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8 Natural Enemies of Checkerspots

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8.1 Introduction

Butterfly eggs, larvae, pupae, and adults are attacked by an array of natural enemies. Many characteristics of butterflies, such as larval crypsis, distastefulness or toxicity, gregariousness, web building, host plant use, and adult wing patterns, are thought to have evolved as defenses against natural enemies (Gilbert and Singer 1975, Bowers 1981, Stamp 1981a, Dempster 1984, Bowers et al. 1985, Sillén-Tullberg 1988, Vulinec 1990, Montllor and Bernays 1993, Weseloh 1993, Ohasaki and Sato 1999, Hunter 2000). But, paradoxically, while population biologists widely agree that natural enemies have shaped the evolution of butterflies, the extent to which the observed abundances, population dynamics, and other ecological processes in butterflies are now influenced by natural enemies is more controversial. What is known from life-table analyses and experiments is that generalist arthropod and vertebrate predators often cause significant and typically density-independent mortality in butterflies and moths (Dempster 1983, Bellows et al. 1992). Disease can also cause massive mortality at high population densities, particularly in moths with outbreak dynamics (Anderson and May 1981, Dwyer 1994, Dwyer et al. 2000, Kamata 2000). In a review covering all insects, Hawkins (1994) found that parasitoids generally cause 20–60% mortality in their hosts, with the maximum level of mortality related to the host feeding niche. Insects feeding externally on leaves, such as butterfly larvae, tend to suffer lower parasitism than leaf miners, but higher parasitism than borers and root feeders. Parasitoid-caused mortality in butterflies is at least occasionally density-dependent and may thereby contribute to host population regulation (Ford and Ford 1930, O. W. Richards 1940, Dempster 1983). In general, the question of whether natural enemies often regulate their insect host populations and keep them at low density remains much debated (Price 1984, Walde and Murdock 1988, Strong 1989, Turchin 1995, Bernstein 2000, Hassell 2000a).

Studies of the natural enemies of checkerspots are necessary for a comprehensive understanding of the ecology and population biology of these butterflies, but such research also contributes to our understanding of the ecology and evolution of host–parasite and predator–prey interactions in general. Parasitoid–host interactions are among the most common interspecific interactions. They also include some of the most specialized relationships and pose challenging research questions about the ecology and evolution of interactions at all levels, from molecular (Henter 1995, Mikio et al. 2001) to population (Cappuccino and Price 1995, Godfray 2000, Hochberg and Ives 2000) to community (Hawkins 1994, Hawkins and Sheehan 1994) and to ecosystem (Marino and Landis 1996, Landis and Menalled 1998, Letourneau 1998).

Informative empirical study of the population biology and dynamics of natural enemies must take place in systems for which the host ecology is well known. This is especially true for parasitoids, as their biology and dynamics are intimately dependent on the dynamics of their hosts. Short-term field and laboratory experiments have shown that the strength of interaction in predator–prey and host–parasitoid systems depends on many factors, including the relative dispersal ability of the species, host density, direct competition, trophic complexity, and host resistance or parasitoid virulence (Morrison and Strong 1980, Rosenheim et al. 1993, Godfray 1994, 2000, Myers and Rothman 1995, Müller and Godfray 1998, Amarasekare 2000, Doak 2000, Hawkins 2000, Hochberg and Ives 2000, Hufbauer 2002, Stefanescu et al. 2003). How the results of such experiments play out over long times and in large areas is unknown. Large-scale empirical work on the population dynamics of parasitoids has been mostly conducted in the context of biological control. In these studies, changes in the sizes of parasitoid populations are measured with reference to the size and persistence of pest insect populations in managed ecosystems, and the two parameters of the greatest interest are the rate of spread of the parasitoid and the degree of host suppression (Clausen et al. 1965, Murdock et al. 1984, 1989, Roland 1994, Landis and Menalled 1998, Bernstein 2000, Hastings 2000). Studies in managed ecosystems are important for pest control and as tools to identify key components of species interactions, but they do not necessarily address the processes involved in long-term stable interactions that occur in natural, unmanaged systems (Hawkins et al. 1999).

Luckily, there are also a few studies of natural systems in which the population dynamics of parasitoids have been addressed along with the dynamics of their hosts: the winter moth *Cyzenis albicans* in the United Kingdom and in the United States, where it is a pest (Hassell 1969, Roland 1994), the forest tent caterpillar *Malacosoma disstria* (Roland and Taylor 1995), the gypsy moth *Lymantria dispar* (Elkinton and Liebhold 1990, Ferguson et al. 1994, Elkinton et al. 1996), the cinnabar moth *Tyria jacobaeae* (van der Meijden and van der Veen-van Wijk 1997), the Tussock moth *Orgyia vetusta* (Harrison 1997), the knapweed gall fly *Urophaga jaceana* (Varley 1947), the goldenrod gall maker (Abrahamson and Weis 1997), and willow gall-making sawflies (Price 1992, Roininen et al. 1996). In all these cases parasitoids appear to play an important role in host population dynamics under some ecological conditions but not under other conditions. Their role depends primarily on habitat structure and heterogeneity, phenology, and weather, but also on the dispersal behavior of the species involved and on their interactions with other species.

Euphydryas editha and *Melitaea cinxia* and their natural enemies provide excellent opportunities for the study of parasitoid biology and population dynamics because of the solid knowledge base provided by long-term studies of the host populations and metapopulations (chapters 3 and 4). Many of the parasitoids attacking checkerspots are specialists, and some of them even have what appear to be specialist hyperparasitoids. An example is the three-species chain *Melitaea cinxia* (host), *Hyposoter horticola* (primary parasitoid), and *Mesochorus* sp. cf. *stigmaticus* (hyperparasitoid) in the Åland Islands in Finland. The theory of host–parasitoid dynamics (reviewed by Holt 1997, Bernstein 2000, Hassell 2000b) is largely concerned with specialist parasitoids; hence well-studied systems like this example provide much needed empirical data to relate to the current theory.

In this chapter we first outline the natural history and general population ecology of checkerspot natural enemies. It is evident from this review that we know much more about parasitoids than about any other type of natural enemies, which probably reflects the generally dominant role of parasitoids among the natural enemies of checkerspot butterflies. We then discuss multitrophic interactions among the parasitoids, the host butterflies and their food plants, as well as interactions among the natural enemies themselves. Next we address the spatial population dynamics of the interacting species. The final section is devoted to some areas of potential future research.

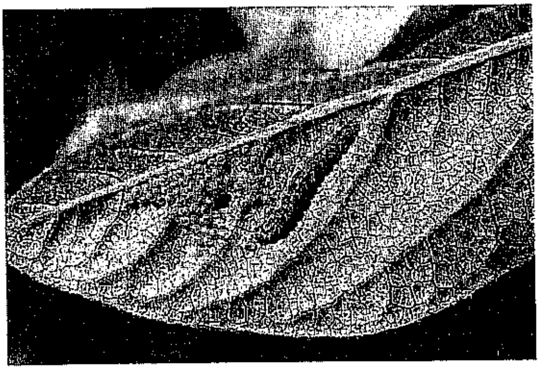
8.2 Natural Enemy Communities Associated with Checkerspots

The natural enemies of checkerspots are united by the biology and behavior of their hosts. Larvae of most checkerspots are conspicuous, gregarious, and web building at least for a part of their lives, and most of them feed on plants that are chemically defended by seco-iridoid or iridoid glycoside secondary compounds (chapters 7 and 11). Generalist predators and parasitoids are to a smaller or greater extent deterred by the toxic chemicals sequestered by or associated with checkerspots (chapter 7;

Bowers 1980, Camara 1997b), and some natural enemies may be hindered by the silken webs and gregarious behavior of the host larvae (Morris 1972a, 1972b, 1976, Stamp 1981a, Moore 1989a). Nonetheless, and in spite of these defenses, larval mortality caused by generalist predators does occur and is occasionally severe (table 8.1 and chapter 7). For example, in the Åland Islands and elsewhere, eggs and larvae of *M. cinxia* are eaten by pentatomid bugs and coccinellid and chrysopid larvae (S.van Nouhuys pers. obs.; figure 8.1), and pupae are parasitized by generalist parasitoid wasps (Lei et al. 1997). Numerous *E. editha bayensis* have been seen with beak-shaped portions of their wings missing, or detached wings have been found on the ground (Bowers et al. 1985). In contrast, we have observed no avian predation of *M. cinxia*, but at least during one year in one region there was significant predation of adults by dragonflies (I. Hanski pers. obs.).

Even if mortality directly caused by generalist predators is limited, the behavioral responses of the prey to these predators may lead to significant population dynamic consequences. A good example is ant predation on *M. cinxia*. Ants do not touch the larvae, apparently because they are distasteful, but the ant species *Myrmica rubra* does attack eggs and adults (table 8.1). Adults can escape, but in the case of ovipositing females, harassment by ants can nonetheless be very detrimental. If ants disturb a female checkerspot during the one hour that it takes to lay a full clutch of eggs, she may be forced to leave early, after having laid only a part of the usual clutch of about 150 eggs. Because larval survival strongly depends on group size, larvae from a small egg cluster have only a limited chance of successful diapause (chapter 7). Thus, although ants are unlikely to catch the female, the disturbance that they cause may drastically reduce the survival of her offspring. It remains to be determined whether abundant ant populations might limit the abundance of local butterfly populations and even increase their risk of extinction. Another species of ant has a positive indirect effect on *M. cinxia*. In this case, larval host plants growing on ant mounds make especially good host plants because of warm microclimate and because the plants do not usually desiccate during the summer. These plants are often used by *M. cinxia* in spite of their proximity to ants, which are frequently seen attacking other, primarily moth, larvae (S.van Nouhuys pers. obs.).

