, which are both competitors and consumers of primary parasitoids, have been reviewed elsewhere (148).

The debate on the ecology of obligate hyperparasitoids has centered on two questions. The first is whether hyperparasitoids disrupt biological control. Most models predict that obligate hyperparasitoids increase the equilibrium density of herbivores (18, 116). However, other models predict that hyperparasitoids exert minimal negative effects on biological control or may actually improve control by stabilizing fluctuations in the densities of the herbivore and the primary parasitoid (11, 111, 127).

A second and more recent controversial hypothesis is that hyperparasitoids do not exert their main adverse effects on biological control through direct mortality of primary parasitoids, but rather by influencing the foraging behavior of primary parasitoids in a way that decreases parasitism of the herbivore (84, 112). In response to spatially density-dependent hyperparasitism, primary parasitoids may abandon incompletely exploited patches of their herbivorous hosts (6, 112, 183) or, on a larger spatial scale, emigrate from fields that have many hyperparasitoids (84).

The hypothesis of early emigration in the face of hyperparasitism was derived from an analysis of seasonal patterns of aphid parasitism and hyperparasitism in cereal fields (84). Parasitoid emigration was inferred indirectly from what

was interpreted as declines in primary parasitism that occurred too early to be explained by direct impacts of hyperparasitism. However, primary parasitism usually declined only after hyperparasitism reached high levels (>50%; see Figure 3 in Reference 84). Thus, the alternate interpretation of direct suppression of primary parasitoids cannot be excluded.

Laboratory experiments have provided mixed support for the hypothesis that hyperparasitoids increase patch-leaving by primary parasitoids. While *Aphidius uzbekistanicus* disperses in response to the presence of its hyperparasitoids (15, 85), neither *Lysiphlebus cardui* nor *Aphidius funebris* do so (180).

Mackauer & Völkl (112) observed that many aphidiid parasitoids leave patches of host aphids long before all hosts are attacked. They suggested that this strategy of spreading offspring among many patches may have evolved to reduce the impact of hyperparasitoids that produce positive spatially density-dependent parasitism and to ameliorate the impact of hyperparasitism on fitness through the "spreading of risk." Departures from partially exploited host patches could be favored for other reasons, however, such as variation in host quality (17) or avoidance of self-superparasitism (149). Risk spreading seems unlikely to favor early patch-leaving. When there is only spatial (and not temporal) variation in offspring survival, risk spreading operates only when populations are unrealistically small (35, 68).

Spatial density-dependence of hyperparasitism is variable. Some hyperparasitoids act in a density-dependent manner and others act independently of primary parasitoid density (49, 151, 185, 186). The fate of dispersing primary parasitoids must be known to determine whether emigration reduces their fitness or simply redistributes them (75, 112). Völkl & Kraus (181) found no risk of mortality for parasitoids foraging within host patches. They did find a high risk of mortality from ensnarement in spider webs during interhost patch flights, supporting the idea that movement can be costly. Direct effects of mortality from hyperparasitism and indirect effects mediated by primary parasitoid foraging behavior are not mutually exclusive possibilities, and these provocative hypotheses should motivate additional research.

A substantial observational literature exists documenting high rates of hyperparasitism (e.g. 4, 16, 20, 84, 125, 177; see also 112, 146, 165). In some of these studies, biological control by primary parasitoids was poor, and researchers have attributed this performance at least in part to hyperparasitism (e.g. 16, 20, 21, 84). However, in other cases, biological control was economically successful despite high levels of hyperparasitism (e.g. 4, 56). Purely observational studies have produced little definitive evidence regarding the impact of hyperparasitism (111).

