Wasp behavior leads to uniform parasitism of a host available only a few hours per year

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The parasitoid wasp, *Hyposoter horticola*, parasitizes a nearly fixed fraction of its host butterfly larvae within a host metapopulation of 300–500 local populations in a 50 × 70-km area. We show, through laboratory observation, that the wasp lays eggs in fully developed larvae that have not yet hatched from the egg, constraining the period of host vulnerability to several hours out of the host's one year lifecycle. The parasitoid achieves a persistent high rate of parasitism over the entire host range despite the extremely limited period of host vulnerability as well as a high rate of host population extinctions and colonizations of new habitat patches every year. It does this in part by being extremely mobile. In addition, we show by using a field experiment and observation of marked wasps foraging for hosts in natural populations, that the wasp finds virtually all host egg clusters in the weeks before the hosts become vulnerable to parasitism, and then later returns to parasitize them. By locating the hosts before their vulnerability, the wasp extends the time available for searching from hours to weeks. After parasitizing about one-third of the larvae in a host cluster the wasp stops, apparently leaving a mark that deters further parasitism by other individuals. The result of this novel combination of mobility and local foraging behavior is a stable population size despite an unstable host that is vulnerable during about one thousandth of its lifecycle. *Key words:* egg parasitism, host marking, *Hyposoter horticola*, *Melitaea cinxia*, population dynamics, spatial learning. *[Behav Ecol 15:661–665 (2004)]*

Host-parasitoid interactions persist via physiological, behavioral, ecological, and epidemiological mechanisms. Parasitoids are limited by host physiological resistance (Fellowes and Godfray, 2000; Quicke, 1997) and behavioral defense or avoidance (Allen, 1990; Briggs and Latto, 1996; Hunter, 2000; Potting et al., 1999; Stamp, 1982), as well as by phenological mismatch (Godfray et al., 1994; Münster-Swendson and Nachman, 1978; van Nouhuys and Lei, 2004) and host density or distribution (Allen, 1990; Godfray, 1994; Lei and Hanski, 1997). Parasitoids overcome these defenses through diverse mechanisms, including virulence and suppression of host immune response (Godfray, 2000; Quicke, 1997), and host regulation (see Moore, 1989), elaborate host finding and handling behavior (Shaw, 1993; Yeargan and Braman, 1986), aggregation (Godfray, 1994; Waage, 1983), learning (Papaj and Lewis, 1993), and unusual life histories (Godfray, 1994; Waage, 1986). Although several of these mechanisms of interaction have been studied in detail, such as parasitoid use of host associated odors (Thaler, 1999; Turlings et al., 1993), and host resistance (Godfray, 2000; Henter, 1995; Quicke, 1997), the mechanisms at play in most host-parasitoid interactions remain unknown (Quicke, 1997; Shaw, 1994), as do their consequences for large scale population dynamics.

The parasitoid, *Hyposoter horticola* (Ichneumonidae: Campopleginae), uses a single species of host butterfly, *Melitaea cinxia* (Lepidoptera: Nymphalidae), in the Åland islands of southwest Finland. The wasp is found throughout the islands and has a consistent population size one-third that of the hosts (van Nouhuys and Hanski, 2002a,b). The spatial and temporal uniformity of parasitism by *H. horticola* is unusual for a parasitoid with a narrow host range (Jones et al., 1994) to a large extent because, at least in a seasonal setting, their success depends entirely on the availability and successful use of a single or limited number of host species, and changes in their population sizes lag behind that of their hosts (Hawkins, 2000). A parasitoid using many host species can compensate for a decrease in abundance of one host by using another.

In search of an explanation of the anomalous pattern of parasitism by a parasitoid with a narrow host range, we investigated the host-finding and host use behavior of adult female *H. horticola*. It has previously been shown that *H. horticola* occupies virtually all host populations in Åland despite extreme habitat fragmentation and a high rate of host population turnover (frequent local extinctions and colonizations of new populations each year) in part because the wasp is extremely mobile, successfully dispersing to both newly colonized and isolated host populations (van Nouhuys and Hanski, 2002a,b). In the present study, we show that wasps find virtually all hosts in a population. However, by observing female *H. horticola* in the laboratory, we find that individual hosts are only available for parasitism for a few hours during their 1-year lifecycle, and only about one-third of the hosts can be parasitized even though they are found by the wasp. This provides a further constraint to parasitism by *H. horticola*. We present observations of marked individuals in the field and a field experiment designed to test the hypothesis that the wasp achieves a high rate of parasitism despite these constraints by locating hosts before they become available for parasitism. This increases the time available for finding hosts from a few hours to several weeks.

