INSECT HYPERPARASITISM

Daniel J. Sullivan

Department of Biological Sciences, Fordham University, Bronx, New York 10458

PERSPECTIVES AND OVERVIEW

Insect hyperparasitism is a highly evolved behavior that is restricted to three orders: the Hymenoptera, Diptera, and Coleoptera. It involves the development of a secondary parasitoid, or hyperparasitoid, at the expense of a primary parasitoid (3, 18, 21, 52, 63–65, 134). Hence, an insect hyperparasitoid attacks another insect that is itself parasitic on a host insect. The host is usually phytophagous, but could also be a predator or a scavenger. The terminology, taxonomy and evolution, bionomics and behavior of selected examples, ecology and host specificity, food web and mathematical models, and finally the impact on biological control of these insect hyperparasitoids are reviewed here. The fundamental theme running through this presentation of insect hyperparasitism is the ecological concept of the "food web" and community structure (2, 33, 54, 78, 98, 99). There exists in nature a complex of interlocking food chains consisting of the host plant, then phytophagous insects, and finally several levels of entomophagous insects that form a two-dimensional ecological community or biocenosis with both inter- and intraspecific components.

Terminology

Obligate hyperparasitoids are always secondary parasitoids; their progeny can develop only in or on a primary parasitoid. There are also *facultative* hyperparasitoids; their progeny can develop as either primary or secondary parasitoids. Another classification of hyperparasitoids is based on their feeding behavior: *endophagous* hyperparasitoids have larvae that feed inside the host, while the larvae of *ectophagous* species feed externally. Finally, *direct* hyperparasitoids attack the primary parasitoid directly by ovipositing in or on it. *Indirect* secondary parasitoids, on the other hand, attack the primary

49

parasitoid's phytophagous host and thus only attack the parasitoid itself indirectly. In this case, the female hyperparasitoid oviposits into the phytophagous host whether it is parasitized or not (31).

TAXONOMY AND EVOLUTION

Only three insect orders (Hymenoptera, Diptera, and Coleoptera) have evolved hyperparasitic behavior. The taxonomic survey by Gordh (43) is summarized below.

Hymenoptera

Most insect hyperparasitism is found in Hymenoptera, especially in the following six superfamilies.

CHALCIDOIDEA   Because so many of the species in this superfamily are parasitoids, it is not surprising that 11 of 17 families display hyperparasitism: Pteromalidae, Encyrtidae, Chalcididae, Aphelinidae, Eulophidae, Eupelmidae, Signiphoridae, Torymidae, Eurytomidae, Elasmidae, and Perilampidae (8,

ICHNEUMONOIDEA   All species are parasitic, but only the Ichneumonidae behave as hyperparasitoids. Hyperparastism is restricted to four subfamilies: Ephaltinae, Gelinae, Mesochorinae, and Tryphoninae. Often their primary parasitoid hosts are other ichneumonids and braconids on Lepidoptera (128).

CYNIPOIDEA   Most members of the family Cynipidae are phytophagous, but the subfamily Alloxystinae has three genera (Alloxysta, Phaenoglyphis, Lytoxysta) that are all hyperparasitic on the primary parasitoids that attack aphids (1, 25, 100).

CERAPHRONOIDEA   Hyperparasitism occurs in two families. Some Ceraphronidae are facultative hyperparasitoids on ichneumonids, braconids, bethylids, and dryinids. Some species of Megaspilidae (Dendrocerus) have evolved a more specialized host range and are hyperparasitic on the primary parasitoids of aphids (19, 30).

PROCTOTRUPOIDEA   In the family Diapriidae there is only one reported case of hyperparasitism, in the genus Ismarus (13, 76).

TRIGONALOIDEA   In this small superfamily, only the family Trigonalidae has hyperparasitoids, which parasitize ichneumonids and tachinids attacking Lepidoptera (17, 127).

Diptera

Although this is also a large order with a number of families that are parasitic, hyperparasitism seems restricted to only two families, Bombyliidae (22a) and Conopidae (102).

Coleoptera

This largest order has only a few examples of hyperparasitism in two families, Rhipiphoridae and Cleridae (89).

Evolution of Hyperparasitism in Hymenoptera

The hymenopteran suborder Symphyta ("Phytophaga" such as the sawflies and horntails) is the most primitive in structure and behavior, and is considered closest to the ancestors of the Hymenoptera. The other suborder, Apocrita ("Heterophaga"), is usually divided into the Parasitica (Terebrantia) and the Aculeata (bees, wasps, and ants).

Concerning primary parasitism, Malyshev (81) held that the Parasitica were derived from the original Symphyta, while the Aculeata originated from primitive Parasitica or together with them from common ancestors. It is not known how phytophagous feeding evolved into entomophagous behavior, but Telenga (126) suggested that the phytophagous sawflies first evolved predation, and later parasitism of coleopteran larvae also living in tree trunks. These primary parasitoids were at first ectophagous, but endophagous parasitism appeared very early in the Parasitica.

Hyperparasitism (except in the Aculeata) evolved from among early Parasitica, probably independently and several times in different taxa. Brues (10) noted that many insect hosts exhibit defense reactions against the parasitic larva, and the greater the taxonomic and physiological distance between parasitoid and host, the stronger this defense reaction. Therefore, if a hymenopteran parasitoid accidentally oviposited in a host of the same order, the primary parasitic larva would find the hymenopteran a very suitable host. Telenga (126) agreed, and added that facultative secondary parasitism provides a transitional stage to obligatory hyperparasitism.

Gordh (43) concluded his taxonomic survey by pointing out that although the host spectrum of hyperparasitoids is broader at the species level than that of primary parasitoids, it is mainly restricted to immature hymenopteran hosts that are natural enemies of phytophagous insects, mainly in three orders: Homoptera, Lepidoptera, and the hymenopteran suborder Symphyta. On the other hand, hyperparasitoids rarely attack the egg and adult stages of primary parasitoids. It is also interesting that some families of insects that are well known for their parasitic behavior have no hyperparasitoids. Such is the case in the hymenopteran families Aphidiidae, Braconidae, Trichogrammatidae,

Mymaridae, Tetracampidae, and Eucharitidae, and in almost the entire super-family Proctotrupoidea. Similarly, in the order Diptera, hyperparasitoids are completely absent in the parasitic families Tachinidae, Acroceridae, Pipunculidae, and Nemestrinidae.

APHID HYPERPARASITOIDS

The most intensive studies of hyperparasitism have been conducted on the Hymenoptera that attack the Homoptera, and in particular the superfamily Aphidoidea (132). That which holds true for aphid hyperparasitoids, however, has relevance for hyperparasitoids that affect primary parasitoids of other insect groups. Hence, aphids are given special coverage in this review.

Taxonomy

Not all of the superfamilies and families listed above in the general taxonomic survey include species of aphid hyperparasitoids. Instead, aphid hyperparasitism is restricted to three hymenopteran superfamilies (52, 87, 119): Chalcidoidea [Pteromalidae: *Asaphes, Pachyneuron, Coruna* (44, 68, 108, 111); Encyrtidae: *Aphidencyrtus* (60–62); and Eulophidae: *Tetrastichus* (8, 90)], Ceraphronoidea [Megaspilidae: *Dendrocerus* (19–21, 30, 113, 121, 142)], and Cynipoidea [Cynipidae (subfamily Alloxystinae): *Alloxysta, Phaenoglyphis,* and *Lytoxysta* (1, 25–29, 100)]. Within some of these five families and nine genera, there are also species that are not aphid hyperparasitoids.

Primary Parasitoid Development

To understand the behavior of aphid hyperparasitoids, a knowledge of the development of the primary parasitoids of aphids is necessary. The latter are classified both taxonomically and behaviorally into only two families, the Aphidiidae (Ichneumonoidea) and the Aphelinidae (Chalcidoidea) (52, 80, 112). A well-studied species is the aphidiid wasp *Aphidius smithi* introduced into North America to control the pea aphid, *Acyrthosiphon pisum,* an exotic pest. The female wasp oviposits into the aphid, and over a period of approximately 8 days the parasitic larva gradually devours the aphid internally and kills it. The fourth instar larva spins a cocoon inside the dead aphid, whose exoskeleton becomes hard and changes color from green to light brown (this is referred to as a "mummy"). The larva then pupates, and approximately 4 days later (or about 12 days after the original oviposition), the new adult primary parasitoid cuts a circular emergence hole in the dorsum of the mummy and pulls itself out.