The literature on hyperparasitism is peppered with warnings concerning the anticipated difficulty of conducting experimental evaluations of hyperparasitoid

impact [e.g. 59, 84, 173; see also Luck et al's critique (111) of DeBach's study (38)]. Studies using enclosures have been deemed unsatisfactory by some workers because of the unnatural constraints on parasitoid movement (84). Nevertheless, Burton & Starks (25) conducted the first experimental test contrasting treatments with and without hyperparasitoids using small cages established within a greenhouse. They showed that the hyperparasitoid *Charips* sp. suppressed the primary parasitoid *Lysiphlebus testaceipes* to very low levels, allowing aphid populations to reach densities close to those observed in the absence of all parasitoids. Unreplicated informal observations of uncaged aphids in greenhouses suggested that either *Charips* sp. or another hyperparasitoid, *Pachyneuron siphonophorae*, effectively suppressed *L. testaceipes*.

Goergen & Neuenschwander (69) reported a similar experimental study using cages in greenhouses to test whether two species of hyperparasitoids could disrupt biological control of the cassava mealybug by its specialist parasitoid. Although neither of the hyperparasitoids tested alone affected mealybug control, an experiment that attempted to simulate field conditions by using realistic mealybug densities and releases of both hyperparasitoids showed a major disruption of biological control. Plant dry weight was reduced to 63% of that observed in the absence of hyperparasitoids. Finally, Shi (152) showed using field cages that the hyperparasitoid *Aphidencyrtus aphidivorus* produced a substantial but incomplete breakdown of aphid control exerted by the primary parasitoid *Trioxys communis*.

Thus, three experimental investigations of hyperparasitism led to a consistent conclusion: Hyperparasitoids disrupt the short-term regulation of hosts by primary parasitoids. The longer-term, multi-generation experiments needed to test the prediction that hyperparasitoids stabilize the herbivore-parasitoid interaction have not been conducted.

Predators of Parasitoids

PREDATION ON IMMATURE STAGES   Immature parasitoids may be attacked not only by hyperparasitoids but also by predators (see 148, 166). A likely influence on the effects of adding a predator to a host-parasitoid system is the relative impact of the predator on parasitized vs unparasitized hosts. Predator impact in turn is a function of encounter rates and attack rates.

The foraging patterns of parasitoids and predators can result in parasitized hosts being under- or over-represented in the pool of potential prey encountered by predators. Three examples demonstrate the range of potential outcomes. Sawfly larvae feed gregariously and display group defenses, thereby concentrating parasitoid and predator attacks in the colony's periphery. As a result, predatory pentatomid bugs encounter and attack a disproportionate fraction of parasitized sawfly larvae (171).

Interactions also occur among natural enemies of the goldenrod gall fly (1). The most important parasitoid, *Eurytoma gigantea*, only attacks galls with radii that are sufficiently small to be traversed by the parasitoid's ovipositor. Predatory larvae of the beetle *Mordellistena unicolor* attack galls of all sizes and therefore encounter parasitized galls in proportion to their abundance. Two birds, however, preferentially attack larger galls and thus bias their attacks on unparasitized gall flies.

Finally, spatial variation in host density can shape predator impact on parasitized hosts (172). Predation by blue tits on a cecidomyiid gall midge was concentrated in areas of high midge density; thus, birds had a greater than proportionate impact on two parasitoids that foraged in areas of high host density, a less than proportionate impact on two parasitoids that foraged in areas of low host density, and a proportionate impact on the remaining four parasitoid species that foraged independently of host density. These effects were balanced, so that the blue tits encountered parasitized hosts in proportion to their overall abundance.

Immature parasitoids may manipulate their host's behavior, altering microhabitat selection and thereby decreasing their likelihood of being encountered by predators (and potentially hyperparasitoids) (20). Behavioral manipulation may extend to the recruitment of host defensive behavior against potential natural enemies even after the parasitoid has emerged from the host and pupated (22, 104).

Not all encounters between predators and potential prey result in successful attacks. Predators may attack only unparasitized hosts, attack only parasitized hosts, or show partial preferences (reviewed in 62, 148, 166). A common pattern is for predators to consume newly parasitized and unparasitized prey indiscriminately but to discriminate increasingly against parasitized prey as the parasite develops and effects more substantial changes in host morphology and physiology. Even parasitoids that have fully consumed their hosts may not be free from predator attack, however, as witnessed by the many predators that attack mummified aphids and parasitoid pupae found with host remains (104, 148, 166, 185).

