

Parasitoid–host metapopulation dynamics: the causes and consequences of phenological asynchrony

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Summary

1. The strength of interaction between the specialist parasitoid *Cotesia melitaearum* and the host butterfly *Melitaea cinxia* is influenced by the coincidence of the adult stage of the parasitoid with the larval stage of the host.
2. We show that there is great variation in this developmental synchrony among local populations and among years, ranging from complete synchrony to complete asynchrony.
3. The causal mechanism is early spring temperature, which affects parasitoid development differently than the development of the host.
4. At cool air temperatures the dark-coloured and mobile host larvae benefit from basking in the sun, while the white and immobile parasitoid cocoons develop slowly in shaded microclimates, becoming adults after hosts have pupated and are no longer available for parasitism. At warm temperatures many adult wasps emerge in time to parasitize host larvae.
5. We show that the host–parasitoid synchrony influences subsequent parasitoid population size and the rate of colonization of previously uninhabited host populations, contributing to parasitoid metapopulation dynamics.
6. We detected no direct effect of the phenological synchrony on local host population size, but the synchrony is likely to be important for overall host metapopulation dynamics via variation in the rate of colonization by the parasitoid.

Key-words: basking, butterfly, *Cotesia melitaearum*, *Melitaea cinxia*, thermoregulation.

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Introduction

For an interaction between a parasitoid and a host to persist the likelihood of all host individuals being parasitized must be low. Preservation of a part of the host population can be due to spatial distribution, physiological or behavioural defence, or it can come about as a result of temporal asynchrony of the vulnerable stage of the host and the adult stage of the parasitoid (Varley 1947; Hassell 1969; Cheng 1970; Godfray, Hassell & Holt 1994; Hochberg & Hawkins 1994; Hassell 2000). In climates with discrete generations the adult stage of a parasitoid coincides roughly with the vulnerable stage of the host (Schoonhoven 1962; Nealis 1988; Godfray 1994; Kaitaniemi & Ruohomäki 1999), but spatial and

temporal variation in phenological synchrony can cause fluctuation of population size, influence persistence (Varley 1947; Griffiths 1969; Hassell 1969; Weseloh 1976; Münster-Swendson & Nachman 1978; Craig, Itami & Price 1990; Godfray *et al.* 1994; Nakata 1995; Thireau & Regniere 1995) and contribute to community structure (Hawkins & Sheehan 1994; Briggs & Latto 1996).

Developmental rate of insects is controlled to a large extent by temperature. Insects control body temperature, and thus their metabolic and developmental rates, behaviourally, morphologically and physiologically (May 1979; Heinrich 1993). Caterpillars regulate their metabolism using colouration, morphology, physical location and behaviour to avoid or to absorb heat (Casey 1976; Casey *et al.* 1988; Fields & McNiel 1988; Joos *et al.* 1988; Weiss, Murphy & White 1988; Stamp & Bowers 1990a,b; Bryant, Thomas & Bale 2000; Frid & Myers 2002). Many dark-coloured caterpillars bask in the sun, increasing their body temperature far above ambient temperature (Porter 1982; Weiss *et al.* 1988; Stamp & Bowers 1990a; Casey 1993; Kuussaari *et al.* 2004). With increased body temperature comes increased growth rate, which generally decreases

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the amount of time spent as a larva. One of the advantages of fast larval development is a short period of vulnerability to larval predators and parasites (Evans 1982; Porter 1983; Clancy & Price 1987; Stamp & Bowers 1990a, b; Benrey & Denno 1997; Bryant *et al.* 2000).

The larvae of the *Melitaea cinxia* (L.) (Glanville fritillary butterfly) are gregarious, dark and bask in the sun, like their close relatives *Euphydryas aurinia* in the United Kingdom (Porter 1982, 1984) and *E. phaeton* in the Eastern United States (Stamp 1982). The wasp *Cotesia melitaearum* (Wilkinson) is a parasitoid of Melitaeine butterflies (van Nouhuys & Hanski 2004). As an egg and larva, the wasp experiences the same environment as the host because it is an internal parasitoid. Consequently, the wasp's rate of development changes with temperature in concert with that of the host (Gould & Elkinton 1990). However, a significant fraction of the life of the parasitoid is spent as a pupa, independent of the host. The parasitoid pupae are white, immobile and often occur in the shade (Lei *et al.* 1997; van Nouhuys & Hanski 2004). While the unparasitized host larvae may increase growth rate behaviourally by basking, the parasitoid cocoons cannot move, and hence their developmental rate depends on where they pupated.