Natural enemies with narrow host ranges, particularly parasitoids, appear to have evolved mechanisms to take advantage of the chemically and physically defended host larvae (Stamp 1981a, Price 1984). Parasitoids with narrow host ranges are involved in the natural enemy communities associated with checkerspots (table 8.2). Unfortunately, knowledge about parasitoid host ranges and systematics in general is limited (Shaw 1994). The parasitoids of checkerspots are no exception, and thus no systematic analysis of the host records can be attempted here. There are only a few checkerspot species for which the ecology of the parasitoids has been studied and published in any detail. These are *Euphydryas editha* (White 1973, 1986, Moore 1989a, 1989b) and *E. phaeton* (Bowers 1980, Stamp 1981a, 1982b, 1984) in North America, *E. aurinia* in England (Ford and Ford 1930, Fraser 1954, Porter 1981, 1983), and



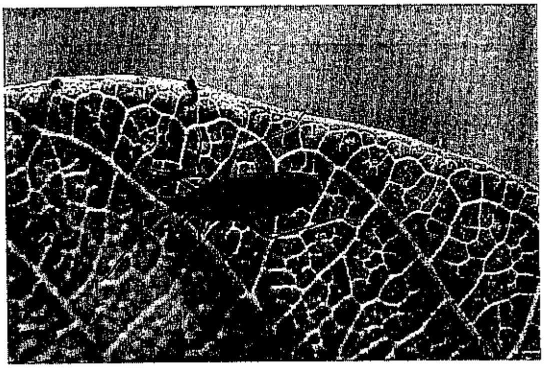


Figure 8.1. While most work on natural enemies of checkerspots has been done on parasitoids, other organisms may have significant impacts on checkerspot populations. For instance, moth larvae (left) attack egg masses and mirid bugs (right) eat hatchlings of *Euphydryas gillettii* in Colorado (see table 8.1). Photos by Paul R. Ehrlich.

Table 8.1. Predators of checkerspot butterflies.

Butterfly	Predator	Prey Stage	Scale of Impact	Reference[a]
Chlosyne lacinia	Fire ant *Solenopsis xyloni*	Larvae	50% mortality in one population	1
	Pentatomid bug *Stiretrus anchorago*	Larvae	Almost entire larval nests in one population	2
	Polistes wasp	Larvae	Almost entire larval nests in one population	2
	Jumping spider	Adult	Unknown	2
	Orb weaving spider	Adult	Unknown	2
Euphydryas aurinia	Bird (Cuckoo)	Larvae	Unknown, one population	3
	Pterostichus versicolor	Larvae	Unknown, one population	3
	Bug	Larvae	Unknown, one population	3
	Frogs and toads	Larvae	Unknown, one population	3
E. chalcedona	Bird	Adults	Significant in some populations	4, 5
E. editha	Stilt bug (Berytidae)	Eggs	Minor	6
	Unknown	Eggs	0–85% mortality in different populations	7
	Herbivore	Eggs, larvae	0–8% in one population, four years	6
	Unknown	Pupae	23–34% in one population, three years	8
	Bird	Adults	Unknown	19, 10
	Spider	Adults	Causes male bias in a population	11
E. gillettii	Myrid bug(Myridae)	Eggs, larvae	Contributes to 30–80% mortality in two populations	12
	Erythraid mites	Eggs, larvae	Contributes to 30–80% mortality in two populations	12
	Beetle larvae	Eggs, larvae	Contributes to 30–80% mortality in two populations	12
E. phaeton	Unknown	Eggs	7% of eggs from 70% of clusters, one population	13
Melitaea cinxia	Lady beetle (Coccinellidae)	Eggs, larvae	Unknown, probably high predation of eggs; entire clusters eaten	14
	Lacewing (Chrysopidae)	Eggs, larvae	Unknown, variable entire egg clusters eaten	14
	Pentatomid bug (Pentatomidae)	Larvae	Unknown	14
	Red ant (*Myrmica rubra*)	Eggs	Unknown fractions of egg clusters eaten	15
	Spider	Adults	Unknown	14
	Dragon fly	Adults	Unknown	16
Melitaea athalia	Small mammals	Pupae	31–41%, one population over three years	17
	Carabid beetle	Pupae	2–6%, one population over three years	17
	Staphylinid beetle	Pupae	0–2%, one population over three years	17

[a]References: 1, Clark (1997b); 2, Drummond et al. (1970); 3, Wilkinson (1907); 4, Brown and Ehrlich (1980); 5, Bowers et al. (1985); 6, Moore (1989a); 7, White (1973); 8, White (1986); 9, Ehrlich (1965); 10, Hendricks (1986); 11, Moore (1987); 12, E. H. Williams et al. (1984); 13, Stamp (1981b); 14, S. van Nouhuys (pers. obs.); 15, J. Ehrnsten (pers. comm.); 16, R. Setchfield (pers. comm.); 17, Warren (1987c).

Table 8.2. Parasitoids of checkerspot butterflies.

Parasitoid[a]	Host	Geographic Area	Reference[b]
Hymenoptera			
Braconidae			
Cotesia acuminata agg. (S)[c]	*Euphydryas maturna*	Europe	1, 2, 3
	Melitaea didyma	Europe	4
	Melitaea latonigena	Siberia	5
	Melitaea phoebe	Europe, Siberia	5, 4
	Melitaea athalia	Europe	4
	Melitaea scotosia	China	4
Cotesia bignellii (S)	*Euphydryas aurinia*	Europe	2, 7
Cotesia cynthia (S)	*Euphydryas cynthia*	Europe	6, 6
Cotesia euphydridis (S)	*Chlosyne harrissii*	North America-E	8
	Euphydryas phaeton	North America-E	8
Cotesia koebelei (S)	*Chlosyne leanira*	North America	8
	Chlosyne neumoegeni	North America	8
	Euphydryas chalcedonia	North America-W	8
	Euphydryas editha	North America-W	8, 9, 10
Cotesia melitaearum (S)	*Euphydryas aurinia*	Europe	7, 5, 11
	Euphydryas aurnia davidi	Siberia	5
	Euphydryas desfontainii	Europe	1
	Euphydryas maturna	Europe	2,4
	Melitaea cinxia	Europe, Asia	12, 6, 5, 13
	Melitaea diamina	Europe	4
	Melitaea didyma	Europe	4
	Melitaea parthenoides	Europe	4
	Melitaea trivia	Europe	4
	Melitaea athalia	Europe	2, 13, 14
	Melitaea deione	Europe	3, 4
Apanteles lunatus	*Chlosyne lacinia*	North America-W	15
Other Ichneumonoidae			
Apechthis compunctor (G, P)	*Euphydryas maturna*	Europe	1
Benjaminia euphydridis (S)	*Chlosyne harrissii*	North America-E	16
	Euphydryas phaeton	North America-E	16
Benjaminia fumigatos (S)	*Melitaea didyma*	Europe	4
Benjaminia fuscipennis (S)	*Euphydryas editha*	North America-W	9
	Euphydryas chalcedonia	North America-W	16
Benjamina sp. (S)	*Melitaea didymoides*	Siberia	5
Benjamina sp. (S)	*Euphydryas gillettii*	North America-W	6
Cratichneumon vinnulus (P)	*Chlosyne lacinia*	North America-W	15
Gelis sp. (G, P)	*Melitaea athalia*	Europe	14
Hyposoter horticola (S)	*Melitaea cinxia*	Europe	12, 13
Hyposoter sp.	*Melitaea cinxia*	Europe	13
	Melitaea phoebe	Siberia	5
Ichneumon cynthiae (S, P)	*Euphydryas cynthia*	Europe	17
Ichneumon balteatus (P)	*Melitaea cinxia*	Europe	17
Ichneumon cinxiae (S, P)	*Melitaea cinxia*	Europe	17
Ichneumon gracilicornis (G, P)	*Euphydryas aurinia*	Europe	2
	Euphydryas maturna	Europe	1, 2
	Melitaea cinxia	Europe	12
Ichneumon pulvinatus (P)	*Melitaea cinxia*	Europe	17
Probolus culpatorius (G, P)	*Euphydryas maturna*	Europe	1
Stenichneumon culpator (G, P)	*Melitaea athalia*	Europe	17
Unknown Ichneumonid	*Chlosyne harrissii*	North America-E	18
	Melitaea cinxia	Siberia	5
	Melitaea deione	Europe	4

(*continued*)

Table 8.2. (*continued*)