Hyperparasitoid Development

Sullivan (115–117), Matejko & Sullivan (83), and others (21, 112) divide aphid hyperparasitoids into two categories based on adult ovipositional and

larval feeding behaviors. (*a*) The female wasp of endophagous species deposits her egg inside the primary parasitoid larva while it is still developing inside the live aphid, before the aphid is mummified. The egg does not hatch until after the mummy is formed, and then the hyperparasitic larva feeds internally on the primary larval host. (*b*) The female wasp of ectophagous species deposits her egg on the surface of the primary parasitoid larva after the aphid is killed and mummified. Then the hyperparasitic larva feeds externally on the primary larval host while both are still within the mummy. Based on these behavioral criteria, the nine genera listed taxonomically above can be arranged as follows: Endophagous hyperparasitoid species in the genera *Alloxysta, Phaenoglyphis, Lytoxysta,* and *Tetrastichus;* Ectophagous hyperparasitoids in the genera *Asaphes, Dendrocerus, Pachyneuron,* and *Coruna;* and *Aphidencyrtus,* a special case in which the larva is essentially endoparasitic but the adult can manifest either ovipositional behavior.

Comparative Attack and Ovipositional Behavior

The behaviors of representative species from four genera of hyperparasitoids are described.

ALLOXYSTA   *Alloxysta* (=*Charips*) *victrix,* in the family Cynipidae (subfamily Alloxystinae), is an example of an endophagous hyperparasitoid (9, 50, 82, 115–117). The female approaches a live, already parasitized aphid and rapidly antennates its surface. She mounts the dorsum of the aphid and assumes a squatting position with her abdomen slightly bent (Figure 1*a*). The female then inserts her ovipositor through the thin exoskeleton of the aphid and deposits her egg inside the primary larva, which is still feeding. The *Alloxysta* egg does not hatch until after the primary larva has completely devoured the aphid internally and killed it in the usual manner as if it had not been hyperparasitized. Only after the dead aphid is mummified does the hyperparasitoid larva hatch from the egg within the primary parasitoid larva. The secondary larva feeds endophagously until it kills and completely consumes the primary larva. Then it metamorphoses into a pupa and emerges from the mummy as an adult approximately 19 days after the original oviposition.

ASAPHES   The first example of an ectophagous hyperparasitoid is *Asaphes californicus* or *A. lucens,* species with similar behavior, in the family Pteromalidae (7, 70, 77, 115–117). The ovipositional behavior differs from that of *Alloxysta* in that the primary larva is not attacked until after the aphid is killed and the mummy is formed. The female mounts the mummy, drills a hole with her ovipositor (Figure 1*b*), and injects a venom into the primary parasitoid larva developing inside the mummy; this results in paralysis and
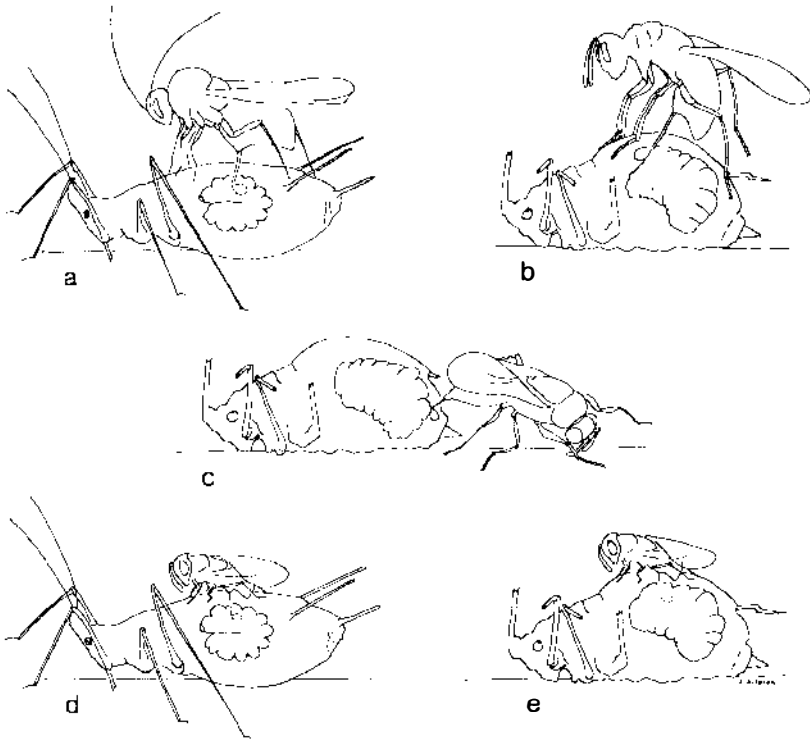
Figure 1 Ovipositional behavior of four genera of aphid hyperparasitoids: (*a*) endophagous *Alloxysta victrix;* (*b*) ectophagous *Asaphes lucens;* (*c*) ectophagous *Dendrocerus carpenteri;* (*d*) endophagous *Aphidencyrtus aphidivorus* ovipositing in primary parasitoid larva inside live aphid; and (*e*) *A. aphidivorus* ovipositing in primary parasitoid larva inside dead mummy. From Sullivan (117) with permission from Elsevier Science Publishers. See text for description.

termination of its development (7). An egg is then laid on the surface of the primary larva, which gradually deteriorates into a soft, blackened mass. In spite of the decay of the host, the newly hatched *Asaphes* larva continues to feed ectophagously. The primary parasitoid is devoured, and after metamorphosis an *Asaphes* adult emerges approximately 21 days after egg deposition.

DENDROCERUS The species of *Dendrocerus,* family Megaspilidae, are also ectophagous hyperparasitoids, but the ovipositional behavior and venom are quite different from those of *Asaphes* (5, 83, 116, 117). Instead of mounting the top of the mummy, the female *Dendrocerus carpenteri* turns around 180°, backs into the side or rear of the mummy, and drills a hole (Figure 1*c*). An egg is deposited on the surface of the primary larva within the mummy. Venom is injected but, whereas the venom of *Asaphes* caused blackening and

decay, the primary larva retains its bright yellow color during feeding by the *Dendrocerus* larva, as clearly shown in the color plate of Bocchino & Sullivan (7). The *Dendrocerus* larva also becomes yellow. Development from egg to adult takes approximately 16 days.

APHIDENCYRTUS   *Aphidencyrtus aphidivorus* in the family Encyrtidae is a special case; it has "dual" ovipositional behavior (69, 116, 117). Although the larva is endophagous, the female hyperparasitoid can attack the primary parasitoid larva either while the aphid is still alive (Figure 1*d*), in the manner of *Alloxysta,* or after the mummy has been formed (Figure 1*e*), like *Asaphes* and *Dendrocerus*. Choice experiments indicate a preference to attack through the mummy. In both cases, however, the egg of *Aphidencyrtus* is laid inside the primary parasite larva, where it feeds endophagously.

Tertiary Hyperparasitism in Aphids

At the next higher trophic level, aphid hyperparasitoids attack each other (Figure 2). Although difficult to prove in the field, it has been demonstrated in the laboratory that both intraspecific tertiary parasitism (or autohyperparasitism) (5, 77) and interspecific tertiary hyperparasitism (or allohyperparasitism) (83, 115) can occur. Success in the competition between hyperparasitic larvae depends on the developmental age of the hyperparasitoid larva already inside the mummy at the time of oviposition by the second hyperparasitoid.

HOST SPECIFICITY

This topic has received greater attention at the level of primary parasitoids (139, 140), for it was thought that hyperparasitoids tended toward polyphagy with little host specificity. Contrary evidence from field and laboratory research, especially that on the well-studied ecosystems in which aphids are the insect pests, was reviewed by van den Bosch (132). He pointed out that feeding behavior involves a continuum, and that "host specificity" can range from monophagy to some level of oligophagy, as shown in the five aphid complexes discussed below. There is indeed some host specificity among the endophagous aphid hyperparasitoids, but much less, if any, in the ectophagous genera.