We hypothesize that during cool but sunny early springs the host larvae benefit from basking in the sun while the parasitoid cocoons do not, so that by the time the parasitoid adults emerge most of their larval hosts have pupated and are no longer vulnerable to parasitism. This would cause the reproductive success of the parasitoid population to be low. During warm springs developmental rates of the two species would differ less, and hence more host caterpillars would be available upon emergence of adult parasitoids, and the reproductive success of the parasitoid would be relatively high. Porter (1983) suggests that a similar interaction occurs between the butterfly *E. aurinia* and the parasitoid *Cotesia bignellii* in one population in the United Kingdom. Here we test and extend the idea, using field survey and temperature data collected from 1993 to 2002 from multiple populations of *M. cinxia* occupied by *C. melitaearum* in the Åland Islands of SW Finland.

Materials and methods

NATURAL HISTORY

In the Åland Islands of south-western Finland the parasitoid *Cotesia melitaearum* parasitizes *M. cinxia* in a large metapopulation of 300–500 local butterfly populations in an area of 50 × 70 km. The butterfly persists as a classical metapopulation inhabiting semi-independent habitat patch networks (Lei *et al.* 1997; Hanski 1999; Nieminen, Siljander & Hanski 2004). Ten to 20% of the butterfly populations are occupied by *C. melitaearum* (van Nouhuys & Hanski 1999). The parasitoid can have a great impact on the host population dynamics, occasionally even driving local host populations to extinction (Lei & Hanski 1997), but currently the few *C. melitaearum*

populations in the Åland Islands remain small and prone to local extinction with little impact on the host (van Nouhuys & Tay 2001; van Nouhuys & Hanski 2002a).

The butterfly lays eggs in clusters on the food plants *Plantago lanceolata* and *Veronica spicata* in June. The larvae hatch and feed gregariously in a communal web until autumn, when they spin a dense silk tent and spend the winter in diapause. In spring the larvae continue to live gregariously until their last larval instar in mid-May, at which point they disperse to pupate (Kuussaari *et al.* 2004). The Åland Islands are located at the northern range limit of *M. cinxia* (Higgins & Riley 1970). The growing season is short and unpredictable, limited variously by late spring thaw, summer drought and early winter frost (Nieminen *et al.* 2004). *M. cinxia* larvae bask gregariously on sunny days throughout their development, but are most conspicuous as large black post-diapause larvae in spring (Kuussaari *et al.* 2004).

The parasitoid *C. melitaearum* has two to three generations during each host generation. The first generation of wasps lays one to two eggs in the first and second instar larvae in the summer. The second generation lays two to four eggs in the larvae ready for diapause in the autumn, and the third generation lays 10–40 eggs in the last or the penultimate instar in the spring (Fig. 1; Lei *et al.* 1997). The larval stage of the first parasitoid generation is often prolonged, resulting in no autumn generation (Saskya van Nouhuys, unpublished data).

The third generation of *C. melitaearum* parasitizes large *M. cinxia* larvae in the spring (Fig. 1). This generation is the only one that we can reliably monitor (Lei & Hanski 1997; Lei & Camara 1999; van Nouhuys & Tay 2001), and it is the most discrete. The success of this generation, in terms of the number of progeny produced, is extremely variable. The potential for wasp population increase is very high, because each parasitized *M. cinxia* larva hosts up to 40 developing wasps, and hundreds of the gregarious caterpillars in a population may be parasitized. However, the number of adult wasps available to lay eggs is generally small to begin with, because the rate of parasitism in the previous autumn is low (2–4% of larvae in parasitoid-occupied populations) (Lei *et al.* 1997) and there is often extremely high mortality of the parasitoid pupae due to hyperparasitism and predation (van Nouhuys & Tay 2001).

RELATIONSHIP BETWEEN AMBIENT TEMPERATURE AND HOST AND PARASITOID BODY TEMPERATURES

In the spring of 1999 we measured the ambient (air) temperature and surface temperatures of *C. melitaearum* cocoons and host larvae in 12 natural populations in order to compare relationship between ambient and body temperature for the host and the parasitoid. A digital thermometer with a copper wire thermistor probe was used to measure the surface temperature of each of the 115 *C. melitaearum* cocoons visited on the 14 sunny or partially sunny days between 27 April and 17 May. The