Parasitoid[a]	Host	Geographic Area	Reference[b]
Chalcidoidea *Coelopisthia caledonica* (G, P)	*Melitaea cinxia*	Europe	12
Pteromalus apum (G,P)	*Euphydryas aurinia*	Europe	19, 20
	Euphydryas maturna	Europe	19
	Melitaea cinxia	Europe	19, 20
	Melitaea didyma	Europe	19
Pteromalus archippi (P)	*Chlosyne lacinia*	North America-W	15
Pteromalus puparum (G, P)	*Euphydryas phaeton*	North America-E	21
	Melitaea cinxia	Europe	12
Pteromalus vanessae (P)	*Euphydryas gillettii*	North America-W	6
Pteromalus sp. (P)	*Melitaea athalia*	Europe	14
Spilochalcis phoenica (P)	*Chlosyne lacinia*	North America-W	15
Trichogramma fasciatium undescribed	*Chlosyne lacinia*	North America-W	15
Trichogrammatid (egg)	*Euphydryas phaeton*	North America-E	22
Unidentified Chalcid (P)	*Euphydryas editha*	North America-W	10
Diptera			
Tachinidae			
	Euphydryas phaeton	North America-E	21
Compsilura concinnata			
Erycia fatua (S)	*Euphydryas aurinia*	Europe	7, 23
	Euphydryas maturna	Europe, Siberia	2, 23
	Melitaea britomartis	Europe	23
	Melitaea cinxia	Europe	24
	Melitaea deione	Europe	24
	Melitaea parthenoides	Europe	3, 23
	Melitaea athalia	Europe	24
Erycia festinans (S)	*Melitaea cinxia*	Europe, Siberia	5, 25
	Melitaea didyma	Europe	23
Erycia fasciata (S)	*Melitaea didyma*	Europe	23
	Melitaea latonigena	Siberia	5
Erycia furibunda (S)	*Euphydryas aurinia*	Europe	2, 3, 6, 23, 25
	Euphydryas desfontainii	Europe	25
	Euphydryas maturna	Europe	23
Eupharoceradaripennis (P)	*Chlosyne lacinia*	North America-W	15
Siphosturmia melitaeae (P)	*Chlosyne lacinia*	North America-W	15
	Euphydryas chalcedonia	North America-W	27
	Euphydryas editha	North America-W	28
Unidentified Tachinid	*Euphydryas editha*	North America-W	10, 29, 30
Other Palearctic Tachinidae genera recorded from Melitaeini	*Exorista, Compsilura, Nemorilla, Phryxe, Huebneria, Palis, Ceromasia, Masicera, Thelymorpha*		23

[a]The parasitoids emerge from the larval stage of the host unless otherwise noted. Species marked with (P) emerge from the host pupa, species marked with (S) are thought to be a specialist of Melitaeini, and species marked with (G) are known to use hosts other than Melitaeine.

[b]References: 1, Eliasson; (1991), 2, Komonen (1997); 3, Komonen (1998); 4, M. Shaw (pers. comm.); 5, Wahlberg et al. (2001); 6, E. H. Williams et al. (1984); 7, Porter (1981); 8, Marsh (1979); 9, White (1973); 10, Moore (1989a); 11, Ford (1930); 12, Lei (1997); 13, S. van Nouhuys (pers. obs.); 14, Warren (1987c), 15, Drummond et al. (1970); 16, Carlson (1979); 17, Meier (1968); 18, Shapiro (1976); 19, Askew and Shaw (1997); 20, Shaw (2002); 21, Stamp (1984); 22, Stamp (1981a); 23, Tschorsnig (pers. comm.); 24, Tschorsnig (1994); 25, Ford et al. (2000); 26, Belshaw (1993); 27, Brown and Ehrlich (1980); 28, White (1986); 29, C. Boggs (pers. comm.); 30, Mattoni et al. (1997).

[c]This is probably at least two species, M. Shaw, personal communication

Melitaea cinxia in Finland (Lei and Hanski 1997, Lei et al. 1997, van Nouhuys and Hanski 2002b).

The general importance of natural enemies for the population dynamics of their checkerspot hosts is largely unknown. This is because the impact of natural enemies is extremely variable, natural enemies have been studied in only one or a few locations for each host species, and the roles of predators, especially, is difficult to measure. There is, however, some indication that natural enemies play a smaller role in the dynamics of the well-studied populations of *E. editha bayensis* and *E. chalcedona* (Ehrlich et al. 1975, Lincoln et al. 1982) than in *E. aurinia* (Porter 1981), *E. phaeton* (Bowers 1980, Stamp 1984), and *M. cinxia* (Lei et al. 1997, van Nouhuys and Hanski 2002b). Such differences might be explained by differences in the larval interactions with host plants, climate, and the composition of the parasitoid communities.

Natural Enemy Community Associated with Melitaea cinxia

The parasitoid complex associated with *Melitaea cinxia* in the Åland Islands consists of two primary larval parasitoids, two abundant hyperparasitoids (figure 8.2), and several generalist pupal parasitoids (Lei et al. 1997). The specialist parasitoid *Cotesia melitaearum* (Wilkinson) (Braconidae: Microgastrinae; plate X) is a gregarious braconid which, depending on weather, has two or three generations per host generation (year) in Åland. *Cotesia melitaearum* is a relatively sedentary wasp that occupies only well-connected host populations (Lei and Camara 1999, van Nouhuys and Hanski 2002a). Where present, *C. melitaearum* can have a great impact on host populations, even to the point of causing local extinctions (Lei 1997). However, *C. melitaearum* is only found in about 10% of host populations, and most frequently it persists as small, extinction-prone populations that have little impact on local host population dynamics (van Nouhuys and Hanski 1999, van Nouhuys and Tay 2001). Because *C. melitaearum* is a poor disperser, the spatial structure of the host metapopulation and therefore the respective habitat patch network largely determines the occurrence and role of *C. melitaearum* in host dynamics (van Nouhuys and Hanski 2002a).

The second primary parasitoid attacking *M. cinxia* is *Hyposoter horticola* (Gravenhorst) (Ichneumonidae: Campoplaginae; plate X), which is a solitary wasp with a single generation per host generation. *Hyposoter horticola* is restricted to a few Melitaeini, and *M. cinxia* appears to be its only host in Åland (Lei et al. 1997, van Nouhuys and Hanski 2002b). Exceptionally, though it is a larval parasitoid, *H. horticola* lays eggs in the host larvae while they are still inside the eggshell (plate X; van Nouhuys and Ehrnsten 2004). The wasp develops within the host larva and pupates inside the host integument the next spring. *Hyposoter horticola* is a large (12 mm body length) and extremely mobile wasp, and it parasitizes about a third of the host larvae in most populations, including very isolated and newly colonized host populations. In contrast to the spatially and temporally dynamic occurrence of *C. melitaearum*, the occurrence of *H. horticola* is stable, and it thereby uniformly suppresses host population sizes without directly causing local host population extinctions (van Nouhuys and Hanski 2002a, van Nouhuys and Ehrnsten 2004).

The two parasitoid species compete directly in those host populations in which they happen to occur together (section 8.3; Lei and Hanski 1998, van Nouhuys and Tay 2001). Additionally, each parasitoid has its own natural enemies. *Cotesia melitaearum* is host to the pseudo-hyperparasitoid *Gelis agilis* (Fabricius) (Ichneumonidae: Cryptinae) and less commonly to three other *Gelis* species (Lei et al. 1997). These species are all abundant wingless, generalist, ectoparasitic ichneumonids parasitizing insects developing in silken cocoons (Schwarz and Shaw 1999). *Gelis* aggregate in response to high host density and can greatly reduce the population size of *C. melitaearum*, probably even causing local extinctions (Lei and Hanski 1997, van Nouhuys and Tay 2001). An additional complication, supported by experimental results reported below, is the possibility that the dynamics of the primary parasitoid *C. melitaearum* is influenced, via apparent competition (Holt 1977), by the alternative prey of the generalist hyperparasitoid *G. agilis* (van Nouhuys and Hanski 2000). Finally, generalist predators kill some 40% of pupae in the early spring generation of *C. melitaearum*, leaving the populations small and prone to extinction (van Nouhuys and Tay 2001).

Hyposoter horticola is parasitized by the solitary ichneumonid hyperparasitoid *Mesochorus* sp. cf. *stigmaticus* (Brischke) (Ichneumonidae: Mesochorinae), which, like its host, is univoltine and very mobile and successfully parasitizes about a third of the host individuals throughout the Åland Islands

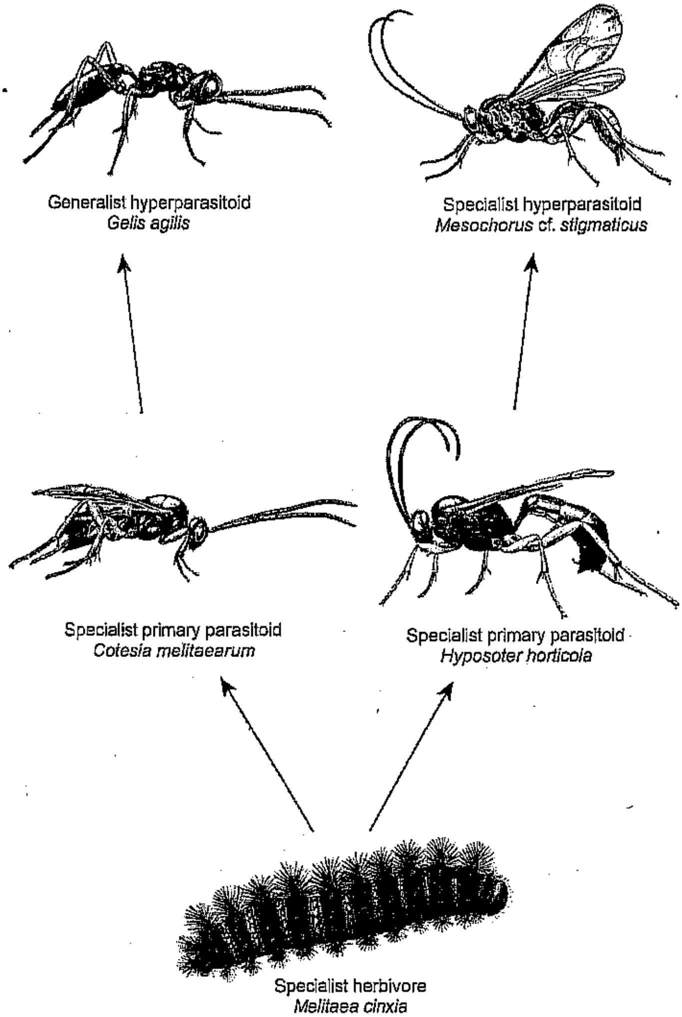


Figure 8.2. The parasitoid food web associated with *Melitaea cinxia* in the Åland Islands, involving two primary parasitoids (*Cotesia melitaearum* and *Hyposoter horticola*) and two hyperparasitoids (*Gelis agilis* and *Mesochorus* sp. cf. *stigmaticus*). Drawings by Zdravko Kolev.