Cabbage Aphid Complex

Hafez (51) studied the seasonal population fluctuations in the relatively stable ecosystem of a brussels sprout–cabbage aphid *(Brevicoryne brassicae)* habitat in the Netherlands. There was strong host specificity and a bimodal phenological synchronization between the endophagous hyperparasitoid, *Alloxysta* (=*Charips*) *ancylocera,* and the primary parasitoid, *Diaeretiella rapae.* On
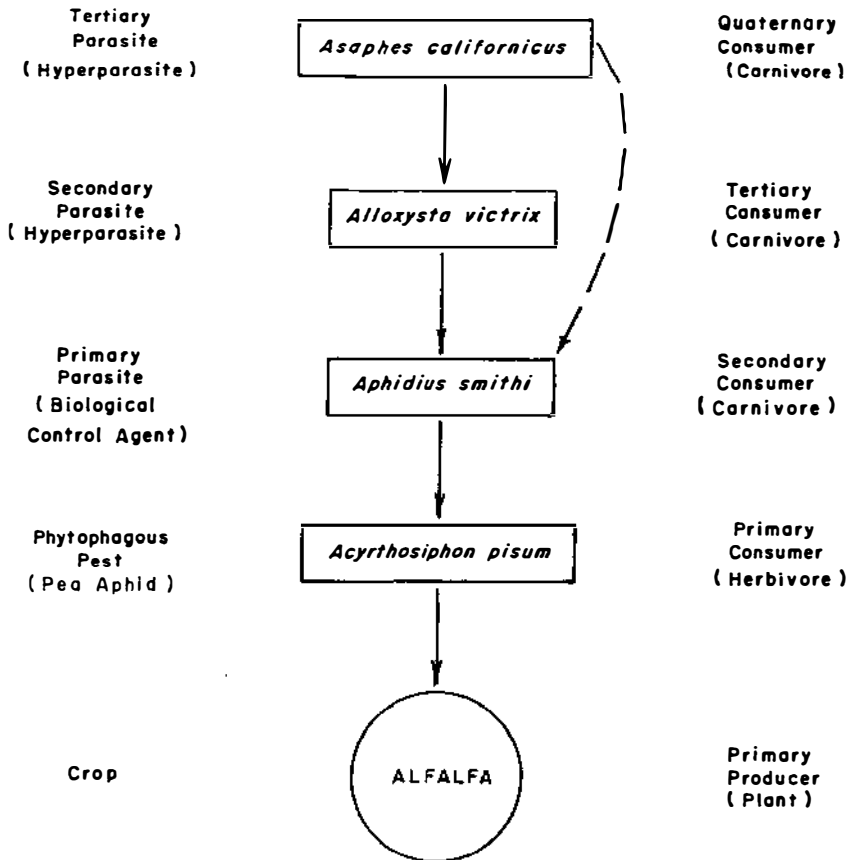
Figure 2   Food chain in alfalfa agroecosystem showing pea aphid, primary parasitoid, and two hyperparasitoids at the secondary, tertiary, and quaternary trophic levels. After van den Bosch et al (134), with permission from Plenum Press.

the other hand, neither host specificity nor phenological synchrony were found between the two ectophagous hyperparasitoids, the pteromalids *Asaphes* and *Pachyneuron,* and the primary parasitoid. Hence, the endophagous *Alloxysta* was the dominant hyperparasitoid. Evenhuis (29) and Chua (14) consider this an example of *Alloxysta*'s strong temporal, behavioral, and biological adaptation for monophagous specificity to a primary host. Chemical cues for habitat selection may also be involved (101, 136).

Two Aphids on Alfalfa

Using a different species, *Alloxysta* (=*Charips*) *victrix,* Gutierrez (45–48) with van den Bosch (49, 50) further substantiated the presence of host

specificity in this endophagous genus. They studied alfalfa fields in California where two different species of aphids coexisted (Figure 3): the pea aphid *(Acyrthosiphon pisum)* and the spotted alfalfa aphid *(Therioaphis trifolii)*. Not only did *Alloxysta* show a preference for potential hosts in the pea aphid over those in the spotted alfalfa aphid, but it even discriminated among nine primary parasitoids, ovipositing in *Aphidius* most frequently. In laboratory experiments Gutierrez demonstrated that *Alloxysta* could distinguish between two primary parasitoids that had parasitized the same species (the preferred pea aphids), and that only *Aphidius* was suitable for the development of the hyperparasitoid's larva (Figure 4).
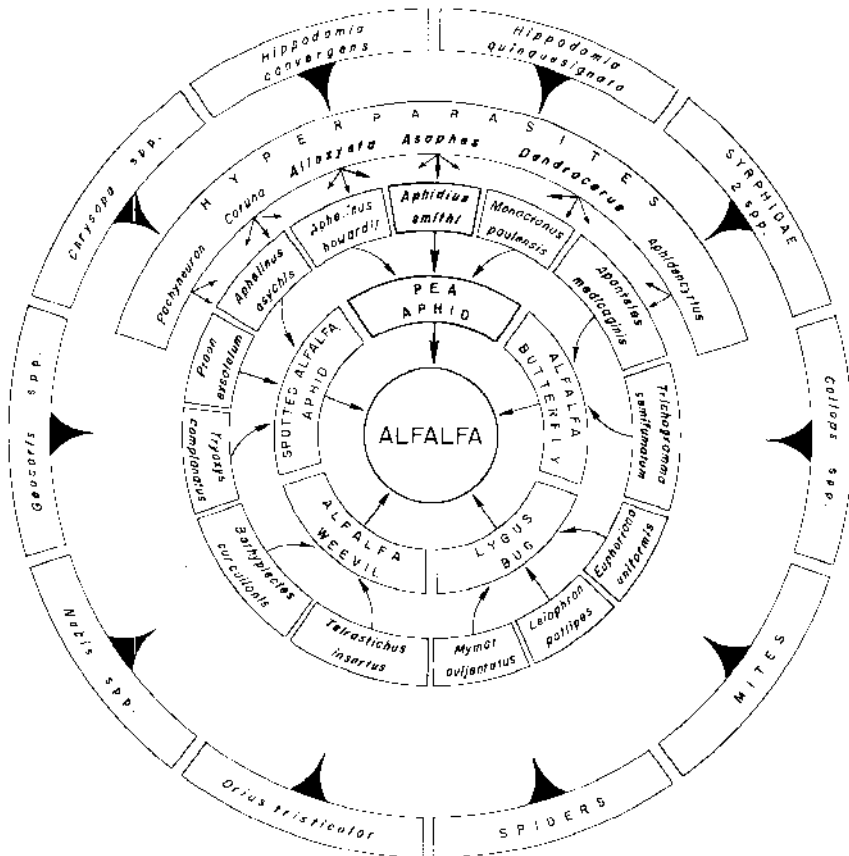

Figure 3 Diagram of food web surrounding alfalfa. Inner ring shows five phytophagous insect pests. Second ring shows entomophagous primary parasitoids and predators, followed by partial ring of hyperparasitoids that attack only aphidophagous parasitoids. In outer ring are other predaceous arthropods associated with this agroecosystem. Redrawn from van den Bosch et al (134), with permission from Plenum Press.
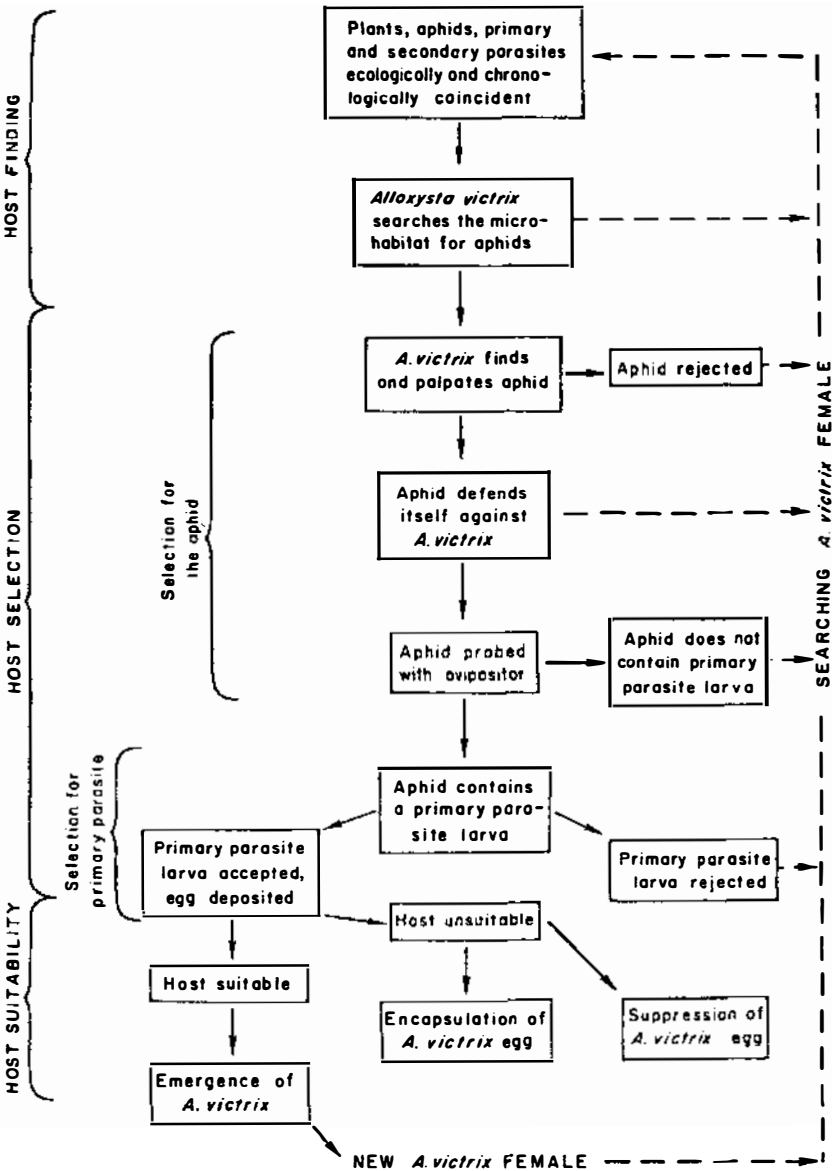
Figure 4   Diagram of host specificity in the endophagous hyperparasitoid *Alloxysta victrix*, showing the interaction of ecological and physiological factors. After the initial host-habitat finding, the sequence of behaviors includes host finding, host selection, and determination of host suitability. From van den Bosch et al (134), with permission from Plenum Press.