METHODS

Natural history

The host butterfly, *M. cinxia*, is an endangered European checkerspot butterfly. In the Åland Islands in southwest Finland, the butterfly persists as a well-studied group of local populations, a classical metapopulation (Hanski, 1999). In this region there are about 4000 suitable habitat patches (open meadows) in an area of 50 × 70 km, 300–500 of which are occupied by small butterfly populations. The butterfly lays

eggs in clusters of 100–200 on the underside of the leaves of its food plants (*Plantago lanceolata* and *Veronica spicata*) in June. An occupied habitat patch has, usually, one to 10 egg clusters that are visually inconspicuous and widely scattered over the patch (typically 0.1–0.5 ha). Upon hatching, larvae live gregariously in silken nests until just before pupation the following spring. The butterfly populations have a high rate of turnover, with an average of about 35% of the local populations newly colonized, and with about 35% of the populations going extinct in a given year. As expected, the smallest populations have the highest probability of extinction (Hanski et al., 1994; Nieminen et al., 2004).

The parasitoid *H. horticola* is restricted to using Melitaeine butterflies as hosts, and uses only *M. cinxia* as a host in the Åland islands (van Nouhuys and Hanski, 2004). Similar to other members of the subfamily Campopleginae, *H. horticola* lays eggs in host larvae and develops as a Koinobiont endoparasitoid (Goulet and Huber, 1993). Single eggs are laid in first instar *M. cinxia* larvae, and the developing wasp resides in the host through the hosts' larval development, including winter diapause, until pupation late the following spring. The wasp pupates within the host integument and, in the Åland islands, emerges as an adult in June while the host butterflies are adults (Lei et al., 1997; van Nouhuys and Hanski, 2004).

Measurement of parasitism in the field

To measure the pattern of parasitism within and among host populations, 67 plants with host egg clusters on them were placed in natural populations during the *H. horticola* flight period and then returned as hatched larvae to the laboratory for dissection. The dissected larvae were scored as parasitized by *H. horticola* or unparasitized. The egg clusters placed in the field were produced by female butterflies from a laboratory colony that were caged with host food plants which had been transplanted into pots from natural populations. In 1999, 32 egg clusters were placed in eight different host populations. Eleven clusters were placed in six host populations in 2000, and finally, 24 clusters were placed in two populations in 2001.

Observation of adult wasps in the laboratory

We observed *H. horticola* parasitizing *M. cinxia* in the laboratory to (1) identify the host stage vulnerable to parasitism, (2) identify which hosts within clusters were vulnerable to parasitism, (3) measure the time individual wasps spent parasitizing host clusters, (4) find out whether wasps visit previously parasitized clusters, and (5) measure the per cluster rate of parasitism. The 30 female *H. horticola* used for laboratory observation were collected in 2001 and 2002 from natural populations while still in the host larvae. Upon emergence, the adult female wasps were kept in mesh cages and fed nectar from fresh flowers and a solution of honey/water, 1:2. We observed the behavior of the wasps parasitizing *M. cinxia* on potted host plants in 0.3 × 0.3 × 0.5-m mesh cages, and dissected host *M. cinxia* larvae to measure the rate of parasitism.

Field observation of adult wasps

Forty-five *H. horticola* were collected as parasitized host larvae from a population in a large (1.5 ha) habitat patch in the spring of 2001. Upon emergence, adult female wasps were marked individually with small spots of paint on the ventral surface of the thorax between the wings. Males were each given identical marks. After marking, the wasps were released back into the patch from which they were collected as larvae. To observe the behavior of wasps upon their encounter with the hosts, eight pairs of host food plants containing host egg clusters from the laboratory were transplanted into the habitat patch and observed daily for 3 weeks (24 June–16 July 2001). The frequency and duration of visits to the focal hosts, by both marked and naturally occurring *H. horticola*, were recorded, along with the behavior of wasps while on or near the host plants.