(van Nouhuys and Hanski 2002b). *Mesochorus* sp. cf. *stigmaticus* also parasitizes *C. melitaearum*, though only occasionally (Lei et al. 1997). The systematics of the Palaearctic species of *Mesochorus* is in need of revision; hence we cannot be sure that the species is *stigmaticus* (Lei et al. 1997). However, *Mesochorus* are usually closely affiliated with the host of their primary parasitoid and are likely to have narrow host ranges. Thus, *M.* sp. cf. *stigmaticus* may be a specialist on *M. cinxia* in Åland (this is indirectly supported by distributional data; section 8.3).

There are at least four species of pupal parasitoids of *M. cinxia* in Åland: *Ichneumon gracilicornis* (Gravenhorst) (Ichneumonidae: Ichneumoninae), *Pteromalus apum* (Retzius) (Pteromalidae: Pteromalinae), *P. puparum* (L.) (Pteromalidae: Pteromalinae), and *Coelopisthia caledonica* (Askew) (Pteromalidae: Pteromalinae). All these species appear to have wide host ranges. Little is known of their impact on *M. cinxia*, apart from the observation that 14% of the pupae put out in a habitat patch used by *M. cinxia* during one season were parasitized (Lei et al. 1997).

Numerous samples of all larval stages suggest that there are no larval-pupal parasitoids in the community (S.van Nouhuys pers. obs.).

Biology of Checkerspot-Associated Parasitoids and Their Communities

Parasitoids in the genus *Cotesia* have been found to use most checkerspot species in Europe and North America. There are 4 recognized species in Europe using 13 different host species, and 2 species in North America using 6 host species (table 8.2). However, recent molecular studies suggest that there may be several more *Cotesia* species associated with checkerspots that have not been recognized by traditional taxonomy (M. Kankare pers. comm.). Additionally, only a few host species have been sampled extensively; thus the host records are likely incomplete. A few generalizations can nonetheless be drawn from the comparison of species in table 8.2. There is no clear pattern in the host ranges of the European *Cotesia* with respect to the phylogeny of the host butterflies (Wahlberg and Zimmermann 2000), nor is there an overall pattern in the use of host larvae on particular host plant species. The two generalist species of *Cotesia*, *C. melitaearum* and *C. acuminata*, share many host species (table 8.2), but they do not appear to coexist locally on the same host. One caveat here is that both *C. melitaearum* and especially *C. acuminata* may actually be aggregate names including two or more species each having a narrow host range (M. Kankare and M. Shaw pers. comm.).

Cotesia is a large genus parasitizing many families of Lepidoptera, but the *Cotesia* that parasitize checkerspots are not known to parasitize any other hosts. *Cotesia* species parasitizing *E. phaeton*, *E. aurinia*, and *M. cinxia* have specialized behaviors that are not characteristic of the genus *Cotesia* as a whole. These behaviors include moving freely inside the dense silken web of the host larvae, attending these webs for hours in the case of *E. phaeton* (Stamp 1981a, 1982b) or even days in the case of *M. cinxia* (Lei and Camara 1999), and often parasitizing only a fraction of the larvae available (Stamp 1981a, Porter 1983, Lei and Camara 1999). *Cotesia* that parasitize checkerspots also share many traits with other species in the genus, such as extreme variation in the number of eggs laid in a host depending on host size and flexible developmental time, both of which contribute to a potentially high rate of population increase. Additionally, at least some *Cotesia* that use checkerspots can control the rate of development of the host (e.g., Stamp 1984, Moore 1989b), and most pupate in clusters around the dead or dying host, as do other *Cotesia* (plate X).

Less is known about the behavior of the remaining parasitoids attacking checkerspots. Stamp (1982c) observed the ichneumonid *Benjaminia euphydryadis* making brief visits to *E. phaeton* larval groups in the field, where it successfully parasitized 4–6% of larvae and appeared to be deterred by larval defensive behavior. The ichneumonid *Hyposoter horticola* completely avoids any larval behavioral defenses of *M. cinxia* by parasitizing first instar larvae while they are still within the eggshell (plate X). This behavior leads to an extremely short window of opportunity for parasitism, only lasting for some hours per generation. It is at first surprising that the parasitoid nonetheless manages to parasitize about a third of the host larvae in most host populations, including the newly established ones. Part of the explanation is the great mobility of *H. horticola* (van Nouhuys and Hanski 2002a). But another reason for the high rate of parasitism, in spite of the short period of time during which the host is vulnerable, is the ability of the female wasps to learn the locations of the host groups before they are at the vulnerable stage for parasitism. By observing marked individuals of *H. horticola* in the field, we know that the wasps are long lived, and they actively forage for *M. cinxia* egg groups for several weeks before the eggs are due to hatch. During this time the wasps apparently memorize the locations of the egg clusters and return to parasitize them just before they hatch (figure 8.3; van Nouhuys and Ehrnsten 2004).

The better studied parasitoid complexes attacking checkerspots exhibit a clear pattern in species composition. Each host has a species of gregarious multivoltine *Cotesia* with complex behavior and extreme population fluctuations, as well as a single other important specialist parasitoid that is a large, solitary, univoltine ichneumonid (table 8.3; with the possible exception of *E. aurinia*, which appears to lack the ichneumonid) or a tachinid fly (table 8.2; Wahlberg et al. 2001). It may well be that coexistence of two *Cotesia* on the same host in the same locality is unlikely because of competition, while coexistence of a species of *Cotesia* and an unrelated parasitoid with contrasting behavior and phenology is possible (section 8.3). Unfortunately, the better studied systems all include just one common checkerspot host species, whereas there are locali-

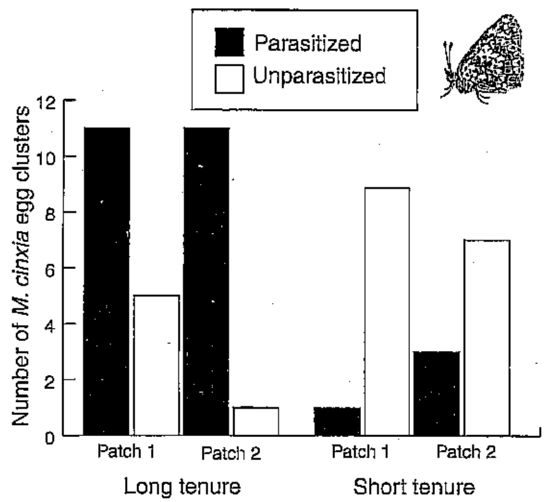


Figure 8.3. Parasitism of *Melitaea cinxia* egg clusters by *Hyposoter horticola* in a field experiment testing the hypothesis that *H. horticola* learn the locations of host egg clusters (van Nouhuys and Ehrnsten 2004). Two habitat patches occupied by both the butterfly and the parasitoid were divided into 144 and 132 2 × 2-m quadrants. Twenty quadrants in each patch were randomly assigned to receive transplanted food plants containing one-week old egg clusters (long-tenure eggs), and 10 quadrants in each were randomly assigned to receive transplanted plants with egg clusters on the day the eggs were to become susceptible (short-tenure eggs). Host egg clusters were laid by butterflies in the laboratory on potted food plants. Short tenure eggs were placed in the field by 9 AM when they began to slightly darken (see plate X), several hours before they became susceptible to parasitism. This assured that both egg cluster types were available for the entire time that they were vulnerable to parasitism. Egg clusters were checked every evening, and upon hatching returned to the laboratory, where the larvae were later dissected and scored as parasitized or unparasitized. The observed parasitism differs from the expected at $p < .01$ (Fisher's Exact test) in each habitat patch. Several of the long-tenure egg clusters in each patch were eaten by predators before the end of the experiment.

ties in Europe and Asia with up to 10 co-occurring checkerspot species. In these communities, several checkerspot species share the same habitat and even the same host plant species. For instance, in the steppe region of Buryatia, Russia, three checkerspot species, *Melitaea cinxia*, *M. latonigena*, and *M. didymoides*, all feed on *Veronica incana*, but they have not been observed to share the same species of *Cotesia* (*M. cinxia* has *C. melitaearum*, *M. latonigena* has *C. acuminata*, while no *Cotesia* was reared from *M. didymoides)*. In contrast, *M. phoebe* and *M. latonigena*, which feed on different host plant species in the same steppe habitat, share *C. accuminata* (Wahlberg et al. 2001). There is much scope for more work on the multihost communities, in which complex parasitoid communities with complex species interactions may occur.