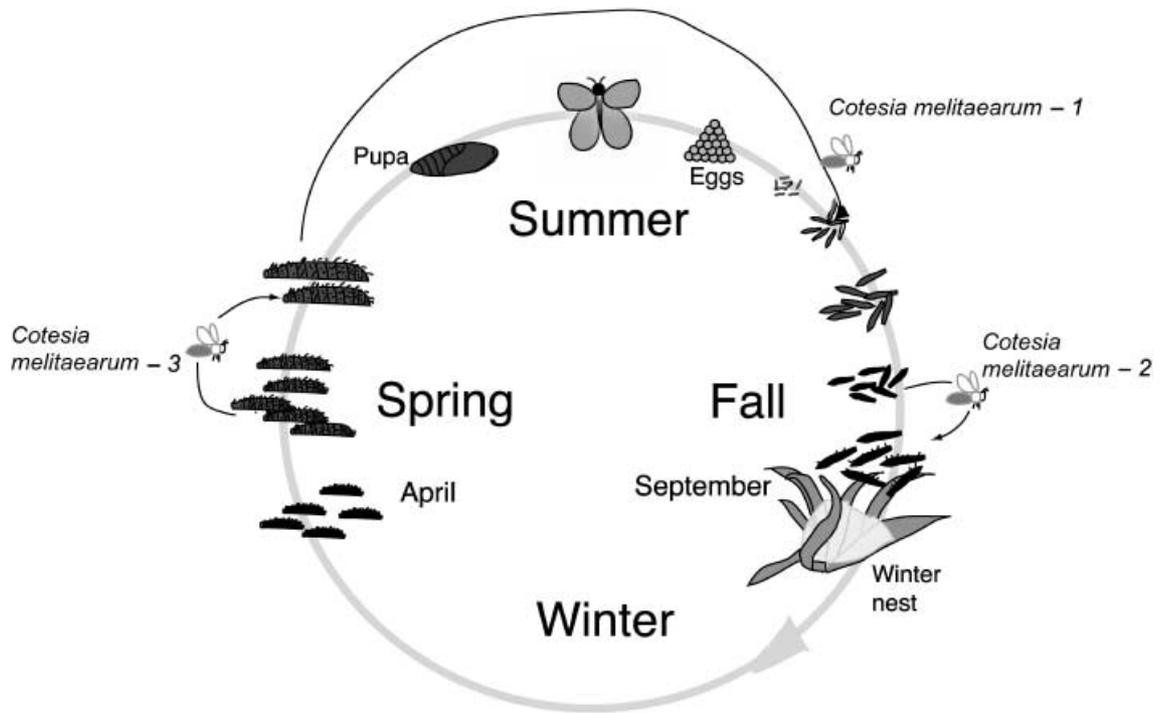


Fig. 1. The life cycle of the butterfly *Melitaea cinxia* and parasitoid *Cotesia melitaearum* in Åland, Finland.

temperature measurements were taken between 9 : 30 h and 18 : 00 h when the sky was clear or partly cloudy. The exposure (sun or shade) and location of each cocoon (in leaf litter, lichen, active or abandoned communal host web) was recorded, as well as the ambient air temperature in the shade. Additionally the surface temperatures of host caterpillars from the same nest were measured by pressing the thermistor probe against the body of the caterpillar. The locations of the caterpillars (basking outside of the communal web, within the web in the sun, within the web in the shade) was recorded. Because caterpillars from a single nest often bask in small groups in different locations, there was a total of 162 measurements of caterpillar temperatures. The surface temperatures of the host caterpillars and parasitoid cocoons were measured rather than the internal temperatures in order not to disturb them. There is only a small difference between the internal and surface body temperatures because the larvae and cocoons are small and ectothermic (May 1979). The differences between cocoon, caterpillar and ambient temperatures was tested using one tailed paired *t*-tests.

MEASUREMENT OF HOST AND PARASITOID DEVELOPMENT IN THE SPRING

Each spring from 1993 to 2002 *M. cinxia* nests were observed from late April, soon after the larvae broke diapause and began to feed, until pupation in mid-May. Every 3–5 days the developmental stage (instar) of the larvae in each larval group was recorded as well as the number remaining available for parasitism. We also counted the number of *C. melitaearum* cocoons and recorded when they became adult parasitoids, were eaten

by predators or were parasitized by the pseudohyperparasitoid *Gelis agilis* (detailed analysis of parasitoid survival in 1999 and 2000 is summarized in van Nouhuys & Tay 2001).

This procedure was followed in 117 host populations. During 1993–95 all the parasitoid populations studied were located close to each other as part of a single dense network of host populations. In 1996 and 1997 the parasitoid populations used were separated spatially more, and in 1998–2001 all parasitoid populations with host populations larger than three nests were used (Table 1). In spring 2002 the host and parasitoid population sizes were recorded in order to measure the performance of those populations observed in 2001.