Experimental test of parasitoid host finding behavior

Two habitat patches occupied by both the butterfly and the parasitoid were divided into 144 and 132 quadrants (2 × 2 m) in the spring of 2001. We estimated, based on the number of host caterpillars in the spring, that there were approximately 40 wasps in the first and 35 wasps in the second population. Twenty quadrants in each patch were randomly assigned to receive transplanted food plants containing 1-week-old egg clusters (long-tenure eggs), and 10 other 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 from a laboratory colony on potted food plants collected from the field. Long-tenure eggs were placed in the field 19–22 June 2001 and hatched from 1–4 July. Week-old clusters were used rather than newly laid eggs to avoid loss owing to predation. Short-tenure eggs were placed in the field 28 June–4 July by 0900 h, when they began to very slightly darken, several hours before they became susceptible to parasitism. This assured that both cluster types were available for the entire time that they were vulnerable to parasitism. Before being put in the field, the short-tenure eggs were kept outside the laboratory so their development was synchronized with that of the long-tenure eggs. 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.

RESULTS

Rate of parasitism in the field

Parasitism of *M. cinxia* by *H. horticola* is remarkably constant throughout the Åland Islands. *H. horticola* is present in virtually every host population (van Nouhuys and Hanski, 2002a), and also finds most larval groups within each host population and parasitizes about one-third of the individuals in each. In 1999 all 32 egg clusters that had been placed in eight different host populations were parasitized. Eleven out of 13 clusters placed in six host populations in 2000 were parasitized, and finally, all 24 clusters placed in two populations in 2001 were parasitized. The fraction of larvae parasitized in each cluster in the field was about 30%, 10% at the lowest and 63% at the highest (Figure 1a,b). Previous studies, in which numerous *H. horticola* have been reared from *M. cinxia* larvae collected from natural populations in Åland, corroborate our finding that larvae from almost every population and egg cluster are parasitized, and they are parasitized at a rate of 30–40% (Lei et al., 1997; van Nouhuys and Hanski, 2002b).

Laboratory observation of parasitism of *M. cinxia* by *H. horticola*

Surprisingly, *M. cinxia* is susceptible to parasitism by *H. horticola* only while the host is a fully developed first instar larva that has not yet broken out of the eggshell (Figure 2a,b). Individual hosts are vulnerable for less than 1 h to several hours, and the hosts from a single egg cluster hatch gradually over several hours to a day. Before this stage, the wasp is interested in eggs, occasionally probing them with her ovipositor, but does not parasitize them. Immediately afterward, when the larvae have
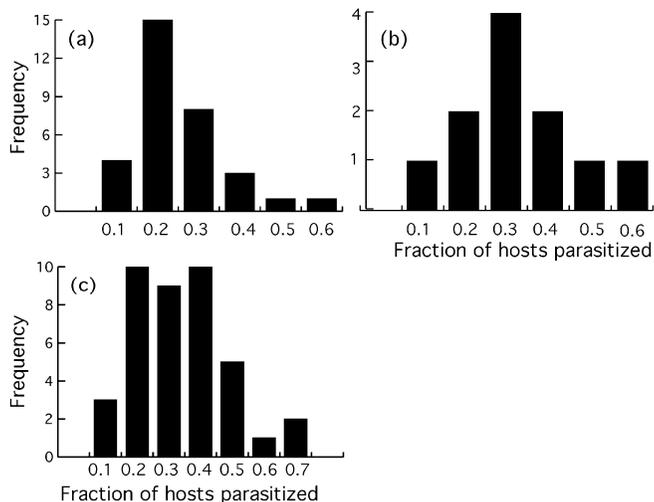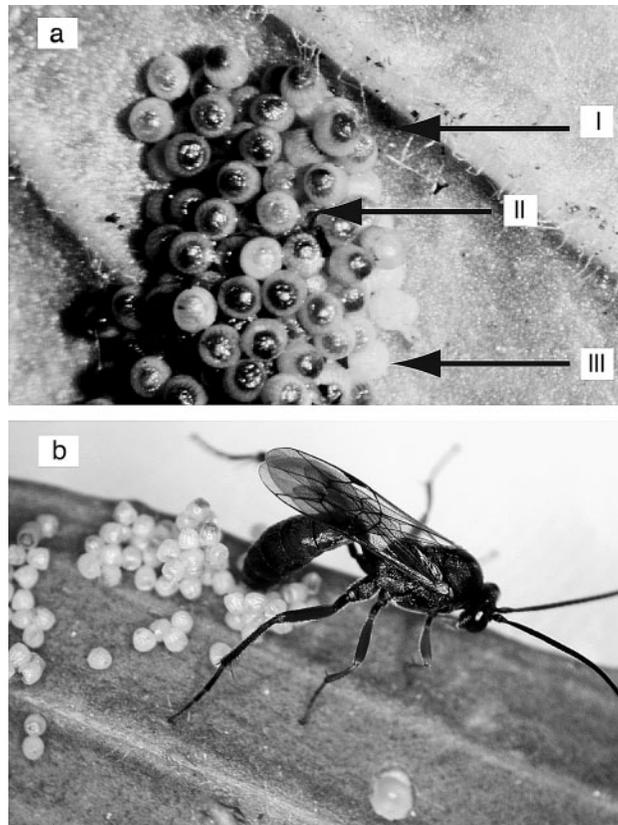
Figure 1
The fraction of larvae parasitized by *H. horticola* in each *Melitaea cinxia* egg cluster in 32 clusters parasitized in 8 host populations in the field in 1999 (a), 11 clusters parasitized in 6 populations in the field in 2000 (b), and 40 clusters (c), each parasitized by a single female in the laboratory.