Four experiments have been reported in which a predator was added to a host-parasitoid system. In all cases, the predator consumed both unparasitized and parasitized hosts. Press et al (141) examined biological control of *Plodia interpunctella* by the parasitoid *Bracon hebetor* and the predator *Xylocoris flavipes* in the laboratory. *X. flavipes* fed directly on the ectoparasitic larvae of *B. hebetor*, but relative preferences for parasitoid vs moth prey were not measured. Although each natural enemy tested alone suppressed *P. interpunctella* populations, the parasitoid was much more effective than the predator. Adding

the predator to the host-parasitoid system disrupted biological control, and *P. interpunctella* densities almost doubled.

Ferguson & Stiling (58) used field cages to assess suppression of the aphid *Dactynotus* sp. by the parasitoid *Aphidius floridaensis* and the coccinellid predator *Cycloneda sanguinea*. *C. sanguinea* preyed upon mummified aphids, but preferences for parasitized vs unparasitized prey were not quantified. Although both natural enemies tested alone suppressed aphids, the parasitoid was again more effective than the predator. Adding the predator to the host-parasitoid complex caused aphid densities to increase slightly, but the main test for interaction was nonsignificant.

Colfer & Rosenheim (33) used field cages with different mesh sizes to study the ability of the parasitoid *Lysiphlebus testaceipes* alone and in combination with the predator *Hippodamia convergens* to regulate populations of the aphid *Aphis gossypii*. Laboratory choice-tests suggested that *H. convergens* was approximately equally likely to consume unparasitized aphids vs aphid mummies (RG Colfer, personal communication), and predation on mummies in the field was heavy. Nevertheless, adding predators to the host-parasitoid system substantially enhanced biological control. These results were mirrored in observational field studies, which documented consistently strong biological control through the combined effects of parasitoids and predators (150a).

Finally, Heinz & Nelson (81) used large cages in greenhouses to test all combinations of the parasitoids *Encarsia formosa* and *Encarsia pergandiella* and the predator *Delphastus pusillus* for control of the whitefly *Bemisia argentifolii*. Laboratory studies showed that *D. pusillus* does not discriminate between unparasitized whiteflies and those harboring parasitoid eggs or young larvae but shows increasingly strong avoidance of hosts harboring mature parasitoid larvae or pupae (80, 83). The predator was a more effective biological control agent than either of the parasitoids, and adding the predator to host-parasitoid systems consistently improved whitefly suppression.

These four studies demonstrate that the addition of predators to host-parasitoid systems can either enhance or disrupt biological control. Additional studies linking levels of herbivore suppression to predator preferences for parasitized vs unparasitized hosts will be especially useful in dissecting the mechanistic basis for these variable outcomes.

PREDATION ON ADULT PARASITOIDS   The traditional view of adult parasitoid ecology has been shaped by an extensive literature of laboratory studies that report parasitoid life-table parameters. In these studies, parasitoids are generally provided with excess hosts, a source of carbohydrate nutrition, and protection from predators and other potentially adverse biotic and abiotic environmental

factors. This literature creates an expectation of substantial longevities and fecundities. For example, species of one intensively studied genus, *Aphytis*, are typically reported as having longevities of 2–6 weeks and lifetime fecundities of 30–80 offspring (147).

Field observations suggest, however, that adult parasitoids have evolved under selection pressures exerted by predators. Parasitoids participate in mimicry complexes, forage at night to avoid predators, and display behavioral, structural, or chemical antipredator defenses (46, 68, 179). Several authors have reported informal observations of parasitoids falling prey to generalist invertebrate predators (79, 130). Studies that quantify parasitoid longevity in the field have produced estimates that are small fractions of laboratory values (78, 86, 143), suggesting that mortality factors that are excluded from the laboratory setting are important in the field.