Further complications occur due to varying host phenologies and development. Checkerspots in mild climates may have two or even three generations per year, in mountain regions host phenology changes with altitude, and in the north larvae may take more than one year to develop (Tolman and Lewington 1997). Examples include *M. cinxia*, which has two generations per year in much of southern France, but in the French Alps at higher altitudes there is only one generation per year (Tolman and Lewington 1997). *Euphydryas maturna* develops facultatively in two years in cool microclimates in Finland (Wahlberg 1998), whereas *E. gillettii* develops in two years at high altitudes in western North America (Stamp 1984). Such variation in host life cycles may have important consequences for host–parasitoid interactions.

8.3 Multitrophic-Level Interactions and Parasitoid Population Dynamics

The size and persistence of parasitoid populations at a local scale are affected by attributes of the host and the host food plants, which influence success

Table 8.3. Parasitoids in four checkerspot communities.

Butterfly[a]	Parasitoid	Host Stage Parasitized	Parasitoid Larval Behavior	Parasitoid Oviposition Behavior	Parasitoid Generations Per Year	% Host Population Parasitized
Melitaea cinxia	*Cotesia melitaearum*	Larvae	Gregarious	Specialist	2–3	Variable, 2–80%
	Hyposoter horticola	Larvae (in egg)	Solitary	Specialist	1	30% uniformly
	Coelopisthia caledonica	Pupae		Generalist		
	Coelopisthia extenta	Pupae		Generalist		
	Pteromalus apum	Pupae		Generalist		
Euphydryas editha	*Cotesia koebelei*	Larvae	Gregarious	Specialist	2	Variable, 0–66%
	Benjaminia fuscipennis	Larvae (?)	Solitary	Specialist	1	Very low, <1.0%
	Siphosturmia melitaeae	Larvae(?)	Solitary	Specialist		1–10%
E. phaeton	*Cotesia euphydridis*	Larvae	Gregarious	Specialist	2	6%
	Benjaminia euphydridis	Larvae			1	4–6% in
	Trichogrammatid	Eggs				<5%
E. aurinia	*Cotesia bignellii*	Larvae	Gregarious	Specialist	2–3	Variable, 0–80%

[a]*Melitaea cinxia* in the Åland Islands, 1993–2002 in a 50 × 70 km area (Lei et al. 1997, van Nouhuys and Tay 2001, van Nouhuys and Hanski 2002b); *Euphydryas editha* in California, USA, several years in coastal populations (Ehrlich 1965, White 1973, 1986), and several years in Sierra populations (Moore 1989a); *E. phaeton* in eastern USA, one population 1979 and 1980 (Stamp 1981a, 1982b); and *E. aurinia* in the United Kingdom, one site 1895–1926 (Ford and Ford 1930), and one site 1977–80 (Porter 1981, 1983).

of parasitism, and by parasitoid mortality caused by competition and natural enemies. At larger spatial scales parasitoid population dynamics may be constrained by the spatial dynamics of the species with which they interact, including factors that influence the extinction–colonization dynamics of the host and the relative range and the rate of dispersal of the interacting species (van Nouhuys and Hanski 2002b). Here we first discuss local tritrophic interactions among the butterflies, their food plants and the primary parasitoids, then local interactions among the parasitoids, and finally the spatial dynamics of the interacting species. All these interactions are primarily illustrated by results for *Melitaea cinxia* and its parasitoids in the Åland Islands, a system in which parasitoids play a significant role in the dynamics of the host butterfly.

Natural Enemies and Checkerspot Larval Host Plants

Natural enemies of herbivorous insects are influenced in various ways by the food plants of their host species (Godfray 1994, De Moraes et al. 1998). As reviewed in chapters 7 and 11, most checkerspots feed on plants containing iridoid glycoside or secoiridoid plant secondary compounds, which deter generalist herbivores. Checkerspot larvae sequester iridoids from their food plants (Bowers and Puttick 1986, Bowers 1988, Suomi et al. 2001), and predation by generalists would probably be higher if the hosts were not chemically defended. Specialist parasitoids appear to tolerate, overcome, or avoid iridoids sequestered by their hosts (Bowers 1981, Stamp 1982b, 1992). In a laboratory experiment using selected lines of *Plantago lanceolata* with high and low iridoid concentrations, Harvey and van Nouhuys (unpubl.) found that the rate of development and the size of *C. melitaearum* developing in *M. cinxia* larvae did not vary significantly with the iridoid content of the plants eaten by the host larvae. In contrast, in the field in the Åland Islands, where parasitoids may choose among hosts feeding on plants containing dissimilar iridoid concentrations, parasitism appears to be associated with low levels of the iridoid glycoside catalpol in the host plant (Nieminen et al. 2003). The apparent difference between the laboratory and field results might reflect a difference in parasitoid preference (which the field results largely or entirely reflect) and parasitoid performance (which the laboratory experiment measured). Alternatively, sequestration or metabolism of iridoid glycosides by host larvae in the laboratory may differ from that in natural conditions, or adult wasps may prefer larvae feeding on low-iridoid plants for reasons not related to the measures taken in the laboratory experiment. Finally, attributes of plants that are correlated with catalpol level may influence the adult oviposition behavior or success of *C. melitaearum* larvae. It would be worthwhile to compare the natural enemy communities associated with iridoid-defended versus undefended checkerspot butterfly species. For example, *Melitaea phoebe*, *M. scotosia*, *M. punica*, and *Chlosyne lacinia* all feed on plants in the family Asteraceae, which do not synthesize iridoids (Wahlberg 2001b). *Chlosyne lacinia* appears to have generalist predators, such as *Polistes* wasps, which have not been recorded for checkerspot larvae feeding on iridoid-producing hosts (table 8.1). The complication, of course, is that these noniridoid plants have a multitude of other secondary chemical compounds with unknown effects on checkerspot larvae and their parasitoids.

Production of toxic chemical compounds consumed and sequestered by herbivores is not the only factor related to plants that might influence natural enemies. For instance, volatile compounds released by herbivore-infested plants attract parasitoid wasps (Vet and Dicke 1992, Turlings et al. 1995). Furthermore, plants differ in their structure, phenology, and dispersion, which can all contribute to the success of a female wasp searching for hosts in which to lay eggs and to the subsequent success of her developing offspring (Godfray 1994). In the Åland Islands, larvae of *M. cinxia* feed on two host plant species, *Veronica spicata* and *Plantago lanceolata*. These plants differ in iridoid glycoside content and concentration (Suomi et al. 2002, Nieminen et al. 2003) and in their distribution within and among habitat patches (chapter 7). *Cotesia melitaearum* uses *M. cinxia* larvae on both host plant species, but observations on the rate of parasitism in natural populations over six years showed that larvae on *V. spicata* were more frequently parasitized than larvae on *P. lanceolata* (van Nouhuys and Hanski 1999). As a consequence, parasitoid populations are largest and persist longest in areas in which the host butterfly feeds predominantly on *V. spicata*. Colonization rate of host populations by the parasitoid also increased with the relative abundance of *V. spicata* in the habitat patch; hence the large-scale distribution of the two host plant species significantly influences the parasitoid metapopulation dynamics (van Nouhuys and Hanski 1999).

The observed superiority of *V. spicata* as a host plant has many possible explanations. Host-occupied *V. spicata* may be easy for female parasitoids to find, or, once larvae on *V. spicata* are discovered, they may be easy to parasitize, or host larvae feeding on *V. spicata* may not be able to defend themselves against the parasitoid eggs or larvae as well as larvae feeding on *P. lanceolata*. Our results support the first explanation rather than the latter two explanations. Possibly, female wasps searching for host larvae find them more easily on *V. spicata* than on *P. lanceolata* because the larval nests on *V. spicata* are generally located closer together than are larval nests on *P. lanceolata* (van Nouhuys and Hanski 1999). Preliminary studies also suggest that *C. melitaearum* is more attracted to the odor of host-occupied *V. spicata* than to the odor of host-occupied *P. lanceolata* (figure 8.4; Anton and van Nouhuys, unpubl. data). Once the host larvae have been located by the wasp, the consequences of the host plant species for the parasitoid are ambiguous. Lei and Camara (1999) found in a laboratory study that host larvae reared on *P. lanceolata* were more readily attacked than larvae reared on *V. spicata* (the larvae were exposed to parasitoids without the host plants). In contrast, Anton and van Nouhuys (unpubl. data) found the opposite: larvae reared on *V. spicata* being more readily attacked. The clutch size and survival of wasp progeny was equal among larvae feeding on the two plant species.

Most other checkerspot butterflies also use several host plant species, which can influence the parasitoid community and population dynamics. For instance, *E. editha bayensis* populations use two host plant species that differ phenologically and that differ in their suitability for larvae depending on the season, weather, and topography. Larvae do not often stay in groups for long, but they move individually from senescent to healthy plant individuals and species (chapters 3 and 7). Such a complex and variable relationship with host plants may render plant-derived host cues unreliable, reducing the efficiency of foraging parasitoids and ultimately the sizes of their populations. This could contribute to the apparent small role of parasitoids in *E. editha* population dynamics (table 8.3). In *E. editha bayensis* in particular, there is typically high larval mortality induced by host plant senescence (chapter 3), which will inevitably lead to high parasitoid mortality as well.