ANALYSIS OF THE ASSOCIATION OF PHENOLOGICAL SYNCHRONY AND EARLY SPRING TEMPERATURE WITH HOST AND PARASITOID POPULATION SIZES

For each population we calculated the fraction of spring generation *C. melitaearum* reaching adulthood while at least some host larvae were available for parasitism (had not dispersed to pupate). This fraction ranged from 0, when the adult wasps were completely unsynchronized with the host population, to 1 when they were completely synchronized ($n = 117$, mean = 0.41, SD = 0.33). The wasp cannot reach adulthood too early because the hosts are available from when they break diapause until they pupate, and the parasitoids leave the hosts to pupate well after the hosts break diapause. The fraction of wasps able to parasitize was the measure of synchrony, and was used to predict the change in population size from one year to

Table 1. Summary of populations monitored from 1993 to 2000

Year	No. of populations	Distribution of populations	Daily temperature (°C) during parasitoid pupation	
			Average	Maximum
1993	9	1 network	10.9	16.7
1994	10	1 network	8.1	13.3
1995	2	1 network	4.9	8.6
1996	21	Several networks	6.0	10.1
1997	7	Several networks	6.3	10.6
1998	15	All networks	8.5	13.2
1999	20	All networks	5.1	9.4
2000	19	All networks	8.7	13.5
2001	14	All networks	8.3	13.3

the next for both the parasitoid and the host populations. Population size of the butterfly was measured as the number of larval groups in the spring, and population size of the parasitoid was measured as the number of host nests containing parasitized larvae in the spring. We used analysis of variance (PROC GLM, SAS Institute Inc. 1992), including year and the initial host and parasitoid population sizes and all interactions as predictor variables. The error terms were distributed normally. Some of the populations persisted over many years so they were censused multiple times. Consequently the 117 observations were not all independent. However, phenological synchrony was not correlated among years within populations censused multiple times. Furthermore, including population identity did not improve the fit of the model nor did a repeated-measures procedure. Treating the observations as independent rather than averaging the change in population size for each year allowed us to use all of our data and, importantly, to test our hypothesis over a wide range of host and parasitoid population sizes.

To test the hypothesis that the parasitoid was more successful following warm springs than following cool springs the average temperature during the period of cocoon development (25 April–15 May) was used to predict the performance (population size in the following year) of the parasitoid and the host using the statistical model described above. Early spring temperature data in central Åland from 1993 to 2001 were provided to us by the Meteorological Institute of Finland. We used the daily mean, maximum and minimum temperatures in our statistical analysis of changes in population sizes and parasitoid colonization rate, as well as to illustrate variation among years.

COLONIZATION OF HOST POPULATIONS BY *C. MELITAEARUM*

Possible association of annual parasitoid colonization rate with host–parasitoid phenological synchrony was measured using linear regression. The average daily maximum temperature in early spring (25 April–15 May) was used as an indicator of phenological synchrony. Parasitoid colonization rate was measured as the number

of host populations colonized divided by the number of possible source populations in the previous year. A colonization was defined as a host population found to be occupied by the wasp one spring but unoccupied in the previous spring. Only those habitat patch networks monitored for the parasitoid during consecutive years were included in the analysis. Seventy colonizations between spring 1994 and spring 2002 were included in the data set (for details of the data set used see van Nouhuys & Hanski 2002a). Yearly variation in the number of host populations available did not contribute significantly to the rate of colonization by *C. melitaeorum* because the number of parasitoid populations was always very small compared to the number of unoccupied host populations.

Results

REGIONAL AND LOCAL VARIATION OF AMBIENT TEMPERATURE

In the early spring when the parasitoid was developing to adulthood and the host larvae were growing to pupation the temperatures were usually low, with an average minimum of 3 °C and an average maximum of 12 °C between 1993 and 2002 (Fig. 2). There was significant variation among years. For example, whereas in 1993, the average daily maximum temperature was 16.7 °C between 20 April and 15 May, in 1995 the average daily maximum temperature during the same interval was only 8.6 °C (Table 1; Fig. 2).