One perhaps unexpected source of information regarding predation on parasitoids comes from studies reporting focal observations of parasitoids freely foraging in the field. These studies, usually conducted for reasons other than quantifying predation, present data sets that might be expected to be too small to be useful for estimating predation rates. The average size of the data sets summarized in Table 1 is 27.8 h of field observations. A predation rate sufficient to depress a laboratory-measured longevity of 4 weeks to a median longevity of 2 weeks would generate only a 5.6% chance of observing one or more predation events during 27.8 h of observations. Nevertheless, 7 of 17 studies did observe predation in the field, and in several systems predation appeared to be common. From these observations we can derive crude estimates of parasitoid half-lives, which are equivalent to projected median longevities. The observed half-lives are very short; for example, two species in the genus *Aphytis* have projected half-lives of less than 1 day. These field observations, taken collectively, reflect rates of predation that must be considered startlingly high.

In the only experimental tests of predation on adult parasitoids, Rees & Onsager (143, 144) used large field-cages and open-plot field experiments to test the impact of asilid flies on the longevity of sarcophagid flies (*Blaesoxipha* spp.) and their ability to parasitize the grasshopper *Melanoplus sanguinipes*. In cages harboring realistic densities of asilids, none of the parasitic flies survived the 13-day experiment, and grasshopper parasitism rates were less than 1%. In cages without asilids, 40% of the parasitoids survived, and grasshopper parasitism averaged 19.3%. Although the asilids also preyed on grasshoppers, overall suppression of grasshopper populations was nearly doubled in the asilid-free cages.

In subsequent open-field plots, attempts were made to catch and remove all asilids from some plots, while other plots were left unmanipulated as controls.

Although the mobility of the asilids, parasitoids, and grasshoppers rendered the asilid-removal treatment only partially effective, parasitism was still enhanced in the predator-removal plots.

These experimental studies and the observational studies in Table 1 suggest strongly that the current view of adult parasitoid ecology is realistic only for the laboratory environment. In the field many parasitoids appear to experience heavy predation, with resultant longevities far below the upper limits set by senescence. This heavy predation may be an important brake on the regulation of host populations by parasitoids.

PREDATORS

Sixty years ago, Balduf (8, 9) highlighted the importance of higher-order consumers of predatory insects. Pathogens (including bacteria, fungi, and protozoans), nematodes, parasitic mites, parasitoids, and invertebrate and vertebrate predators were described as natural enemies of predatory insects. Balduf also catalogued the defensive strategies of predatory insects against their enemies.

Interactions between insect predators and their natural enemies continue to be studied (e.g. 48, 92, 114, 148, 166, 182, 184, 194). Insect predators are often embedded in a complex network of trophic interactions not only with their herbivorous prey but also with each other (e.g. 136, 148, 166, 193). For example, predatory green lacewings are attacked by 36 genera of hymenopteran parasitoids; egg, larval, prepupal/pupal, and adult stages are attacked (5, 126). Lacewings are also exploited by parasitic mites and flies and by invertebrate and vertebrate predators (5, 9, 150). Lacewings have evolved defenses against their natural enemies, including the use of stalked eggs, camouflaging materials, and the deployment of defensive chemicals (9, 48, 121). Despite the omnipresent nature of these interactions, no experiments have examined the influence of natural populations of pathogens or parasitoids on the ability of predatory arthropods to regulate herbivore populations.

Experimental work has evaluated the impact of predator-predator interactions on the regulation of insect herbivore populations. The biological control literature is replete with comparisons of a predator-addition treatment with a no-release control. Predators are generally chosen for testing because they are thought to be effective regulators of a pest population, and predators are often tested in isolation from other members of the natural enemy community. Although not all trials report successful control of pest populations, it is rare to find reports of pest populations increasing in response to predator introductions.