Figure 2
(a) Maturing *M. cinxia* butterfly egg cluster containing soon-to-hatch dark topped eggs vulnerable to parasitism (1), light brown eggs not yet vulnerable (2), and bright yellow eggs with no sign of the maturing larvae inside (3). (b) The parasitoid wasp *H. horticola* parasitizing a cluster of *M. cinxia* eggs.

hatched, the wasp appears to have no interest. Under laboratory conditions a wasp spends 30 min to 1 h parasitizing eggs in a single cluster ($N = 50$ parasitism events observed; mean = 38 min; SD = 11). At any one instant, only a fraction of the host larvae in a cluster are sufficiently developed but unhatched (Figure 2a), so a wasp present for less than an hour has access to only a fraction of the hosts in an egg cluster. *H. horticola* is able to reach the interior of egg clusters by using the abdomen to move eggs on the surface, and we found an equal rate of parasitism among hosts from the interior and surface layers of eggs ($N = 11$ clusters; $48 \pm 11\%$ of surface eggs; $43 \pm 8\%$ of interior eggs).

Once a wasp had stopped parasitizing an egg cluster, she groomed, walked back and forth dragging her abdomen across the egg cluster and surrounding leaves for several minutes, and then flew away. On none of the 14 occasions that we presented host egg clusters that had been parasitized to a second individual did the second wasp attempt to parasitize the eggs. In four cases the second wasp palpated the eggs briefly with her antennae, and in the remaining trials the wasp did not approach the parasitized host cluster. Each of the wasps used had experienced parasitizing during the previous days, and these that were tested (six) subsequently parasitized egg clusters that had not been visited previously. The fraction of larvae parasitized per egg cluster by single wasps in the laboratory is similar to that found in the field (Figure 1), suggesting that each of the parasitized hosts in a cluster in a natural population is the offspring of a single wasp during one visit.

Observation of *H. horticola* visiting *M. cinxia* in the field

Of the 45 wasps we marked and released for observation, we were able to identify individual marked female wasps landing on or near the focal food plants, and observe their behavior and the behavior of naturally occurring individuals on and around the egg clusters. None of the 17 marked males was observed after release. Of the 28 marked females, six were seen on multiple occasions over 3 weeks both visiting new egg clusters and visiting previously visited egg clusters. Eleven others were seen visiting host egg clusters only on 1 day. One marked female was observed both in the original host

population and in a nearby one, several hundred meters away. In addition, we observed unmarked wasps, most likely originating from other host populations, visiting the focal host plants on 21 occasions. The maximum life-span recorded was 32 days, which is consistent with the observation that adult female *H. horticola* live about 1 month when kept under sheltered ambient conditions with access to honey and nectar (Lei et al., 1997). We have observed *H. horticola* visiting host egg clusters in natural populations early in the season while adult butterflies are still laying eggs, through to the end of the egg hatching period.