Three Apple-Infesting Aphids

Evenhuis (24–29) reported that three different species of endophagous hyperparasitoids had each selected specific primary parasitoid hosts that in turn were specific on each of three different aphids: *Alloxysta quateri–Binodoxys–Aphis pomi, Alloxysta* sp.*–Ephedrus–Dysaphis plantaginea, Phaenoglyphis–Monoctonus–Rhopalosiphum insertum.* In contrast, however, the three ectophagous hyperparasitoids present *(Dendrocerus, Asaphes,* and *Pachyneuron)* all shared the three primary parasitoid hosts. As a result of this difference in host specificity, the alloxystines were the dominant hyperparasitoids.

Potato Aphid Complex

Sullivan & van den Bosch (119) in California reported a similar pattern of host specificity in two species of the endophagous *Alloxysta* that were hyperparasitic on potato aphids *(Macrosiphum euphorbiae).* Among six species of hyperparasitoids, *Alloxysta victrix* was the most abundant and showed the strongest preference for *Aphidius,* which in turn was the dominant primary parasitoid. Another *Alloxysta* species showed host specificity for a different primary parasitoid, *Aphelinus.* Perhaps because of this competition, the ectophagous *Asaphes* showed some host specificity by concentrating on the third primary parasitoid, *Ephedrus,* and was the most numerous of the six hyperparasitoids that attacked it. The remaining hyperparasitoids *(Pachyneuron, Dendrocerus,* and *Aphidencyrtus)* showed little host specificity and were of minor importance.

Walnut Aphid Complex

Frazer & van den Bosch (38) and van den Bosch et al (133) reported on the biological control program against the walnut aphid *(Chromaphis juglandicola)* in California, in which the imported primary parasitoid was *Trioxys pallidus.* In the Palearctic region, where both the walnut aphid and *Trioxys* are native, the dominant hyperparasitoids are the endophagous alloxystines; this follows the pattern demonstrated in the previous examples. In California, however, where the walnut aphid is an invader and the primary parasitoid was introduced, the alloxystines are insignificant in the walnut aphid ecosystem. Instead, this ecological niche is filled by another hyperparasitoid, *Aphidencyrtus aphidivorus,* which has become dominant.

FACULTATIVE HYPERPARASITISM

Some hyperparasitoids behave both as typical secondary and primary parasitoids (23, 36, 37, 88, 96, 114, 145, 146). Kfir et al (71–75) studied an

interesting case of facultative hyperparasitism in the pteromalid *Pachyneuron concolor,* a cosmopolitan and polyphagous secondary parasitoid that attacks encyrtid primary parasitoids in soft scale insects, mealybugs, aphids, and coccinellid larvae. *P. concolor* can also develop as a tertiary parasitoid on members of its own species or on various other chalcidoids that have developed as secondary parasitoids on an encyrtid host (74).

Of special interest here, however, is the proof that *P. concolor* is truly a facultative hyperparasitoid, since it also develops as a primary parasitoid of fly puparia (104). Host selection appears to be based on locating a soft-bodied host within a hard, dry shell, independent of whether the host is a dipterous pupa in its puparium or a primary parasitoid in its mummified host. Unfortunately, when *P. concolor* behaves as a primary parasitoid, the dipterous host that it attacks happens to be a beneficial aphidophagous fly. Hence, *P. concolor* could be detrimental to a biological control program.

ADELPHOPARASITISM IN THE APHELINIDAE

"Adelphoparasitism" is unique to the Aphelinidae; this unusual autoparasitic behavior involves a hyperparasitic male larva attacking a primary female larva of its own species. Most Aphelinidae are primary parasitoids of Homoptera (Aphidoidea, Aleyrodoidea, and Coccoidea); Viggiani (138) reviewed the bionomics of this interesting chalcidoid family. Although some species of Aphelinidae exhibit hyperparasitism, it is not widely distributed (only 11 of 42 genera). The females of three of these genera *(Marietta, Ablerus,* and *Azotus)* attack primary parasitoids of Homoptera, and the hyperparasitic development of both sexes is quite normal. Abnormal behavior or deviant male ontogeny is associated with sex differentiation in the host relations of some species in the eight remaining genera *(Aneristus, Coccophagus, Coccophagoides, Euxanthellus, Encarsia, Lounsburyia, Physcus,* and *Prococcophagus).* The female larvae always develop as primary endoparasitoids in Homoptera (mealybugs, scale insects, and whiteflies), while the male ontogeny is deviant.

Adelphoparasitism as an example of deviant male ontogeny is better understood in light of the categories of sex differentiation in primary-parasitoid hosts (137, 144, 147, 149, 150): (*a*) In some species, the male is a primary parasitoid of the same host as the female, but the haploid egg has been laid externally (not internally as with the female) and the male larva feeds ectophagously. (*b*) In other species, the male is again a primary parasitoid, but in a different host from the female; the haploid egg has been laid internally, so the male larva feeds endophagously as does the female larva. (*c*) Finally, in some species the male larva develops as an external or internal secondary parasitoid of preimaginal stages of a primary parasitoid. This has been well studied in

species of *Coccophagus* (34, 35). Behavior in which a male hyperparasitoid attacks a female larva of its own species is termed autoparasitism; in this special case of a male hyperparasitoid it is termed adelphoparasitism. Examples of adelphoparasitoids are *Coccophagoides similis* and *C. utilis*. This sex differentiation in host relations and deviant male ontogeny (especially adelphoparasitism) must be taken into consideration when using Aphelinidae in biological control programs (32). It may be necessary to release unmated females after mated females to produce males at the correct time.

FOOD WEBS AND MATHEMATICAL MODELS

In the last 20 years there has been an increasing number of field studies of phytophagous insects (usually economic pests) that include not merely primary parasitoids, but also hyperparasitoids in the food web (14, 22, 24, 36, 37, 39, 41, 49, 51, 66, 67, 87, 91–95, 97, 103, 105, 107, 109, 110, 119, 122–124, 131, 136, 142, 143, 148). Two food webs are used as examples.

Alfalfa Agroecosystem

This food web (Figure 3) is composed of a two-dimensional, multilevel ecological community. Horizontally, at the same trophic level, there is both inter- and intraspecific competition; vertically, at different trophic levels, there are several food chains (134). Alfalfa, as the central plant, is the producer at the first trophic level, with phytophagous insects such as the pea aphid and the spotted alfalfa aphid among the herbivorous consumers at the second trophic level (Figure 2). The aphid food chain continues with the carnivorous consumers or entomophagous insects at the third level, e.g. aphidophagous predators and primary parasitoids. These in turn are fed upon by secondary parasitoids or hyperparasitoids (*Alloxysta, Asaphes, Dendrocerus, Aphidencyrtus*, etc.) at the fourth trophic level. Tertiary parasitism may also exist (83), making a fifth trophic level. Yet this aphid food chain constitutes just one component of the food web in this alfalfa agroecosystem.

Cassava Mealybug Complex

Another interesting food web is associated with the cassava plant (*Manihot esculenta*), which was brought to Africa from South America by the Portuguese about 300 years ago. In 1973, the cassava mealybug, *Phenacoccus manihoti*,
ica. Before the cassava mealybug arrived in Africa, the only insects commonly found in large numbers on cassava were grasshoppers (*Zonocerus* spp.).

As the mealybug spread across the African cassava belt, so did the diversity of the associated insect fauna. This became especially noticeable in 1981,

when the encyrtid wasp *Epidinocarsis lopezi* was introduced from South America as a primary parasitoid of the cassava mealybug. *E. lopezi* is now the only common primary parasitoid of the cassava mealybug in Africa (91), despite defensive behavior by the mealybug involving encapsulation and melanization of the wasp's eggs and larvae; the wasp has coevolved to overcome this defense by laying extra eggs (118). About 12 other species of primary parasitoids that attack *P. manihoti* are indigenous to Africa, but most are adapted to other species of mealybugs and therefore have not been effective biological control agents of the cassava mealybug. Although exotic hyperparasitoids were carefully excluded during importation of the natural enemies from South America, four species of indigenous hyperparasitoids followed their normal primary parasitoid hosts into the cassava mealybug ecosystem and began attacking *E. lopezi* as well. In addition, the cassava complex includes several introduced and native coccinellid predators with their parasitoids and hyperparasitoids. The complex food web associated with the cassava mealybug and its introduced primary parasitoid now consists of about 110 species of insects.