Within the broader ecological literature, we often find, however, that at least some elements of the herbivore community increase in response to predator introductions (reviewed in 154). A series of field experiments examined the

Table 1 Direct observations of predation on parasitoids foraging freely in the field

Species (family)	Stage; field vs outplant[a]	Habitat/host plant	Total observation time (h) and [number of observations]	Number of predation events	Predators	Prey half-life (h)	Reference
Aphelinus asychis (Aphelinidae)	Adult males and females; outplanted	Barley	7.5 [100]	0	—	—	57; X Fauvergue, personal communication
Aphytis aonidiae (Aphelinidae)	Adult females; field	Almond orchard	87.3 [212]	5	*Zelus renardii* *Linepithema humile* Salticidae Thomisidae	12.2 (95% CI = 7.0–82.5)	79
Aphytis vandenboschi (Aphelinidae)	Adult females; field	Almond orchard	2.3 [23]	1	*Linepithema humile*	1.6	79; GE Heimpel, personal communication
Anicetus beneficus (Encyrtidae)	Adult females; field	Mandarins	2.4 [26]	0	—	—	96a; T Itioka, personal communication
Comperiella bifasciata (Encyrtidae)	Adult females; field	Mandarins	110.4 [280]	0	—	—	PJ Ode, personal communication
Closterocerus tricinctus (Eulophidae)	Adult females; field	Oak trees	11 [103]	0	—	—	34; EF Connor, personal communication
Leptopilina clavipes (Eucoilidae)	Adult females; field	Mushrooms in a forest	33.9 [49]	0	—	—	46
Leptopilina heterotoma (Eucoilidae)	Adult females; field	Fermenting fruits; sap fluxes	8.3 [27]	0	—	—	98, 99; A Janssen, personal communication

Aphidius rosae (Aphidiidae)	Adult females; field	Wild rose	28.5 [22]	1	Web-building spider (Linyphiidae)	19.8	178; W Völkl, personal communication
Lysiphlebus cardui (Aphidiidae)	Adult females; field	Creeping thistle	22 [43]	0	—	—	176; W Völkl, personal communication
Pauesia pinicollis (Aphidiidae)	Adult females; field	Pine trees	16 [11]	2	Web-building spiders	5.5	W Völkl, personal communication
Pauesia unilachni (Aphidiidae)	Adult females; field	Pine trees	73.7 [37]	4	Web-building spiders	12.8	181; W Völkl, personal communication
Trioxys angelicae (Aphidiidae)	Adult females; field	Spindle bush	4 [7]	2	*Lasius niger*	1.4	W Völkl, personal communication
Trioxys betulae (Aphidiidae)	Adult females; field	Birch trees	39 [18]	5	*Formica polyctena*	5.4	179; W Völkl, personal communication
Agathis thompsoni (Braconidae)	Adult females; field	*Lomatium dissectum*	14.3 [7]	0	—	—	167; JN Thompson, personal communication
Aphaereta scaptomyzae (Braconidae)	Adult females; field	Fermenting fruits; sap fluxes	4.8 [10]	0	—	—	A Janssen, personal communication
Asobara tabida (Braconidae)	Adult females; field	Fermenting apples and pears; sap fluxes	7.8 [16]	0	—	—	98, 99; A Janssen, personal communication

[a]The subjects of the focal observations were either members of naturally occurring populations (field) or were outplanted by the experimenters (outplanted).

effects of praying mantids on arthropod communities inhabiting old fields and pastures (53, 54, 90, 123). The addition of mantids suppressed some herbivores, had no effect on others, and caused still other herbivore populations to expand. For example, when Fagan & Hurd (54) calculated the strength of per capita interactions between *Mantis religiosa* and ten diverse arthropod taxa, the strongest interactions were as follows: (*a*) *M. religiosa* caused a large decrease in densities of predators in the family Nabidae, apparently as a result of direct predation; and (*b*) *M. religiosa* caused a large increase in densities of herbivorous Miridae, apparently as an indirect effect of predation on other members of the arthropod community.

Similarly, studies manipulating the presence of lizards, which are dominant insectivores in some tropical ecosystems, have shown that densities of herbivores (and associated plant damage) may decrease, remain unchanged, or increase (45, 131, 159). Lizards consistently suppressed spider populations, thereby allowing some insect populations to increase.

Although these studies document potentially disruptive effects of higher-order predators, it is difficult to pinpoint the interactions leading to increased herbivore densities. For example, some herbivores may increase in density not because of a release from predation, but because of a release from competition for food resources when predators suppress populations of other herbivores.