RELATIONSHIP OF AMBIENT TEMPERATURE WITH HOST AND PARASITOID BODY TEMPERATURE

In the spring of 1999 there were *C. melitaeorum* cocoons for about 20 days. The ambient temperature, measured between 9 : 30 h and 18 : 00 h, ranged from 3.6 to 18.3 °C, and was on average 12.7 °C. During this period both the caterpillars and the cocoons were on average above ambient temperature (paired *t*-test, $n_{\text{caterpillar}} = 115$, $t_{\text{caterpillar}} = 20.6$, $P = 0.0001$; $n_{\text{cocoon}} = 107$, $t_{\text{cocoon}} = 13.7$, $P = 0.0001$), and both were warmer in the sun than in the shade

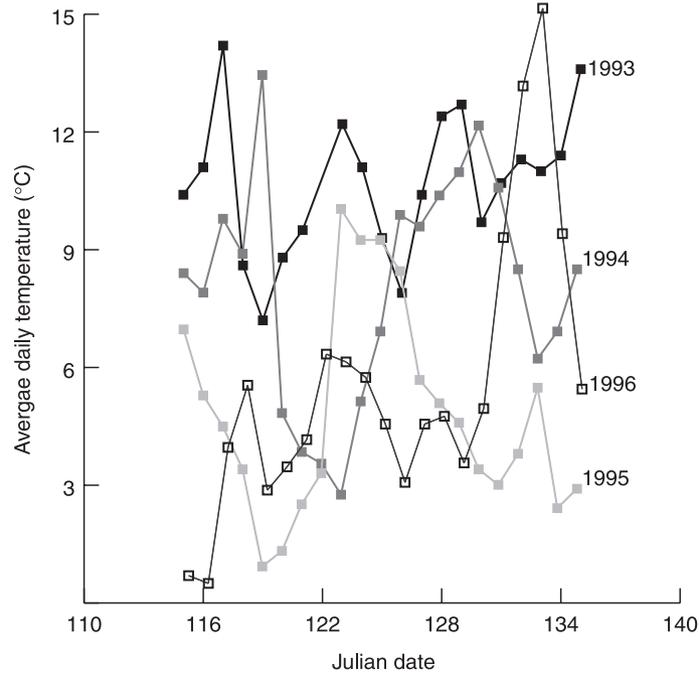


Fig. 2. Average temperature during *C. melitaeorum* pupation in the spring (25 April–15 May) during 4 years at the Jomala weather station in Åland.

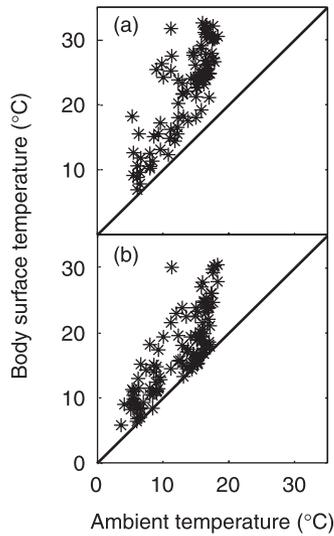


Fig. 3. Ambient versus surface temperature of (a) *M. cinxia* larvae and (b) *C. melitaeorum* cocoons measured on 115 visits to cocoons and associated unparasitized host larvae in 21 different populations during 14 days in early spring 1999.

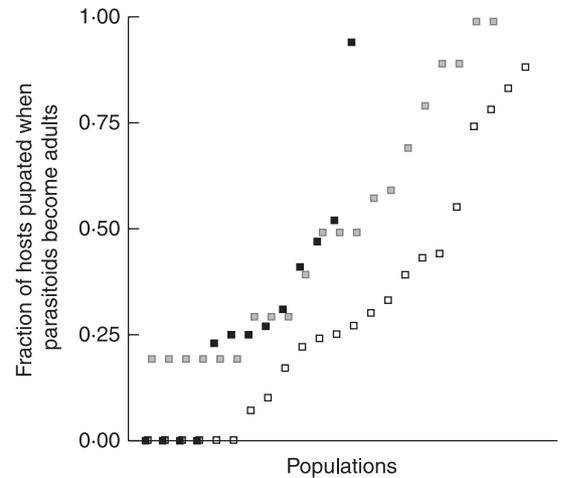


Fig. 4. The fraction of *M. cinxia* larvae that had already pupated (were no longer available for parasitism) when *C. melitaeorum* adults emerged in populations in 1993 (black squares), 1994 (open squares) and 1996 (grey squares). Each point is a population.

($P = 0.0001$). However, 80% of the caterpillars were found basking gregariously in the sun whereas only 30% of the cocoons were in the sun. The caterpillars were on average 3.3 °C warmer than the cocoons (Fig. 3a,b). Additionally, where cocoons and caterpillars were found in the sun together (both in the same web) the caterpillars were 2.8 °C warmer than the cocoons (paired t -test, $n = 13$, $t = 3.17$, $P = 0.008$). High ambient temperatures, above 16 °C, occurred during the middle of continuously sunny days. At these times the temperatures of both insect species increased sharply (Fig. 3).