Mathematical Models

There is a commonly held thesis in population ecology that increasing the complexity of the food web automatically leads to increased community stability. Based on mathematical models, however, May (84) expressed some reservations, for in some cases the reverse may be true. The history, evolution, and equations of mathematical models should be consulted (15, 40, 54–59, 85, 98, 135, 151). Many models do not explicitly include hyperparasitoids, but several groups of researchers have indeed included them. Luck et al (79) based their model on the Hassell & Varley (57) modification of the Nicholson-Bailey equation, using Q_h as the quest constant or "area of discovery" of an obligate hyperparasitoid. Hassell & Waage (58) reviewed the multispecies interactions of primary parasitoids and hyperparasitoids, and noted that there have been relatively few attempts to assess the ecological impact of obligate hyperparasitoids (16, 49, 71, 119) and to analyze this mathematically (4, 53, 54, 85).

The mathematical models indicate that although an obligate hyperparasitoid contributes to the complexity of the food web and may add stability, it also raises the host's equilibrium and increases pest abundance. Hence, obligate hyperparasitoids are usually detrimental to biological control programs.

IMPACT ON BIOLOGICAL CONTROL

Although hyperparasitoids have traditionally been considered harmful to the beneficial primary parasitoids of insect pests, obligate hyperparasitoids should be distinguished from facultative, and exotic from indigenous.

Obligate Hyperparasitoids

It has been the policy in biological control projects to exclude exotic hyper-parasitoids when introducing foreign natural enemies. Bennett (6) discussed the problems inherent in trying to exclude exotic, obligate hyperparasitoids at each of the standard steps (64, 134) in importation for biological control. Once introduced and colonized, however, the primary parasitoid faces the danger of indigenous hyperparasitoids in its new habitat (12, 106). After the primary parasitoid has been introduced, there is a gradual transition from the colonizing stage to permanent establishment. The role of the hyperparasitoids also changes, so that sometimes what was expected to be a major threat by secondary parasitoids has not in fact impeded the success of the primary ones. Moreover, the diversity of species as well as the numbers of hyperparasitoids can vary greatly from place to place and from year to year, making their long-term influence on the primary parasitoids difficult to predict. Although there is a need for more field data and mathematical modeling, Bennett (6), Luck et al (79), Hassell & Waage (58, 141), and other researchers have concurred that exotic obligate hyperparasitoids should continue to be ex-cluded during the foreign importation part of a biological control program. Little can be done about indigenous hyperparasitoids, since they antedate the exotic primary parasitoid and move easily into the food web.

Facultative Hyperparasitoids

Bennett (6) and others (23, 146) also considered the more complex situation of importing facultative hyperparasitoids (which behave both as primary and also as secondary parasitoids). Species are evaluated according to whether the hyperparasitic behavior is predominant or only occasional. Species that are predominantly hyperparasitic are treated as if they were obligatory hyperpar-asitoids and hence are excluded. The problem is with those species that are usually primary but only occasionally secondary parasitoids. In a serious pest situation where there are no normal primary parasitoids available for biologi-cal control, perhaps a calculated risk should be taken as a last recourse.

SUMMARY AND CONCLUSIONS

Based on this limited review, a "laundry list" for future research projects might include the following. More research is needed on the components of the behavior of hyperparasitoids that result in host specificity (host-habitat finding, host location, host acceptance, and determination of host suitability), in order to see how widespread oligophagy is among endophagous and perhaps even ectophagous hyperparasitoids. Related to this are morphological and physiological studies on chemoreception of pheromones and kairomones.

Host suitability also involves defense mechanisms on the part of the host, such as encapsulation and melanization; yet reports of primary parasitoids using this phenomenon against hyperparasitoids are rare. There is also a dearth of ethological studies on courtship and mating behavior of hyperparasitoids that might lead to control measures. Comparative biochemical analyses of the venoms of endophagous and ectophagous hyperparasitoids could reveal useful components.

Finally, the consensus remains that exotic obligate hyperparasitoids should be excluded as part of biological control programs. Whether or not exotic facultative hyperparasitoids should be imported must be evaluated separately for each candidate species depending on the availability of conventional natural enemies and the seriousness of the insect pest problem. Indigenous hyperparasitoids already form part of the existing food web and may or may not interfere significantly with exotic primary parasitoids introduced in a biological control program. Realistically, they cannot be eliminated from the ecosystem, but monitoring of their impact on the primary parasitoids is important and must continue. Indigenous hyperparasitoids add complexity to the food web, but more field studies to complement mathematical modeling are needed to analyze their impact on stability. If the influence is positive, and the extreme oscillations of primary parasitoids are dampened, then some insect hyperparasitoids might even be considered beneficial.

Literature Cited

1. Andrews, F. G. 1978. Taxonomy and host specificity of Nearctic Alloxystinae with a catalog of the world species (Hymenoptera: Cynipidae). *State Calif. Dep. Food Agric. Occas. Pap. Entomol.* 25:1–128
2. Askew, R. R. 1961. On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. *Trans. R. Entomol. Soc. London* 14:237–68
3. Askew, R. R. 1971. *Parasitic Insects.* London: Heinemann. 316 pp.
4. Beddington, J. R., Hammond, P. S. 1977. On the dynamics of host-parasite-hyperparasite interactions. *J. Anim. Ecol.* 46:811–21
5. Bennett, A. W., Sullivan, D. J. 1978. Defensive behavior against tertiary parasitism by the larva of *Dendrocerus carpenteri*, an aphid hyperparasitoid. *J. NY Entomol. Soc.* 86:153–60
6. Bennett, F. D. 1981. Hyperparasitism in the practice of biological control. In *The Role of Hyperparasitism in Biological Control: A Symposium. Priced Publ. 4103*, ed. D. Rosen, pp. 43–49. Berkeley, Calif: *Div. Agric. Sci. Univ. Calif.*

7. Bocchino, F. J., Sullivan, D. J. 1981. Effects of venoms from two aphid hyperparasitoids, *Asaphes lucens* and *Dendrocerus carpenteri* (Hymenoptera: Pteromalidae and Megaspilidae), on larvae of *Aphidius smithi* (Hymenoptera: Aphidiidae). *Can. Entomol.* 113:887–89

8. Bouček, Z., Askew, R. R. 1968. *Index of Entomophagous Insects. Palearctic Eulophidae (exc. Tetrastichinae) (Hym. Chalcidoidea).* Paris: Le Francois. 260 pp.

9. Broussal, G. 1964. Comparaison des fécondités de *Charips ancylocera* (Hymenoptère: Cynipidae), hyperparasite et d'*Aphidius brassicae* (Hyménoptère: Aphidiidae), parasite primaire de *Brevicoryne brassicae* (Homoptère: Aphididae). *Ann. Univ. Reims Assoc. Rég. Étud. Réch. Sci. (ARERS)* 2:135–37

10. Brues, C. T. 1921. Correlation of taxonomic affinities with food habits in Hymenoptera with special reference to parasitism. *Am. Nat.* 55:134–64, 636–38

11. Burks, B. D. 1979. Family Pteromalidae. In *Catalog of Hymenoptera in America North of Mexico*, Vol. 1, ed. K. V. Krombein, P. D. Hurd, D. R. Smith, B. D. Burks, pp. 768–835. Washington, DC: Smithsonian Inst. 1198 pp.

12. Burton, R. L., Starks, K. L. 1977. Control of a primary parasite of the greenbug with a secondary parasite in greenhouse screening for plant resistance. *J. Econ. Entomol.* 70:219–20

13. Chambers, V. H. 1955. Some hosts of *Anteon* spp. (Hym., Dryinidae) and a hyperparasite *Ismarus* (Hym., Belytidae). *Entomol. Mon. Mag.* 91:114–15

14. Chua, T. H. 1977. Population studies of *Brevicoryne brassicae*, its parasites and hyperparasites in England. *Res. Popul. Ecol.* 19:125–39

15. Chua, T. H. 1978. A model of an aphid-parasite-hyperparasite system, with reference to timing of attack. *J. Malays. Agric.* 51:375–86

16. Chua, T. H. 1979. A comparative study of the searching efficiencies of a parasite and a hyperparasite. *Res. Popul. Ecol.* 20:178–87

17. Cooper, K. W. 1954. Biology of eumenine wasps. IV. A trigonalid wasp parasitic on *Rygchium rugosum* (Saussure). (Hymenoptera: Trigonalidae). *Proc. Entomol. Soc. Wash.* 56:280–88

18. DeBach, P., ed. 1964. *Biological Control of Insect Pests and Weeds.* London: Chapman & Hall. 844 pp.

19. Dessart, P. 1972. Révision des éspèces Européennes du genre *Dendrocerus* Ratzeburg, 1852 (Hymenoptera: Ceraphronoidea). *Mém. Soc. R. Belge Entomol.* 32:1–312

20. Dessart, P. 1974. Compléments à l'étude des *Dendrocerus* Européens (Hymenoptera: Ceraphronoidea, Megaspilidae). *Bull. Ann. Soc. R. Belge Entomol.* 110:69–84

21. Dessart, P. 1985. A propos des Hymenoptères parasites. *Nat. Belg.* 66:97–120

22. des Vignes, W. G. 1977. Seasonal distribution of *Diatraea* spp., their parasites and hyperparasites on sugar cane and grasses. *Caroni Research Station, Annual Report,* 1977:234–37. Carapichaima, Trinidad: Caroni Res. Stn.