Perhaps the most definitive approach to identifying the effects of predator-predator interactions on herbivore population suppression is to conduct studies in which two or more predators, one or both of which is known to prey upon the other, are tested singly and in combination (23, 32, 36, 37, 60, 91, 117, 132, 150, 158, 160; see also 145). Such studies show clearly that adding predators to existing predator-prey systems does not consistently enhance the suppression of herbivores. Instead, herbivore populations often show no response, and in four of the nine systems studied to date some herbivore populations actually increased.

Spiller (158) demonstrated that the spider *Metepeira grinnelli* displaced and killed the spider *Cyclosa turbinata*, resulting in an overall decrease in predation on small arthropod prey compared to predation by *C. turbinata* alone. Combinations of three predatory mites were generally superior in controlling herbivorous mites than species tested singly, but in some cases the predator *Zetzellia mali* disrupted mite control by preying on the eggs of another predator, *Metaseiulus occidentalis* (36, 37). Brødsgaard & Enkegaard (23) demonstrated that control of the mite *Tetranychus urticae* by the predator *Phytoseiulus persimilis* was delayed by introducing the predatory bug *Orius majusculus*, which preyed upon *P. persimilis*. Finally, field studies in cotton have shown that the most effective predator of aphids, the lacewing *Chrysoperla carnea*, is itself subject to heavy predation by *Nabis* spp. and all developmental stages of the assassin

bug, *Zelus renardii*, resulting in a release of aphid populations from top-down control (32, 150). Direct observations of neonate lacewings foraging freely in the field confirmed the results of these caging studies by documenting intense rates of predation on lacewing larvae by a complex of hemipteran predators (neonate lacewing half-life = 34.7 h; JA Rosenheim, D Limburg, RG Colfer, unpublished data). Studies conducted to date on predator-predator interactions suggest strongly that higher-order predators may represent a powerful brake on the regulation of herbivores by predators.

CONCLUSIONS

This review suggests some conclusions that, although not surprising when viewed in the context of recent developments in community ecology (30, 119, 136, 138, 194), argue for a fundamental change in our view of natural enemy ecology.

First, natural enemies of herbivores are generally not top predators within the food web. While the intermediate position of primary parasitoids in food webs involving hosts (often herbivores) and hyperparasitoids is widely recognized, most other biological control agents have been viewed as being largely free of their own consumers. Entomopathogenic microbes, entomopathogenic nematodes, insect parasitoids, and insect predators are, however, all associated with a rich community of their own natural enemies. Many exploiters are unlikely to define potential hosts or prey simply on the basis of whether they are herbivores.

Second, higher-order predators may represent potent constraints on the efficacy of biological control. Experimental work with higher-order predators is still in its infancy, but patterns are emerging. Natural control exerted by pathogenic bacteria can be disrupted by bacteriophages; control by nematodes can be disrupted by fungi; control by parasitoids can be disrupted by predators or hyperparasitoids; and control by predators can be disrupted by other predators.

Interactions between biological control agents need not lead to less effective suppression of herbivores. Many examples exist of natural enemy combinations that produce enhanced control (23, 36, 37, 60, 91, 145, 158, 160), and even synergistic interactions are possible (110, 166). The conclusion based on decades of concerted work on the regulation of insect herbivore populations is likely to be appropriate for biological control agents as well: both bottom-up and top-down effects are important.

Given that biological control agents occupy an intermediate position in complex trophic webs, there may be little theoretical justification for expecting

consistently strong top-down influences on insect herbivores. The HSS model of three discrete trophic levels may not be a suitable template for biological control theory. The view of natural enemy communities that has emerged from this review is more consistent with models that have proposed indistinct trophic levels, widespread omnivory, trophic interactions among natural enemies, and dynamically significant higher-order predators (136, 138, 194). The historical successes of biological control have been reaped despite the action of higher-order predators; future work in biological control should be enhanced by a fuller understanding of their ecology.

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