PHENOLOGICAL SYNCHRONY,
 TEMPERATURE AND SUBSEQUENT
 POPULATION SIZE

The fraction of hosts available to adult *C. melitaeorum* varied greatly among populations and years. At one extreme it appeared that no hosts were available for parasitism by the time most of the *C. melitaeorum* became adults, while in other populations the majority of host larvae were still vulnerable to parasitism upon emergence of adults (Fig. 4). During warm early springs

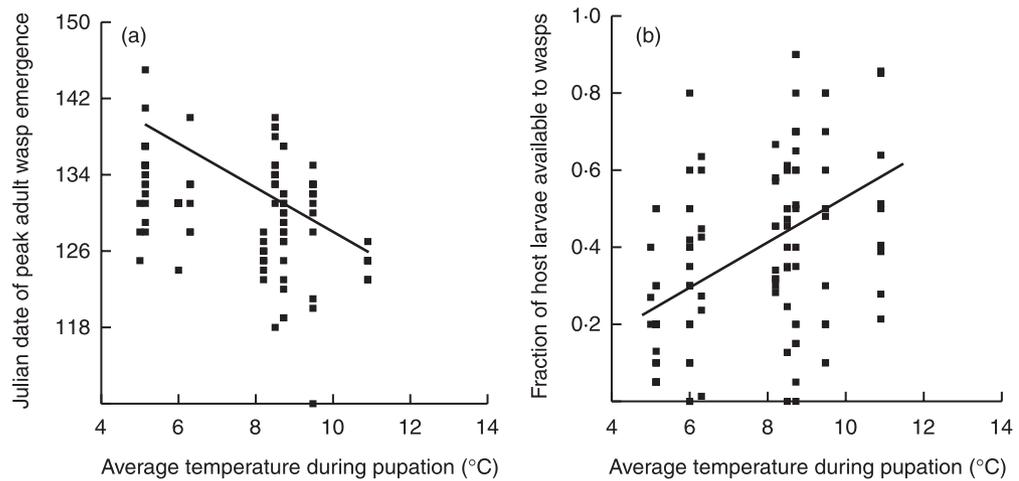


Fig. 5. The association of average daily temperature during wasp pupation in the spring and (a) Julian date the majority of wasps had emerged, and (b) the fraction of larvae that were still available for parasitism at adult wasp emergence. Each point is a population during one year ($n = 117$).

wasps became adults earlier on average than during cool early springs (significant coefficient of regression at $P < 0.0001$ and $r^2 = 0.18$; Fig. 5a). During warm early springs there were also more host larvae still available for parasitism when wasps had emerged than there were during cool early springs (significant coefficient of regression at $P = 0.001$ and $r^2 = 0.23$; Fig. 5b).

Spring butterfly population size was unrelated to degree of synchrony with the parasitoid in the previous spring. Early spring temperature also did not predict butterfly population size in the following spring. Instead, butterfly population size was predicted principally by the size of its own population in the previous year (Fig. 6). Parasitoid populations, on the other hand, were larger following years in which they were well synchronized with their host (Table 2) and when the average temperatures during pupal development in the spring were high (Table 3). As expected, parasitoid population size was also dependent on their population size the spring before, as well as the population size of the host (Tables 2 and 3).

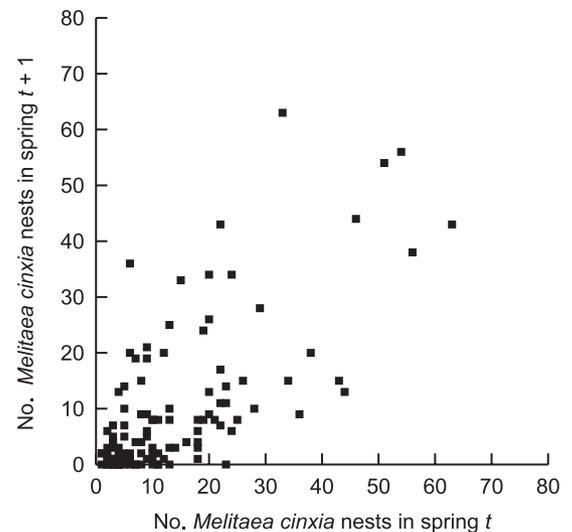


Fig. 6. The association of *M. cinxia* population size (number of larval nests in spring) from one year to the next. $n = 119$ pairs. All populations were occupied by *C. melitaearum* at least during the first year.