22a. Du Merle, P. 1975. Les Hôtes et les stades pré-imaginaux des diptères Bombyliidae: Révue bibliographique annottée. *Bull. Sect. Rég. Ouest Paléarct. (SROP)* 289 pp.

23. Ehler, L. E. 1979. Utility of facultative secondary parasites in biological control. *Environ. Entomol.* 8:829–32

24. Evenhuis, H. H. 1964. The interrelations between apple aphids and their parasites and hyperparasites. *Entomophaga* 9:227–31

25. Evenhuis, H. H. 1971. Studies on Cynipidae Alloxystinae. 1. The identity of *Alloxysta rubriceps* (Kieffer, 1902), with some general remarks on the subfamily. *Entomol. Ber. Amsterdam* 31:93–100

26. Evenhuis, H. H. 1972. Studies on Cynipidae Alloxystinae. 2. The identity of some species associated with aphids of economic importance. *Entomol. Ber.* 32:210–17

27. Evenhuis, H. H. 1973. Studies on Cynipidae Alloxystinae. 3. The identity of *Phaenoglyphis ruficornis* (Foster, 1869). *Entomol. Ber.* 33:218–19

28. Evenhuis, H. H. 1974. Studies on Cynipidae Alloxystinae. 4. *Alloxysta macrophadna* (Hartig, 1841) and *Alloxysta brassicae* (Ashmead, 1887). *Entomol. Ber.* 34:165–68

29. Evenhuis, H. H. 1976. Studies on Cynipidae Alloxystinae. 5. *Alloxysta citripes* (Thompson) and *Alloxysta ligustri* n. sp., with remarks on host specificity in the subfamily. *Entomol. Ber.* 36:140–44

30. Fergusson, N. D. M. 1980. A revision of the British species of *Dendrocerus* Ratzeburg (Hymenoptera: Ceraphronoidea) with a review of their biology as aphid hyperparasites. *Bull. Br. Mus. Nat. Hist. Entomol. Ser.* 41:255–314

31. Flanders, S. E. 1943. Indirect hyper-

parasitism and observations on three species of indirect hyperparasites. *J. Econ. Entomol.* 36:921–26

32. Flanders, S. E. 1959. Differential host relations of the sexes in the parasitic Hymenoptera. *Entomol. Exp. Appl.* 2: 125–42

33. Flanders, S. E. 1963. Hyperparasitism, a mutualistic phenomenon. *Can. Entomol.* 95:716–20

34. Flanders, S. E. 1964. Dual ontogeny of the male *Coccophagus gurneyi* Comp. (Hymenoptera: Aphelinidae): a phenotypic phenomenon. *Nature* 204:944–46

35. Flanders, S. E. 1967. Deviate ontogenies in the aphelinid male (Hym.) associated with the ovipositional behavior of the parental female. *Entomophaga* 12: 415–27

36. Force, D. C. 1970. Competition among four hymenopterous parasites of an endemic host. *Ann. Entomol. Soc. Am.* 63:1675–88

37. Force, D. C. 1974. Ecology of insect host-parasitoid communities. *Science* 184:624–32

38. Frazer, B. D., van den Bosch, R. 1973. Biological control of the walnut aphid in California: the interrelationship of the aphid and its parasite. *Environ. Entomol.* 2:561–68

39. Gambino, P., Sullivan, D. J. 1982. Phenology of emergence of the spotted tentiform leafminer, *Phyllonorycter crataegella* (Lepidoptera: Gracillariidae), and its parasitoids in New York. *J. NY Entomol. Soc.* 90:229–36

40. Getz, W. M., Gutierrez, A. P. 1982. A perspective on systems analysis in crop production and insect pest management. *Ann. Rev. Entomol.* 27:447–66

41. Gonzales, D., Mizakoki, M., White, W., Takada, H., Dickson, R., Hall, J. 1979. Geographical distribution of *Acyrthosiphon kondoi* Shinji (Homoptera: Aphididae) and some of its parasites and hyperparasites in Japan. *Kontyu* 47:1–7

42. Gordh, G. 1979. Family Encyrtidae. See Ref. 11, pp. 890–967

43. Gordh, G. 1981. The phenomenon of insect hyperparasitism and its taxonomic occurrence in the Insecta. See Ref. 6, pp. 10–18

44. Graham, M. W. R. de V. 1969. The Pteromalidae of north-western Europe (Hymenoptera: Chalcidoidea). *Bull. Br. Mus. Nat. Hist. Entomol. Suppl.* 16:1–908

45. Gutierrez, A. P. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 3. Host suitability studies. *Ann. Entomol. Soc. Am.* 63:1485–91

46. Gutierrez, A. P. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 4. The effect of age of host on host selection. *Ann. Entomol. Soc. Am.* 63:1491–94

47. Gutierrez, A. P. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 5. Host selection. *Ann. Entomol. Soc. Am.* 63: 1495–98

48. Gutierrez, A. P. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 6. Description of sensory structures and a synopsis of host selection and host specificity. *Ann. Entomol. Soc. Am.* 63:1705–9

49. Gutierrez, A. P., van den Bosch, R. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 1. Review of hyperparasitism and the field ecology of *Charips victrix*. *Ann. Entomol. Soc. Am.* 63:1345–54

50. Gutierrez, A. P., van den Bosch, R. 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 2. The bionomics of *Charips victrix*. *Ann. Entomol. Soc. Am.* 63:1355–60

51. Hafez, M. 1961. Seasonal fluctuations of population density of the cabbage aphid, *Brevicoryne brassicae* (L.) in the Netherlands, and the role of its parasite *Aphidius (Diaeretiella) rapae* (Curtis). *Tijdschr. Plantenziekten* 67:445–548

52. Hagen, K. S., van den Bosch, R. 1968. Impact of pathogens, parasites, and predators on aphids. *Ann. Rev. Entomol.* 13:325–84

53. Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems.* Princeton, NJ: Princeton Univ. Press. 237 pp.

54. Hassell, M. P. 1979. The dynamics of predator prey interactions, polyphagous predators, competing predators and hyperparasitoids. *Br. Ecol. Soc. Symp.* 20:283–306

55. Hassell, M. P., May, R. M. 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42:693–726

56. Hassell, M. P., May, R. M. 1974. Aggregation of predators and insect

parasites and its effect on stability. *J. Anim. Ecol.* 43:567–94

57. Hassell, M. P., Varley, G. C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* 223:1133–37

58. Hassell, M. P., Waage, J. K. 1984. Host-parasitoid population interactions. *Ann. Rev. Entomol.* 29:89–114

59. Hassell, M. P., Waage, J. K., May, R. M. 1983. Variable parasitoid sex ratios and their effect on host parasitoid dynamics. *J. Anim. Ecol.* 52:889–904

60. Hoffer, A. 1970. Erster Beitrag zur Taxonomie der Palaearktischen Arten der Gattung *Aphidencyrtus* Ashm. (Hymenoptera: Chalcidoidea, Encyrtidae). *Stud. Entomol. For.* 1:25–42

61. Hoffer, A. 1970. Zweiter Beitrag zur Taxonomie der Palaearktischen Arten der Gattung *Aphidencyrtus* Ashm. (Hymenoptera: Chalcidoidea, Encyrtidae). *Stud. Entomol. For.* 1:65–80

62. Hoffer, A., Starý, P. 1970. Zur Biologie der Palaearktischen Arten der Gattung *Aphidencyrtus* Ashm. (Hymenoptera: Chalcidoidea, Encyrtidae). *Stud. Entomol. For.* 1:81–95

63. Huffaker, C. B., ed. 1980. *New Technology of Pest Control.* New York: Wiley-Interscience. 500 pp.

64. Huffaker, C. B., Messenger, P. S., eds. 1976. *Theory and Practice of Biological Control.* New York: Academic. 788 pp.

65. Huffaker, C. B., Rabb, R. L., eds. 1984. *Ecological Entomology.* New York: Wiley-Interscience. 844 pp.

66. Hughes, G. Hammond, P. S., des Vignes, W. G. 1982. Population cycles of the small moth-borers of sugar cane, *Diatraea* spp., and their primary and secondary parasitoids, in Trinidad, West Indies. *Agro-Ecosyst.* 8:13–25

67. Humble, L. M. 1985. Final-instar larvae of native pupal parasites and hyperparasites of *Operophtera* spp. (Lepidoptera: Geometridae) on southern Vancouver Island. *Can. Entomol.* 117:525–34

68. Kamijo, K., Takada, H. 1973. Studies on aphid hyperparasites of Japan. II. Aphid hyperparasites of the Pteromalidae occurring in Japan (Hymenoptera). *Insecta Matsummurana* 2:39–76

69. Kanuck, M. 1981. *The biology and host preference behavior of Aphidencyrtus aphidivorus (Mayr), an aphid hyperparasitoid (Hymenoptera: Encyrtidae).* PhD dissertation. Fordham Univ., New York, NY. 146 pp.