Competition among Natural Enemies

Any predator or parasitoid that has an impact on the host population size is potentially involved in competitive interactions with other natural enemies. Thus the egg, larval, and pupal parasitoids and predators of checkerspots, which have at least occasionally a large impact on local host population size (Ford and Ford 1930, White 1973, 1986,

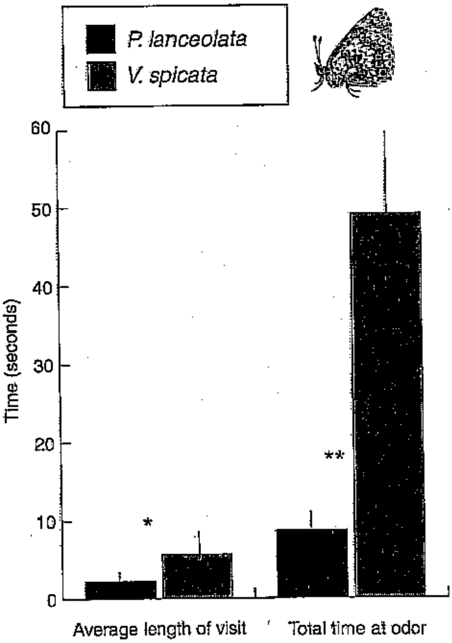


Figure 8.4. The relative attractiveness of the odor of herbivore-damaged *Plantago lanceolata* and *Veronica spicata* to the parasitoid *Cotesia melitaearum*. The gray bar is the host-damaged *V. spicata* + frass treatment. The black bar is the host-damaged *P. lanceolata* + frass treatment. The average visit length is the amount of time a wasp spent palpating and walking during one visit to an odor source. The total time at odor is the average sum of all visits to the odor source during the 5-minute observation period ($n = 15$ independent choice trials under laboratory conditions, $^{*}p < .05$; $^{**}p < .005$).

Moore 1989a, Lei and Hanski 1997), most likely compete with each other.

The two primary larval parasitoids of *M. cinxia* in the Åland Islands, *C. melitaearum* and *H. horticola*, coexist in about 10% of host populations, and the majority of the remaining host populations are occupied by *H. horticola* alone, as this species has a wider range of dispersal than the host and a much wider dispersal range than *C. melitaearum* (van Nouhuys and Hanski 2002a). Coexistence of the competing parasitoids would be enhanced if the superior disperser would be the inferior competitor locally (Nee et al. 1997). *Hyposoter horticola* is always the first one to parasitize a host individual because it oviposits in first instar host larvae while they are still within the eggshell (van Nouhuys and Ehrnsten 2004). *Cotesia melitaearum* does not appear to distinguish between unparasitized hosts and those parasitized by *H. horticola* (E. Punju unpubl. data). Therefore, upon hatching, host larvae already parasitized by *H. horticola* are still vulnerable to parasitism by two or three generations of *C. melitaearum*. In natural butterfly populations occupied by both wasp species, successful parasitism by *H. horticola* is lower than in populations in which it is alone, suggesting that *C. melitaearum* has a substantial competitive impact on *H. horticola* (Lei and Hanski 1998). Laboratory experiments have revealed that both parasitoids suffer from competition, but also that the outcome of competition depends on when, during the host life cycle, the larva is parasitized by *C. melitaearum*. Competition between the two parasitoids takes the form of both physical combat and physiological suppression (E. Punju, unpubl. data). Unexpectedly, it is only during the second (autumn) generation of the three *C. melitaearum* generations that *H. horticola* is the weaker competitor (E. Punju, unpubl. data; figure 8.5). One might have expected *H. horticola* larvae to perform poorly in competition in the smallest host larvae, in which the size difference between the parasitoids should favor *C. melitaearum*, but at this stage *H. horticola* is the superior competitor (figure 8.5).

Natural Enemies of the Natural Enemies

A major source of mortality of insect natural enemies is other natural enemies, in the forms of predation and hyperparasitism, intraguild predation and parasitism, and incidental consumption along with the host (Rosenheim et al. 1993, Godfray 1994, Stiling and Rossi 1994, Colfer and Rosenheim 2001, Snyder and Ives 2001). Because we know relatively little about generalist predators of checkerspots, we also know little about incidental and intraguild predation. What we do know about the hyperparasitoids and predators of *C. melitaearum* in Åland supports the notion that secondary natural enemies play an important role in insect population dynamics and community structure.

The two primary parasitoids of *M. cinxia* in the Åland Islands both suffer substantial parasitism, even though for one of them, *H. horticola*, such mortality is spatially and temporally relatively constant, while for the other one, *C. melitaearum*, mortality is variable and possibly density dependent. As we have already mentioned, *H. horticola* parasitizes about a third of the host larvae in Åland, of which about a third again are parasitized by the solitary hyperparasitoid *M.* sp. cf. *stigmaticus* (figure 8.2). This pattern has remained relatively stable over hundreds of local populations over several years (van Nouhuys and Hanski 2002b). In contrast, the generalist pseudohyperparasitoid *Gelis agilis* (and other less common *Gelis* species) attacking *C. melitaearum* appears to aggregate in response to high host density (Lei and Hanski 1997, van Nouhuys and Hanski 2000), and the fraction of *C. melitaearum* cocoons parasitized by *Gelis* varies from none to virtually 100% in different local populations (figure 8.6). Predation of *C. melitaearum* cocoons can also be high, and it varies greatly both spatially and temporally (figure 8.6). Together the parasitoids and predators of *C. melitaearum* probably cause local extinctions of high-density populations (Lei and Hanski 1997, van Nouhuys and Tay 2001). Because *Gelis* have many host species and aggregate, the local density of alternative hosts for *Gelis* can influence its impact on *C. melitaearum*. Such an indirect interaction, called apparent competition (Holt 1977), was demonstrated in a field experiment in which alternative hosts for *Gelis* (*Cotesia glomerata*) were placed in substantial numbers in natural *C. melitaearum* populations and the population sizes of *C. melitaearum* were compared with untreated control populations (van Nouhuys and Hanski 2000). All three treated populations declined, two of them to extinction, while the control populations remained relatively stable.

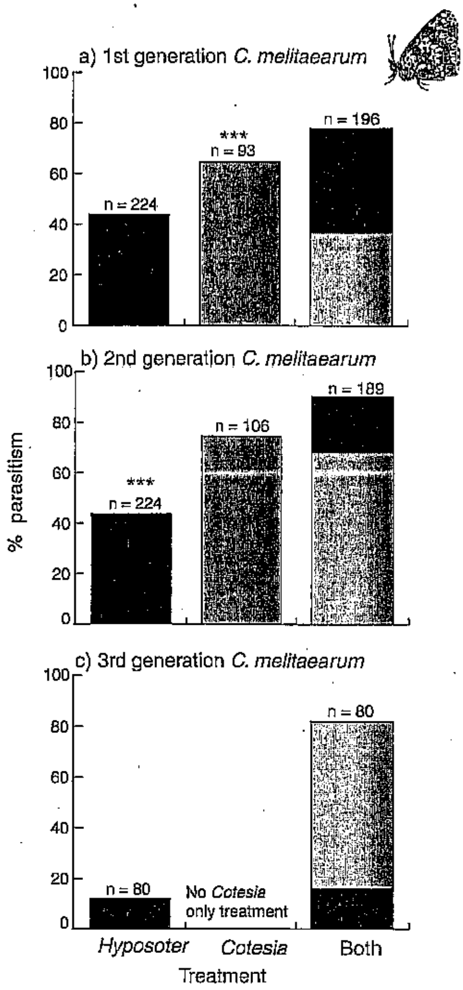


Figure 8.5. The outcome of direct competition between immature parasitoid wasps within *Melitaea cinxia* larvae in laboratory experiments. The gray bars represent successful parasitism by *Cotesia melitaearum*, and the black bars represent successful parasitism by *Hyposoter horticola*. (a) First-generation *C. melitaearum* attacks second instar *M. cinxia* larvae. If the host is already occupied by *H. horticola*, then *C. melitaearum* suffers ($\chi^2 = 12.66$, $p < .001$). (b) Second-generation *C. melitaearum* attacks fourth instar *M. cinxia* larvae. If the host is already occupied by *H. horticola* then *H. horticola* suffers ($\chi^2 = 20.25$, $p < 0.001$). (c) Third-generation *C. melitaearum* attacks sixth instar *M. cinxia* larvae. If the host is already occupied by *H. horticola*, then *C. melitaearum* dies (no significant difference in success of *H. horticola* with and without *C. melitaearum*). Data for panels (a) and (b) are from E. Punju (unpubl.), and for (c) from van Nouhuys and Tay (2001). Note that the initial rate of parasitism by *H. horticola* in (c) was lower than in (a) and (b).

If *Gelis* were absent, and not replaced by an equivalent other natural enemy, the population sizes of *C. melitaearum* would probably increase rapidly, and the butterfly populations would in turn decrease in size and be more prone to local extinction. The deletion of the hyperparasitoid *M.* sp. cf. *stigmaticus* from the species chain *M. cinxia–H. horticola–M. stigmaticus*, in contrast, would probably have no effect on host population dynamics because *H. horticola* is extremely efficient and parasitizes a fraction of almost every egg cluster in Åland. Eggs that escape parasitism have been found by *H. horticola*, but they remain unparasitized because the eggs in one batch mature over several hours (plate X) but are attended by an ovipositing wasp for less than one hour (van Nouhuys and Ehrnsten 2004; figure 8.3). Presumably, it would not pay for the wasp to spend several hours attending one egg cluster.