Experimental test of foraging behavior by *H. horticola*

Our observations of parasitoid behavior led us to hypothesize that *H. horticola* locates young egg clusters and uses information gained in that encounter to return to them later on, when the eggs become susceptible to parasitism. In both replicates of the field experiment designed to test this hypothesis a higher fraction of long-tenure egg clusters (placed in the field 1 week after butterfly oviposition) than the short-tenure egg clusters (placed in the field only just before becoming susceptible) were parasitized (78% long-tenure versus 20% short-tenure; Table 1; the difference between observed and expected cell counts using Fisher's Exact test for site ID 119, $P = .005$; and for site ID 41, $P = .006$). If wasps were to search randomly, an equal fraction of egg clusters in each category would be parasitized. These results demonstrate that the presence of host eggs before their susceptibility is advantageous for *H. horticola*.

Table 1

Observed and expected ( ) parasitism of *M. cinxia* egg clusters by *H. horticola*

	Field tenure*	Parasitized	Unparasitized
Site ID 119	long	11 (7.4)	5 (8.6)
	short	1 (4.6)	9 (5.4)
Site ID 41	long	11 (7.6)	1 (4.4)
	short	3 (6.4)	7 (3.6)

There were initially 20 egg clusters in each long-tenure treatment, some of which were eaten by predators or desiccated prior to the end of the experiment. There were 10 egg clusters in each short-tenure treatment.

DISCUSSION

Theoretical models of persistent host-parasitoid (or predator-prey) interactions often predict asynchronous fluctuation of population sizes of each species over time and (or) space (Hassell, 2000), and the population sizes of parasitoids with narrow host ranges indeed fluctuate greatly (Hochberg and Ives, 2000; Maron and Harrison, 1997; Murdoch, et al., 1984; Roland and Taylor, 1997; Várkonyi et al., 2002). For example, the second specialist parasitoid of the butterfly *M. cinxia* in the Åland Islands, *Cotesia melitaearum* (Wilkinson; Hymenoptera: Braconidae), is present in only a fraction of host populations, fluctuates greatly in population size, and can contribute to or causes local host population extinctions (Lei and Hanski, 1997; van Nouhuys and Tay, 2001).

H. horticola, instead, maintains a population size one-third the size of the hosts. This pattern can be explained by their dispersal, host finding, and host use behavior. First, as mentioned previously, *H. horticola* is present in practically every host population by being dispersive (van Nouhuys and Hanski 2002a). Once in a population, the wasps are able to find and parasitize hosts in essentially all egg clusters by locating them before they become available for parasitism, increasing the time available for host searching from hours to weeks. There are two possible mechanisms by which parasitism by *H. horticola* is increased by their exploration of host eggs that are not yet vulnerable to parasitism. First the wasps may deposit a long-range and long-term marker on the eggs that that they later use to orient to the mature eggs. Second, the wasps may learn the spatial locations of the egg clusters. We believe that spatial learning is a more plausible explanation than is marking, although an experiment would have to be conducted to distinguish between the two explanations before the true mechanism is known.

Long-range marking, rather than learning, is an unlikely mechanism because the distances between clusters is tens and frequently hundreds of meters. Known parasitoid markers are nonvolatile or short range and water-soluble, and host and patch marking is known only as a deterrent (Godfray, 1994; Nufio and Papaj, 2001; Quicke, 1997) rather than as an attractant. In addition, marking would make the eggs known to conspecific parasitoids, which would be detrimental in highly competitive setting. There are no examples of true parasitoids learning the locations of unused resources (host individuals) and visiting them repeatedly. However, many elegant studies of aculeate Hymenoptera (bees, predatory wasps, and ants) demonstrate their use of spatial memory to move between their nests and food (Collett and Lehrer, 1993; Gould, 1986; Rosenheim, 1987; Wehner and Räber, 1979; Zeil et al., 1996), and parasitoids (nonaculeate Hymenoptera) are known to learn odors, colors, and shapes and patterns associated with prey (Turlings et al., 1993; Wäckers and Lewis, 1999), and even

to avoid previously searched (but empty) host feeding sites (Sheehan et al., 1993).