70. Keller, L. J., Sullivan, D. J. 1976. Oviposition behavior and host feeding of *Asaphes lucens,* an aphid hyperparasi-

toid (Hymenoptera: Pteromalidae). *J. NY Entomol. Soc.* 84:206–11

71. Kfir, R., Podoler, H., Rosen, D. 1976. The area of discovery and searching strategy of a primary parasite and two hyperparasites. *Ecol. Entomol.* 1:287–95

72. Kfir, R., Rosen, D. 1981. Biology of the hyperparasite *Cheiloneurus paralia* (Walker) (Hymenoptera: Encyrtidae) reared on *Microterys flavus* (Howard) in brown soft scale. *J. Entomol. Soc. South. Afr.* 44:131–39

73. Kfir, R., Rosen, D. 1981. Biology of the hyperparasite *Marietta javensis* (Howard) (Hymenoptera: Aphelinidae) reared on *Microterys flavus* (Howard) in brown soft scale. *J. Entomol. Soc. South. Afr.* 44:141–50

74. Kfir, R., Rosen, D. 1981. Biology of the hyperparasite *Pachyneuron concolor* (Forster) (Hymenoptera: Pteromalidae) reared on *Microterys flavus* (Howard) in brown soft scale. *J. Entomol. Soc. South. Afr.* 44:151–63

75. Kfir, R., Rosen, D., Podoler, H. 1983. Laboratory studies of competition among three species of hymenopterous hyperparasites. *Entomol. Exp. Appl.* 33:320–28

76. Kozlov, M. A. 1971. Proctotrupoids (Hymenoptera: Proctotrupoidea) of the USSR. *Tr. Vses. Entomol. Ova.* 54:3–67 (In Russian)

77. Levine, L., Sullivan, D. J. 1983. Intraspecific tertiary parasitoidism in *Asaphes lucens* (Hymenoptera: Pteromalidae), an aphid hyperparasitoid. *Can. Entomol.* 115:1653–58

78. Liss, W. J., Gut, L. J., Westigard, P. H., Warren, C. E. 1986. Perspectives on arthropod community structure, organization, and development in agricultural crops. *Ann. Rev. Entomol.* 31:455–78

79. Luck, R., Messenger, P. S., Barbieri, J. F. 1981. The influence of hyperparasitism on the performance of biological control agents. See Ref. 6, pp. 34–42

80. Mackauer, M., Finlayson, T. 1967. The hymenopterous parasites (Hymenoptera: Aphidiidae et Aphelinidae) of the pea aphid in eastern North America. *Can. Entomol.* 99:1051–82

81. Malyshev, S. I. 1966. *Genesis of the Hymenoptera and the Phases of Their Evolution.* London: Methuen. 319 pp.

82. Matejko, I., Sullivan, D. J. 1979. Bionomics and behavior of *Alloxysta megourae,* an aphid hyperparasitoid (Hymenoptera: Cynipidae). *J. NY Entomol. Soc.* 87:275–82

83. Matejko, I., Sullivan, D. J. 1984. In-

terspecific tertiary parasitoidism between two aphid hyperparasitoids: *Dendrocerus carpenteri* and *Alloxysta megourae* (Hymenoptera: Megaspilidae and Cynipidae). *J. Wash. Acad. Sci.* 74:31–38

84. May, R. M. 1973. *Stability and Complexity in Model Ecosystems.* Princeton, NJ: Princeton Univ. Press. 235 pp.

85. May, R. M., Hassell, M. P. 1981. The dynamics of multiparasitoid-host interactions. *Am. Nat.* 117:234–61

86. Deleted in proof

87. Mertins, J. W. 1985. Hyperparasitoids from pea aphid mummies, *Acyrthosiphon pisum* (Homoptera: Aphididae), in North America. *Ann. Entomol. Soc. Am.* 78:186–97

88. Muesebeck, C. F. W. 1931. *Monodontomerus aereus* Walker, both a primary and secondary parasite of the brown-tail moth and the gypsy moth. *J. Agric. Res.* 43:445–60

89. Muesebeck, C. F. W., Dohanian, S. M. 1927. A study in hyperparasitism, with particular reference to the parasites of *Apanteles melanoscelus* (Ratzeburg). *US Dep. Agric. Bull.* 1487:1–36

90. Nealis, V. G. 1983. *Tetrastichus galactopus* (Hym.: Eulophidae) a hyperparasite of *Apanteles rubecula* and *Apanteles glomeratus* (Hym.: Braconidae) in North America. *J. Entomol. Soc. BC* 80:25–28

91. Neuenschwander, P., Hennessey, R. D., Herren, H. R. 1985. Food web of insects associated with the cassava mealybug. In *IITA Annual Report for 1984*, pp. 130–33. Ibadan, Nigeria: Int. Inst. Trop. Agric. 220 pp.

92. Oatman, E. R. 1973. Parasitization of natural enemies attacking the cabbage aphid on cabbage in southern California. *Environ. Entomol.* 2:365–67

93. Paetzold, D., Vater, G. 1967. Populationsdynamische Untersuchungen an den Parasiten und Hyperparasiten von *Brevicoryne brassicae* (L.) (Homoptera: Aphididae). *Acta Entomol. Bohemoslov.* 64:83–90

94. Paetzold, D., Vater, G. 1968. Zur Teratologie der Primär-Hyperparasiten von *Brevicoryne brassicae.* *Dtsch. Entomol. Z.* 15:409–26

95. Paetzold, D., Vater, G. 1969. Untersuchungen zum Einfluss der Hyperparasiten auf die Populationsdynamik von *Diaeretiella rapae* (McIntosh) (Hymenoptera: Aphidiidae). *Ber. 10te Wanderversamml. Dtsch. Entomol., Dresden, 1965* 80:365–75. Berlin, GDR: Dtsch. Akad. Landwirtschaftswiss.

96. Patnaik, N. C., Satpathy, J. M. 1984. Facultative hyperparasitism/predation on *Platygaster oryzae*, an egg-larval parasite of the rice gall midge, *Orseolia oryzae.* *J. Entomol. Res. New Delhi* 8:106–8

97. Polgar, L. 1984. Some new records of parasites, predators and hyperparasites of aphids and a leaf-miner fly, *Cerodonta incisa* (Diptera: Antomyiidae), living in maize ecosystems in Hungary. *Folia Entomol. Hung.* 45:191–94

98. Price, P. W. 1984. *Insect Ecology.* New York: Wiley-Interscience. 607 pp. 2nd ed.

99. Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., Weis, A. E. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol. Syst.* 11:41–65

100. Quinlan, J., Evenhuis, H. H. 1980. Status of the subfamily names Charipinae and Alloxystinae (Hymenoptera: Cynipidae). *Syst. Entomol.* 5:427–30

101. Read, D. P., Feeny, P. P., Root, R. B. 1970. Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and the hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). *Can. Entomol.* 102:1567–78

102. Rettenmeyer, C. W. 1961. Observations on the biology and taxonomy of flies found over swarm raids of army ants (Diptera: Tachinidae, Conopidae). *Univ. Kans. Sci. Bull.* 52:993–1066

103. Rosen, D. 1967. The hymenopterous parasites and hyperparasites of aphids on citrus in Israel. *Ann. Entomol. Soc. Am.* 60:394–99

104. Rosen, D., Kfir, R. 1983. A hyperparasite of coccids develops as a primary parasite of fly puparia. *Entomophaga* 28:83–88

105. Santas, L. A. 1979. Distribution of aphids on citrus and cotton and their parasites in Greece. *Biol. Gallo-Hell.* 9:315–19

106. Schlinger, E. I. 1960. Diapause and secondary parasites nullify the effectiveness of rose-aphid parasites in Riverside, California, 1957–1958. *J. Econ. Entomol.* 53:151–54

107. Sedlag, U. 1964. Zur Biologie und Bedeutung von *Diaeretiella rapae* (McIntosh) als Parasit der Kohlblattlaus (*Brevicoryne brassicae* L.). *Nachrichtenbl. Dtsch. Pflanzenschutzdienst Berlin* 18:81–86

108. Sekhar, P. S. 1958. Studies on *Asaphes fletcheri* (Crawford), a hyperparasite of *Aphidius testaceipes* (Cresson) and

Praon aguti (Smith), primary parasites of aphids. *Ann. Entomol. Soc. Am.* 51:1–7

109. Shands, W. A., Simpson, G. W., Muesebeck, C. F. W., Wave, H. E. 1965. Parasites of potato-infesting aphids in northeastern Maine. *Maine Agric. Exp. Stn. Tech. Bull.* T19:1–77

110. Soteres, K. M., Berberet, R. C., McNew, R. W. 1984. Parasitic insects associated with lepidopterous herbivores on alfalfa in Oklahoma. *Environ. Entomol.* 13:787–93

111. Specht, H. B. 1969. Hyperparasitism of the pea aphid parasite *Aphelinus semiflavus* by *Asaphes vulgaris* in a greenhouse. *Ann. Entomol. Soc. Am.* 62:1207

112. Starý, P. 1970. *Biology of Aphid Parasites (Hymenoptera: Aphidiidae) with Respect to Integrated Control.* The Hague: Junk. 643 pp.