Spatial Population Dynamics of Interacting Species

At large spatial scales, species interactions may depend on both the structure of the landscape and the dispersal behavior of the interacting species. There is an extensive body of theory dealing with interspecific interactions in fragmented landscapes (Holt 1997, 2002, Nee et al. 1997, Hanski 1999b, Hassell 2000b). Prey and inferior competitors may escape enemies and superior competitors by dispersing to currently unoccupied habitat (temporary refuge). Over time, space may allow for sufficiently asynchronous local dynamics to be maintained to pre-

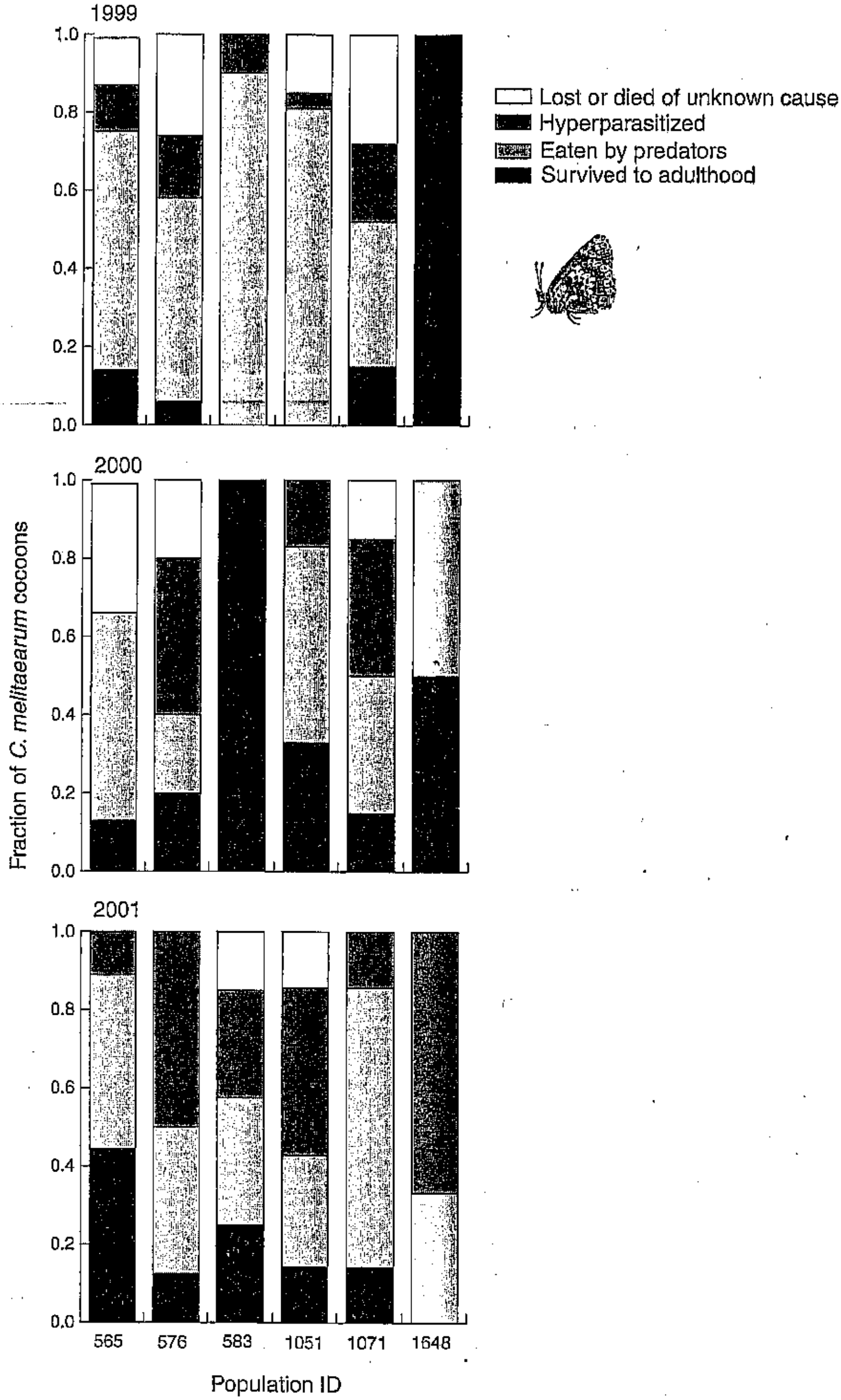


Figure 8.6. The fate of cocoons of the spring generation of *Cotesia melitaearum* in six populations in 1999, 2000, and 2001. Data for 1999 and 2000 are from van Nouhuys and Tay (2001).

vent metapopulation extinction. A critical issue is the rate and the scale of dispersal, which should be sufficient to allow for recolonization of currently empty habitat but not so extensive as to eliminate spatial asynchrony in local dynamics.

Butterfly movements within and among habitat patches have been much studied (Baguette and Nève 1994, Hill et al. 1996, Roland et al. 1999, Baguette et al. 2000, Ries and Debinski 2001), including the movement behavior of checkerspots (chapters 3 and 4). Checkerspots are convenient for the study of spatial population dynamics because the butterflies are relatively sedentary and because the habitat patches they use can often be delimited easily. In contrast, large-scale movements of insect predators and parasitoids are difficult to study and have rarely been measured in any system (Godfray, 1994; for exceptions, see Hopper 1984, Antolin and Strong 1987).

Studies conducted in the Åland Islands have produced unique data on the rates and ranges of colonization by *M. cinxia* and its two primary parasitoids, measured in field experiments and inferred from long-term observations on the presence and absence of the species in habitat patches (van Nouhuys and Hanski 2002a). This research shows that *M. cinxia* persists as a classic metapopulation in the Åland Islands (chapter 4). van Nouhuys and Hanski (2002a) found that *H. horticola*, the large ichneumonid, experiences the host as a single, patchily distributed population because of its high rate of dispersal and long colonization distances. In contrast, most of the local butterfly populations are temporally or more permanently inaccessible to *C. melitaearum*, the small braconid wasp, which has a limited dispersal range and therefore persists only in tightly clustered networks of host populations (figure 8.7). At the regional scale, the butterfly may escape *C. melitaearum* by colonizing empty habitat, but host dispersal does not limit parasitism by *H. horticola*, which consequently must be limited by local interaction. *Hyposoter horticola* suffers where it competes directly with *C. melitaearum*, but it mostly avoids direct competition because the majority of *H. horticola* populations occur outside the range of dispersal by current *C. melitaearum* populations.

The three-species chain *Melitaea cinxia–Hyposoter horticola–Mesochorus* sp. cf. *stigmaticus* forms a tightly linked group of interacting species. Hyperparasitoids are generally thought to be less specialized than primary parasitoids (Gordh 1981, Brodeur 2000), presumably because it is difficult to be a successful specialist at a high trophic level (Pimm 1991, Holt 1997). Both *H. horticola* and *Mesochorus* sp. cf. *stigmaticus* are very good dispersers, which facilitates metapopulation-level persistence. The island of Kumlinge, east of the main Åland Island (figure 2.3), is a notable exception. Here the hyperparasitoid is absent, but the butterfly and the primary parasitoid are present, most likely because the relatively small habitat patch network makes long-term persistence of the specialist hyperparasitoid unlikely.

Melitaea cinxia lives in a highly fragmented landscape in the Åland Islands, and hence its local populations are prone to extinction (chapter 4). In other localities, checkerspot butterflies and their natural enemies live in less fragmented landscapes and have

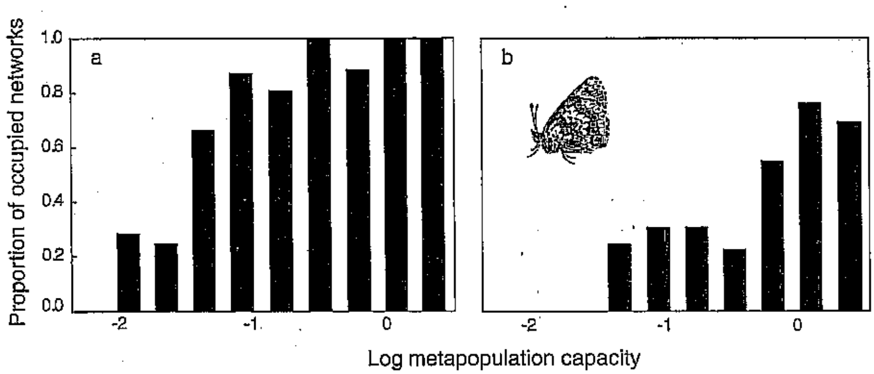


Figure 8.7. The fraction of habitat patch networks occupied by (a) *Melitaea cinxia* only and (b) those occupied by both *M. cinxia* and *Cotesia melitaearum* as a function of the metapopulation capacity of the network (van Nouhuys and Hanski 2002a). See box 12.1 for an explanation of metapopulation capacity.

larger populations. It is possible that *Cotesia* parasitoids in these less fragmented landscapes have generally larger populations and influence the host populations more strongly than in the Åland Islands. Checkerspot-associated *Cotesia* are relatively sedentary and typically have a high intrinsic rate of population increase because they are gregarious and have several generations per host generation. At high host density in an unfragmented habitat, this may lead to a parasitoid outbreak like the ones described by Ford and Ford (1930): a dramatic decline and increase, and then again a decline of *Euphydryas aurinia* populations near Carlisle, UK, in 1881–1929 (figure 1.5), accompanied by increase, decrease, and increase of parasitism by *C. bignellii*. Without having actual data on this, we may speculate that *Cotesia* populations are often kept in check by their own effective natural enemies, such as *Gelis agilis* in the Åland Islands, regardless of the habitat structure. Either way, comparison of the spatial population dynamics of the parasitoids in more and less fragmented landscapes would be welcome.