A parasitoid population cannot persist if all hosts are parasitized. In this case, a majority of the hosts in each egg cluster remains unparasitized. This happens in part because the hosts within an egg cluster mature asynchronously. Although parasitoids all lay eggs in or on a specific life stage of their host (Quicke, 1997), and host phenology is known to influence the rate of successful parasitism at the population level (Godfray et al., 1994; van Nouhuys and Lei, 2004), we are not aware of any other examples of parasitoids depending on such a short interval of individual host development. Moreover, we found no examples in the literature of a larval parasitoid using a host that had not yet hatched from the egg. This behavior limits the amount of time the host is susceptible to parasitism, but it may confer a competitive advantage over later arriving larval parasitoids (Godfray, 1994; Salt, 1961). Furthermore, the parasitoid may avoid encapsulation by the host by entering before the larval immune system is functional (Quicke, 1997).

H. horticola avoids larval defense but is still confronted with the defense of the egg. The eggshell appears to be too tough for the ovipositor to penetrate throughout most of the egg stage. However, as the first instar larva prepares to leave the shell weakens and the wasp ovipositor easily penetrates. Egg clustering is known to render host individuals of some species physically inaccessible to egg parasitoids (Friedlander, 1985; Hondo et al., 1995; Weseloh, 1972). *M. cinxia* egg clusters are usually several layers thick. We have shown that physical inaccessibility of eggs within a cluster is not a constraint for *H. horticola*. The wasp equally successfully reaches eggs both at the surface of the cluster and within.

Not only are individual hosts available for a short time, but the ovipositing wasp spends only one half an hour parasitizing hosts in an egg cluster. Upon departure, she apparently leaves an odor mark that deters herself and conspecifics from visiting the egg cluster. Many parasitoids mark parasitized hosts, thus avoiding superparasitism by themselves and conspecifics (Godfray, 1994; Sheehan et al., 1993; van Lenteren, 1981). True egg parasitoids are known to sometimes mark the entire group while parasitizing only a fraction of the individuals in the group (Roitberg and Mangel, 1988). We do not know why *H. horticola* leaves after parasitizing only a fraction of eggs rather than wait for the remaining eggs in a cluster to mature. Perhaps an individual wasp leaves because mortality of entire host groups is high (Kuussaari et al., 2004) so the wasp may benefit by parasitizing many different egg clusters (Krebs and McCleery, 1984), and not putting all of her "eggs in one basket" (but for an argument against the evolution of intra-generational bet hedging except at very small population sizes, see Hopper et al., 2003).

REFERENCES

Allen GR, 1990. Influence of host behavior and host size on the success of oviposition of *Cotesia urabae* and *Dolichogenidea eucalypti*. J Insect Behav 3:733–749.

Briggs CL, Latto J, 1996. The window of vulnerability and its effect on relative parasitoid abundance. Ecol Entomol 21:128–140.

Collett TS, Lehrer M, 1993. Looking and learning: a spatial pattern in the orientation flight of the wasp *Vespula vulgaris*. Proc R Soc Lond B 252:129–134.

Fellowes MDE, Godfray HCJ, 2000. The evolutionary ecology of resistance to parasitoids by *Drosophila*. Heredity 84:1–8.

Friedlander TP, 1985. Egg mass design relative to surface-parasitizing parasitoids, with notes on *Asterocampa clyton* (Lepidoptera: Nymphalidae). J Res Lepidoptera 24:250–257.

Godfray HCJ, 1994. Parasitoids: behavioural and evolutionary ecology. Princeton, New Jersey: Princeton University Press.

Godfray HCJ, 2000. Host resistance, parasitoid virulence, and population dynamics. In: Parasitoid population biology (Hochberg ME, Ives AR, eds). Princeton, New Jersey: Princeton University Press; 121–138.