113. Starý, P. 1977. *Dendrocerus* hyperparasites of aphids in Czechoslovakia (Hymenoptera: Ceraphronoidea). *Acta Entomol. Bohemoslov.* 74:1–9

114. Strand, M. R., Vinson, S. B. 1984. Facultative hyperparasitism by the egg parasitoid *Trichogramma pretiosum* (Hym.: Trichogrammatidae). *Ann. Entomol. Soc. Am.* 77:679–86

115. Sullivan, D. J. 1972. Comparative behavior and competition between two aphid hyperparasites: *Alloxysta victrix* and *Asaphes californicus* (Hymenoptera: Cynipidae; Pteromalidae). *Environ. Entomol.* 1:234–44

116. Sullivan, D. J. 1986. Aphid hyperparasites: taxonomy and ovipositional behavior. In *Ecology of Aphidophaga*, ed. I. Hodek, pp. 511–18. Prague: Academia

117. Sullivan, D. J. 1987. Aphid hyperparasites. In *Aphids, Their Biology, Natural Enemies and Control*, ed. P. Harrewijn, A. K. Minks. Amsterdam: Elsevier. In press

118. Sullivan, D. J., Neuenschwander, P. 1985. Melanization: the mealybug defends itself. See Ref. 91, pp. 127–29

119. Sullivan, D. J., van den Bosch, R. 1971. Field ecology of the primary parasites and hyperparasites of the potato aphid, *Macrosiphum euphorbiae*, in the East San Francisco Bay Area (Homoptera: Aphididae). *Ann. Entomol. Soc. Am.* 64:389–94

120. Tachikawa, T. 1974. Hosts of the Encyrtidae (Hymenoptera: Chalcidoidea). *Mem. Coll. Agric. Ehime Univ.* 19:185–204

121. Takada, H. 1973. Studies on aphid hyperparasites of Japan. I. Aphid hyperparasites of the genus *Dendrocerus* Ratzeburg occurring in Japan (Hymenoptera: Ceraphronidae). *Insecta Matsummurana* 2:1–37

122. Takada, H. 1976. Studies of aphids and their parasites on cruciferous crops and potatoes. I. Parasite complex of aphids. *Kontyu* 44:234–53 (In Japanese with English summary)

123. Takada, H. 1976. Studies of aphids and their parasites on cruciferous crops and potatoes. II. Life-cycle. *Kontyu* 44:366–84 (In Japanese with English summary)

124. Takada, H., Takenaka, Y. 1982. Parasite complex of *Myzus persicae* on tobacco (Japan). *Kontyu* 50:556–68

125. Tanton, M. T., Epila, J. S. O. 1984. Description of the planidium of *Perilampus tasmanicus* (Hymen.: Chalcidoidea), a hyperparasitoid of larvae of *Paropsis atomaria* (Coleop.: Chrysomelidae). *J. Aust. Entomol. Soc.* 23:149–52

126. Telenga, N. A. 1952. *Origin and Evolution of Parasitism in Hymenoptera Parasitica and Development of Their Fauna in the USSR.* Acad. Sci. Ukr. SSR, Inst. Entomol. Phytopathol., Kiev. Transl. Isr. Prog. Sci. Transl. Jerusalem, 1969. 112 pp.

127. Townes, H. 1956. The Nearctic species of trigonalid wasps. *US Natl. Mus. Proc.* 106:295–304

128. Townes, H. 1969. The genera of Ichneumonidae, Pt. 1. *Mem. Am. Entomol. Inst. Ann Arbor* 11:1–300

129. Trjapitzin, V. A. 1973. Classification of parasitic Hymenoptera of the family Encyrtidae (Hymenoptera: Chalcidoidea), Pt. 1. Survey of the systems of classification. The subfamily Tetracneminae Howard, 1892. *Entomol. Rev.* 52:118–25

130. Trjapitzin, V. A. 1973. Classification of parasitic Hymenoptera of the family Encyrtidae (Chalcidoidea), Pt. 2. Subfamily Encyrtinae Walker, 1837. *Entomol. Rev.* 52:287–95

131. Valentine, E. W. 1975. Additions and corrections to Hymenoptera hyperparasitic on aphids in New Zealand. *NZ Entomol.* 6:59–61

132. van den Bosch, R. 1981. Specificity of hyperparasites. See Ref. 6, pp. 27–33

133. van den Bosch, R., Hom, R. R., Matteson, P., Frazer, B. D., Messenger, P. S., Davis, C. S. 1979. Biological control of the walnut aphid in California: impact of the parasite, *Trioxus pallidus*. *Hilgardia* 47:1–13

134. van den Bosch, R., Messenger, P. S.,

Gutierrez, A. P. 1982. *An Introduction to Biological Control.* New York: Plenum. 247 pp.

135. Varley, G. C., Gradwell, G. R., Hassell, M. P. 1973. *Insect Population Ecology.* Oxford: Blackwell. 212 pp.

136. Vater, G. 1971. Dispersal and orientation of *Diaeretiella rapae* with references to the hyperparasites of *Brevicoryne brassicae. Z. Angew. Entomol.* 68: 187–225

137. Viggiani, G. 1981. Hyperparasitism and sex differentiation in the Aphelinidae. See Ref. 6, pp. 19–26

138. Viggiani, G. 1984. Bionomics of the Aphelinidae. *Ann. Rev. Entomol.* 29: 257–76

139. Vinson, S. B. 1976. Host selection by insect parasitoids. *Ann. Rev. Entomol.* 21:109–33

140. Vinson, S. B., Iwantsch, G. F. 1980. Host suitability for insect parasitoids. *Ann. Rev. Entomol.* 25:397–419

141. Waage, J. K., Hassell, M. P. 1982. Parasitoids as biological control agents—a fundamental approach. *Parasitology* 84:241–68

142. Walker, G. P., Cameron, P. J. 1981. Biology of *Dendrocerus carpenteri,* parasite of *Aphidius* spp., and field observations of *Dendrocerus* spp. as hyperparasites of *Acyrthosiphon* sp. *NZ J. Zool.* 8:531–38

143. Walker, G. P., Nault, L. R., Simonet, D. E. 1984. Natural mortality factors acting on potato aphid *(Macrosiphum euphorbiae)* populations in processing tomato fields in Ohio. *Environ. Entomol.* 13:724–32

144. Walter, G. H. 1983. Divergent male ontogenies in Aphelinidae (Hymenoptera: Chalcidoidea): a simplified classification and a suggested evolutionary

sequence. *Biol. J. Linn. Soc.* 19:63–82

145. Weseloh, R. M. 1969. Biology of *Cheiloneurus noxius,* with emphasis on host relationships and oviposition behavior. *Ann. Entomol. Soc. Am.* 62: 299–305

146. Weseloh, R. M., Wallner, W. E., Hoy, M. 1979. Possible deleterious effects of releasing *Anastatus kashmirensis,* a facultative hyperparasite of the gypsy moth. *Environ. Entomol.* 8:174–77

147. Williams, J. R. 1977. Some features of sex-linked hyperparasitism in Aphelinidae (Hymenoptera). *Entomophaga* 22: 345–50

148. Wilson, C. G., Swincer, D. E. 1984. Hyperparasitism of *Therioaphis trifolii* f. *maculata* (Hom.: Aphididae) in South Australia. *J. Aust. Entomol. Soc.* 23:47–50

149. Zinna, G. 1961. Ricerche sugli insetti entomofagi. II. Specializzazione entomoparassitica negli Aphelinidae: studio morfologico, etologico e fisiologico del *Coccophagus bivittatus* Compere, nuovo parassita del *Coccus hesperidum* L. per l'Italia. *Boll. Lab. Entomol. Agrar. F. Silvestri Portici* 19:301–58

150. Zinna, G. 1962. Ricerche sugli insetti entomofagi. III. Specializzazione entomoparassitica negli Aphelinidae: interdipendenze biocenotiche tra due specie associate. Studio morfologico, etologico e fisiologico del *Coccophagoides similes* (Masi) e *Azotus matritensis* Mercet. *Boll. Lab. Entomol. Agrar. F. Silvestri Portici* 20:73–184

151. Zwölfer, H. 1971. The structure and effect of parasitoid complexes attacking phytophagous host insects. In *Dynamics of Populations,* ed. P. J. den Boer, G. R. Gradwell, pp. 405–18. Wageningen: Cent. Agric. Publ. Doc. 611 pp.

CONTENTS

viii   CONTENTS   *(continued)*