Table 2. Analysis of variance of *C. melitaearum* population size during spring 2 as a function of phenological synchrony* and host and parasitoid population sizes during spring 1

Source	d.f.	SS(III)	F	P > F
Model	18	326.02	6.08	0.0001
Year	8	38.80	1.36	0.22
Host-parasitoid synchrony spring 1 (= HPS)	1	29.20	8.17	0.005
Number of host nests spring 1	1	14.04	3.93	0.05
Number of parasitized host nests spring 1	1	39.20	10.97	0.001
HPS × host nests spring 1	1	7.75	2.17	0.14
HPS × parasitized host nests	1	41.13	11.51	0.001
Host nests × parasitized host nests	1	20.50	5.74	0.02
HPS × host nests × parasitized host nests	1	30.71	8.60	0.004
Error	101	360.90		

*The fraction of wasps in a population reaching adulthood while hosts were still available for parasitism during the previous spring.

Table 3. Analysis of variance of *C. melitaeorum* population size during spring 2 as a function of early spring temperature and host and parasitoid population sizes during spring 1

Source	d.f.	SS(III)	F	P > F
Model	7	309.43	12.76	0.0001
Mean early spring temperature spring 11 (= MET)	1	15.89	4.59	0.03
Number of host nests spring 1	1	2.75	0.79	0.37
Number of parasitized host nests spring 1	1	19.64	5.67	0.19
MET × host nests	1	7.14	2.06	0.15
MET × parasitized host nests	1	23.92	6.91	0.01
Host nests × parasitized host nests	1	38.66	11.16	0.001
MET × host nests × parasitized host nests	1	39.25	11.33	0.001
Error	109	377.49		

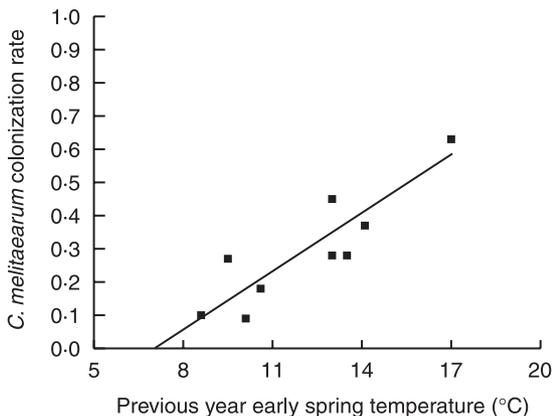


Fig. 7. Rate of colonization by *C. melitaeorum* (the number of host populations colonized divided by the number of extant parasitoid populations in the previous spring) and mean early spring temperature at the Jomala weather station in the previous year (1993–2001). Each point is 1 year.

COLONIZATION OF HOST POPULATIONS BY *C. MELITAEARUM*

There was a strong positive association between parasitoid colonization rate and early spring temperature (significant coefficient of regression at $P = 0.002$ and $r^2 = 0.78$; Fig. 7). The rate of colonization following the two coolest springs (1995 and 1996) was about 0.10 colonized populations per existing population, whereas after the warmest spring (1993) the colonization rate was over 0.60. This pattern suggests that large *C. melitaeorum* populations developed during warm springs and produced many colonists.

Discussion

AMBIENT TEMPERATURE AND THE TEMPERATURES OF HOST LARVAE AND PARASITOID COCOONS

In only 38 of the 115 nests in which both host larvae and parasitoid cocoon temperatures were measured were there any host larvae found in the shade. Those in

the shade appeared to be there simply because the sun had shifted and they had not yet moved or because they were moulting. Six of these larvae were at or below ambient temperature, whereas all the larvae in the sun ($n = 150$) were above ambient temperature (Fig. 3a). Many parasitoid cocoons were at or near ambient temperature (Fig. 3b), both because fewer cocoons were in the sun and because even in the sun, cocoons were cooler than adjacent host larvae.

The optimal temperatures for the development of *M. cinxia* larvae and *C. melitaeorum* cocoons are unknown, but other caterpillars are known to forage for food or metabolize food best between 25 and 35 °C (Porter 1982; Casey *et al.* 1988; Fields & McNiel 1988; Stamp & Bowers 1990a, 1994; Casey 1993; Bryant *et al.* 2000; Frid & Myers 2002). The optimal temperature for the development of the cocoons of the parasitoid *C. melanoscela*, a close relative of *C. melitaeorum*, is 30 °C (Gould & Elkinton 1990), which suggests that the ambient early spring temperatures in Åland are suboptimal for both insects. Our data indicate that while on average both insect species were warmer than ambient, below 16 °C the host larvae increase their body temperatures more than did the parasitoid cocoons. At higher temperatures, many individuals of both species maintain high body temperatures, although only a few reached what may be the optimal temperature for development (Fig. 3).