Godfray HCJ, Hassell MP, Holt RD, 1994. The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. J Anim Ecol 63:1–10.

Gould JL, 1986. The locale map of honey bees: do insects have cognitive maps? Science 232:861–863.

Goulet H, Huber JT, eds., 1993. Hymenoptera of the world: an identification guide to families. Ottowa: Center for Land and Biological Resources Research, Ottowa Agricultural Research Branch Canada.

Hanski I, 1999. Metapopulation ecology. Oxford: Oxford University Press.

Hanski I, Kuussaari M, Nieminen M, 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762.

Hassell MP, 2000. The spatial and temporal dynamics of host-parasitoid interactions. London: Oxford University Press.

Hawkins BA, 2000. Species coexistence in parasitoid communities: does competition matter? In: Parasitoid population biology (Hochberg ME, Ives AR, eds). Princeton, New Jersey: Princeton University Press; 198–214.

Henter HJ, 1995. The potential for coevolution in a host-parasitoid system, 2: genetic variation within a population of wasps in the ability to parasitize an aphid host. Evolution 49:439–445.

Hochberg ME, Ives AR, eds., 2000. Parasitoid population biology. Princeton, New Jersey: Princeton University Press.

Hondo M, Onodera T, Morimoto N, 1995. Parasitoid attack on a pyramid shaped egg mass of the Peacock butterfly *Inachis io* geisha (Lepidoptera: Nymphalidae). Appl Entomol Zool 30:271–276.

Hopper RK, Rosenheim JA, Oppenheim SJ, 2003. Within-generation bet hedging: a seductive explanation? Oikos 101:219–222.

Hunter AF, 2000. Gregariousness and repellent defenses in the survival of phytophagous insects. Oikos 91:213–224.

Jones TH, Hassell MP, May RM, 1994. Population dynamics of host-parasitoid interactions. In: Parasitoid community ecology (Hawkins BA, Sheehan W, eds). Oxford: Oxford University Press; 371–396.

Krebs JR, McCleery RH, 1984. Optimization in behavioural ecology. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific; 91–121.

Kuussaari M. van Nouhuys S, Hellmann J, Singer MC, 2004. Larval biology of checkerspot butterflies. In: On the wings of checkerspots: a model system for population biology. (Ehrlich PR, Hanski I, eds). Oxford: Oxford University Press; 138–160.

Lei GC, Hanski I, 1997. Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos 78:91–100.

Lei GC, Vikberg V, Nieminen M, Kuussaari M, 1997. The parasitoid complex attacking the Finnish populations of Glanville fritillary *Melitaea cinxia* (Lep: Nymphalidae), an endangered butterfly. J Nat Hist 31:635–648.

Maron JL, Harrison S, 1997. Spatial pattern formation in an insect host-parasitoid system. Science 278:1619–1621.

Moore SD, 1989. Regulation of host diapause by an insect parasitoid. Ecol Entomol 14:93–98.

Münster-Swendson M, Nachman G, 1978. Asynchrony in host-parasite interaction and its effect on stability, studied by a simulation model. J Anim Ecol 47:159–171.

Murdoch WW, Reeve JD, Huffaker CB, Kennett CE, 1984. Biological control of olive scale and its relevance to ecological theory. Am Nat 123:371–392.

Nieminen M, Siljander M, Hanski I, 2004. Structure and dynamics of *Melitaea cinxia* metapopulations. In: On the wings of checkerspots: a model system for population biology. (Ehrlich PR, Hanski I, eds). Oxford: Oxford University Press; 63–91.

Nufio CR, Papaj DR, 2001. Host marking behavior in phytophagous insects and parasitoids. Entomol Exp Appl 99:273–293.

Papaj DR, Lewis AC, Eds, 1993. Insect learning: ecological and evolutionary perspectives. New York: Chapman & Hall.

Potting RPJ, Vermeulen NE, Conlong DE, 1999. Active defense of herbivorous hosts against parasitism: Adult parasitoid mortality risk involved in attacking a concealed stemboring host. Entomol Exp Appl 91:143–148.

Quicke DLJ, 1997. Parasitic wasps. London: Chapman and Hall.