8.4 Conclusions and Outstanding Research Questions

Considering the numbers of species of predators and parasitoids in insect communities and their abundances, relatively little is known about them (Shaw 1994). This is in spite of the indisputable ecological importance of predators and parasitoids (Hochberg and Ives 2000, Shaw and Hochberg 2001), and their economic importance in pest control (Hochberg and Hawkins 1994, Barbosa 1998). Our lack of understanding of their taxonomy, natural history, and broader ecology is especially clear when we consider their absence from conservation plans. Invertebrate natural enemies, particularly parasitoid wasps, are prone to extinction because they are both high on food chains and specialized, yet they are part of very few conservation programs worldwide (Hochberg 2000, Shaw and Hochberg 2001).

The natural enemies associated with checkerspot butterflies represent a convenient system in which to learn more about the systematics, natural history, and population and community ecology of predators and parasitoids because we already have such a good understanding of the host ecology. In this final section we discuss four areas for further research, which are all relevant both for basic ecology and conservation as well as for the management of invasive species and biological control.

Role of Natural Enemies in the Dynamics of Checkerspots

We are aware of several examples of natural enemies having great influence on the dynamics of checkerspots, including the early observations by Ford and Ford (1930) of huge fluctuations in population size of *E. aurinia* over 30 years coinciding with great changes in the rate of parasitism by *C. bignellii*, and the metapopulation-level decline of *M. cinxia* in Åland after high levels of parasitism by *C. melitaearum* (Lei and Hanski 1997). Some species, like the ichneumonid *H. horticola* parasitizing *M. cinxia*, influence host population dynamics primarily by imposing a relatively constant rate of mortality in host populations (van Nouhuys and Ehrnsten 2004). The impact of yet other species remains poorly known. There is anecdotal evidence of generalist predation being occasionally very high (table 8.1), there are parasitoids that appear to be specialists but are rare, such as *Benjaminia fuscipennis* parasitizing *E. editha bayensis*, and there are pupal parasitoids, sometimes abundant, which we know little about.

Here we mention several directions for further research on the role of natural enemies in the dynamics of checkerspots. First, further study of the natural history and host ranges of the predators and parasitoids would yield useful information, fleshing out tables 8.1 and 8.3. Second, comparisons could be made of host–parasitoid interactions in communities structured around ephemeral versus more stable host plant species, among populations living in continuous versus fragmented landscapes, and among communities in which different numbers of checkerspot and host plant species co-occur. Third, population dynamics of host–parasitoid and competitive interactions could be analyzed using mathematical models parameterized for the species and ecological settings for which information is available. Two examples of this, though of limited ecological scope, are studies by Lei and Hanski (1997) and Hill and Caswell (2001). Finally, it would advance our understanding of the role of plant defensive chemistry on the natural enemies of herbivores if comparisons were available of the natural enemy communities associated with checkerspots feeding on host plants that do not confer chemical defenses (e.g., plants in the family Asteraceae) and those containing iridoid glycosides. The same question can be addressed experimentally, either by taking advantage of the natural variation in iridoid concentration (Stamp and Bowers 2000a, 2000b, Nieminen et al. 2001), by using artificial diet (Bowers and Puttick 1986, Lei and Camara 1999), or by using selected laboratory lines of the host plant species (Marak et al. 2000, Harvey and van Nouhuys unpubl. data).

Parasitoid Community Structure

Parasitoids are part of most terrestrial communities, in which they occupy several trophic levels and have complex direct and indirect interactions with many species (Hawkins and Sheehan 1994). Several theoretical expectations of community ecology can be illustrated using the parasitoid complex associated with *Melitaea cinxia* in Åland. First, as has been elucidated by theory (Nee and May 1992), the coexistence of the two competing primary parasitoids is at least to some extent facilitated by a negative association between competitive and dispersal abilities. *Hyposoter horticola* is clearly a better colonizer than *C. melitaearum*, but a worse competitor at least during one part of the host life cycle (figure 8.5; van Nouhuys and Hanski 2002a). Second, patterns in food chain length (section 8.3) support the notion that a minimum landscape area is needed to support high trophic levels (Holt 2002). The island of Kumlinge in Åland with a relatively small patch network (around 100 patches) that supports *M. cinxia* is also occupied by the primary parasitoid *H. horticola* but not by the hyperparasitoid *Mesochorus* sp. cf. *stigmaticus*. Third, a field experiment demonstrated apparent competition (Holt 1977, Bonsall and Hassell 1998) between two primary parasitoids sharing a common hyperparasitoid (van Nouhuys and Hanski 2000). A challenge for further empirical research is to analyze host–parasitoid relationships in communities of several coexisting checkerspot species and to relate such studies to predictions of the processes thought to maintain community structure.

Parasitoid Life-History Variation

Patterns of life-history variation within and among animal and plant populations reflect interactions and environmental conditions that are ecologically important. Parasitoids of checkerspots find their hosts in a range of habitats and use hosts with different phenologies. Some northern populations take several years to develop; most populations in central Europe and North America are univoltine, and southern populations are multivoltine (Tolman and Lewington 1997). There are checkerspot species that diapause in winter when it is cool and in summer during summer drought, and there are populations in which diapause is variable (chapters 7 and 11). The larvae feed on many plant species including herbs and shrubs, annuals and perennials, and the landscapes in which the host butterflies live range from vast open grasslands in Asia (I. Hanski pers. obs.) to highly fragmented meadows such as in the Åland Islands (chapter 4). *Cotesia* use conspecific host individuals ranging in size from tenths of milligrams to hundreds of milligrams, depending on the host instar. Therefore, although a parasitoid may have a narrow host range, it is able to use the host species under a variety of environmental and physiological conditions.

Characteristics of life history and behavior are likely to differ among populations of a single parasitoid species because natural selection on characters affecting longevity, fecundity, mating, and dispersal in each population may lead to local or regional specialization. Indeed, researchers have found genetic differences in life-history and behavioral traits among natural populations of parasitoids. For example, Ellers and van Alphen (1997) showed that the ratio of lipid storage to egg production differed among populations of the parasitic fly *Asobara tabida*, and Fleury et al. (1995) found differences in diurnal activity patterns among populations of the parasitoid *Leptopilina heteroma* collected from different latitudes. There are several examples of *Cotesia* populations differing in their searching behavior and attraction to the food plant species used by the host (Kester and Barbosa 1994, Benrey et al. 1997, van Nouhuys and Via 1999).

The extent to which checkerspot-specializing parasitoids have adapted to the particulars of their hosts deserves further study. For example, it would be interesting to know whether parasitoids of unrelated gregarious web-building caterpillars, such as the specialist parasitoid of the forest tent caterpillar *Malacosoma disstria* (Roland and Taylor 1997), behave like *Cotesia* attacking checkerspots. It is interesting that an unrelated specialist parasitoid of the forest moth *Hyphantria cunea* does attend the gregarious larval nests of their hosts for days (Morris 1976) like some *Cotesia* of checkerspots do. The costs and benefits of living in groups have been addressed to some extent using checkerspot larvae (chapter 7), but the costs and benefits for parasitoids of using a group-living host have not. We know that parasitism of *M. cinxia* and *E. phaeton* increases with the size of the host larval group (Stamp 1981a, Lei and Camara 1999), and *Cotesia* adults observed in the field appear to be unhindered by the silken web spun by the host larvae. However, inexplicably, they parasitize only a small fraction of the larvae available (Stamp 1982b, Lei et al. 1997). Finally, *Cotesia* parasitizing checkerspots often form very small local populations, which raises questions about mating behavior, possible inbreeding depression, and sex ratio (Crozier 1977, Kaitala and Getz 1992, Antolin 1999, Fauvergue et al. 1999).

The other side of the story is life histories of host butterflies evolving in response to their interaction with parasitoids (section 8.1). Although demonstrating host life-history evolution in experiments would be difficult, one can use the comparative approach to test predictions based on our knowledge of the host–natural enemy interaction and the biology of the species. For instance, the group-living behavior of checkerspot larvae, which shows great variation within and among the species (chapter 11) and which may have evolved in response to mortality caused by natural enemies, would be an interesting topic for comparative research. In another vein, parasitism of *E. aurinia* by *C. bignellii* late in the season has been shown to lead to a male-biased butterfly population (Porter 1984). How common such an effect might be is unknown, but butterfly dynamics are greatly influenced by adult sex ratio (chapter 5).

Parasitoid Phylogenies and Host Range

The host range of a parasitoid is influenced by the physiology, phenology, feeding niche, host food plant, habitat type, and evolutionary history of potential host species (Shaw 1994). Of the well-known Old World species, *Cotesia melitaearum* and *C. acuminata* use many checkerspot species feeding on different host plants over a large geographic area, whereas *C. bignellii* and *C. cynthia* appear to be entirely species specific (table 8.2). However, recent molecular results suggest that the picture is more complicated (M. Kankare and M. Shaw pers. comm.). For instance, a distinct haplotype of *C. melitaearum* has been reared from *Melitaea athalia* in the Åland Islands. These individuals have not been observed to parasitize *M. cinxia* (S. van Nouhuys pers. obs.); hence there may be two cryptic species using the two syntopic checkerspots in the Åland Islands. *Cotesia acuminata* is also likely to include two or several species using different host butterflies (M. Kankare and M. Shaw pers. comm.). Further studies will show the extent to which *Cotesia* associated with checkerspots have evolved or perhaps speciated in concert with their hosts. In other cases, parasitoids may have been specialized at least locally to host plant chemistry or habitat type rather than to host species. It will be particularly exciting to examine *Cotesia* in communities of many checkerspot species in which strong ecological dynamics may become intimately intertwined with local adaptation.