Roitberg BD, Mangel M, 1988. On the evolutionary ecology of marking pheromones. Evol Ecol 2:289–315.

Roland J, Taylor PD, 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710–713.

Rosenheim JA, 1987. Host location and exploitation by the cleptoparasitic wasp *Argochrysis armilla*: the role of learning (Hymenoptera: Chrysididae). Behav Ecol Sociobiol 21:401–406.

Salt G, 1961. Competition among insect parasitoids. Symp Soc Exp Biol 15:97–119.

Shaw MR, 1994. Parasitoid host ranges. In: Parasitoid community ecology (Hawkins BA, Sheehan W, eds). Oxford: Oxford University Press; 111–144.

Shaw SR, 1993. Observations on the ovipositional behavior of *Neoneurus mantis*, an ant-associated parasitoid from Wyoming (Hymenoptera: Braconidae). J Insect Behav 6:649–658.

Sheehan W, Wäckers FL, Lewis WJ, 1993. Discrimination of previously searched, host-free sites by *Microplitis croceipes* (Hymenoptera: Braconidae). J Insect Behav 6:323–331.

Stamp NE, 1982. Behavioral interactions of parasitoids and Baltimore checkerspot caterpillars (*Euphydryas phaeton*). Environ Entomol 11: 100–104.

Thaler JS, 1999. Jasmonite-inducible plant defenses cause increased parasitism of herbivores. Nature 399:686–688.

Turlings TCJ, Wäckers, FL, Vet LEM, Lewis WJ, Tumlinson JH, 1993. Learning of host-finding cues by hymenopterous parasitoids. In: Insect learning: ecological and evolutionary perspectives (Papaj DR, Lewis AC, eds). New York: Chapman and Hall; 51–78.

van Lenteren JC, 1981. Host discrimination by parasitoids. In: Semiochemicals: their role in pest control (Nordlund DA, Jones AL, Lewis WJ, eds). New York: John Wiley; 153–180.

van Nouhuys S, Hanski I, 2002a. Colonisation rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. J Anim Ecol 71:630–650.

van Nouhuys S, Hanski I, 2002b. Multitrophic interactions in space: metacommunity dynamics in fragmented landscapes. In: Multitrophic level interactions (Tscharntke T, Hawkins BA, eds). Cambridge: Cambridge University Press; 124–147.

van Nouhuys S, Hanski I, 2004. Natural enemies of checkerspot butterflies. In: On the wings of checkerspots: a model system for population biology. (Ehrlich PR, Hanski I, eds). Oxford: Oxford University Press.

van Nouhuys S, Lei GC, 2004. Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. J Anim Ecol 73:526–535.

van Nouhuys S, Tay WT, 2001. Causes and consequences of mortality in small populations of a parasitoid wasp in a fragmented landscape. Oecologia 128:126–133.

Várkonyi G, Hanski I, Rost M, Itämies J, 2002. Host-parasitoid dynamics in periodic boreal moths. Oikos 98:421–430.

Waage JK, 1983. Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera, Ichneumonidae). Ecol Entomol 8:447–453.

Waage JK, 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: Insect parasitoids. (Waage JK, Greathead D, eds). London: Academic Press; 63–96.

Wäckers FL, Lewis WJ, 1999. A comparison of color-, shape- and pattern-learning by the hymenopteran parasitoid *Microplitis croceipes*. J Comp Physiol A 184:387–393.

Wehner R, Räber F, 1979. Visual spatial memory in dessert ants, *Cataglyphis bicolor*. Experimentia 35:1569–1571.

Weseloh RM, 1972. Influence of gypsymoth egg mass dimensions and microhabitat distribution on parasitism by *Ooencyrtus kuwanai*. Ann Entomol Soc Am 65:64–69.

Yeargan KV, Braman SK, 1986. Life history of the parasite *Diolcogaster facetosa* (weed) (Hymenoptera: Braconidae) and its behavioral adaptation to the defense response of a lepiopteran host. Ann Entomol Soc Am 79:1029–1033.

Zeil J, Kelber A, Voss R, 1996. Structure and function of learning flight in bees and wasps. J Exp Biol 199:245–252.