PHENOLOGICAL SYNCHRONY, TEMPERATURE AND SUBSEQUENT POPULATION SIZE

C. melitaeorum appeared to benefit from warm air temperatures during pupation in the spring generation, emerging as adults early, while a fraction of host larvae were still available for parasitism. In years when the air temperature was high during that period populations of *C. melitaeorum* grew and in the following spring more host nests were parasitized, whereas after a cool early spring the parasitoid populations were smaller.

It is apparent that phenological synchrony in the spring is controlled by air temperature during parasitoid pupation. At cool but sunny temperatures the host basks in the sun, increasing its rate of development while the

parasitoids are immobile pupae. At warm air temperatures basking is less of an advantage, and the wasp pupae develop sufficiently quickly to become adults while hosts are still available. Population dynamics of *C. melitaeorum* are thus influenced by variation in host–parasitoid phenological synchrony driven by differences in temperature among years and among populations. Host population size in the previous year, in addition to synchrony (or temperature), is also associated with parasitoid population size. This may be due simply to the increased number of hosts available for parasitism, but it is probably also because within-population phenological overlap would increase with host population size in topographically diverse habitat patches where larval groups experience different microclimates.

We did not detect an association of butterfly population size with early spring temperature or host–parasitoid phenological synchrony. One would expect that if the parasitoid population would grow, then the host population should shrink. However, many other factors such as summer drought and winter cold affect *M. cinxia* population size more than does *C. melitaeorum* (Kuussaari *et al.* 2004; Nieminen *et al.* 2004).

The degree of phenological synchrony between *M. cinxia* and *C. melitaeorum* is likely to influence adult butterfly sex ratio, because *M. cinxia* are protandrous with male larvae tending to pupate a few days earlier than female larvae (Boggs & Nieminen 2004). *C. melitaeorum* generally miss host individuals that pupate early, hence adult butterflies in populations occupied by *C. melitaeorum* may be male-biased. Such a bias was found by Porter (1982) in *E. aurinia*, presumably as a consequence of parasitism by *C. bignellii*. Variation of butterfly sex ratios due to variation in synchrony with the parasitoid is likely to contribute to population dynamics of the butterfly.

METAPOPULATION DYNAMICS OF THE PARASITOID

Regional persistence of the parasitoid *C. melitaeorum* depends on its ability to colonize new host populations to compensate for extinctions, due to a high rate of local host population turnover (Hanski 1999; van Nouhuys & Hanski 2002a) and due to density-dependent predation and hyperparasitism (van Nouhuys & Tay 2001; van Nouhuys & Hanski 2002b). The potential for colonization of host populations is highest during the first parasitoid generation, the progeny of those parasitizing the largest host larvae in the spring (Fig. 1). This is because the adult stage is long, from soon after the butterflies pupate until there are first or second instar host larvae (about 5 weeks) and there are potentially many adult wasps. Furthermore, it is only in this generation that the wasps must discover new larval groups, and may need to find new host populations if the local host population has gone extinct during the previous generation. During the second and third generations the wasps are rather sedentary (Lei & Camara 1999), and can potentially parasitize host larvae remaining in the nests they came from.

We found a strong positive association of temperature during *C. melitaeorum* pupal stage in the spring and colonization of previously unoccupied host population (Fig. 7). This suggests that spatial and temporal variation of temperature during the 2–3 weeks of spring parasitoid pupation contributes to the metapopulation dynamics of *C. melitaeorum* by affecting directly the number of colonists produced. This is an important aspect of the population ecology of *C. melitaeorum* in the Åland Islands because the overall abundance of the wasp is low and is limited by its dispersal ability (van Nouhuys & Hanski 2002a).

METAPOPULATION DYNAMICS OF THE HOST BUTTERFLY

Although we found no direct effect of host–parasitoid phenological synchrony on host population size, the effect of weather conditions on parasitoid colonization (above) may be important for the butterfly. The parasitoid has been observed to decrease the host population size in one high-density host population network (Lei & Hanski 1997). Other such well-connected populations exist but have remained uncolonized by *C. melitaeorum* (van Nouhuys & Hanski 2002a). A high rate of colonization, due to warm spring weather occurring over several years, would probably lead to the colonization of susceptible (high population density) host population networks. Species interactions such as between this host and parasitoid, which depend on precise phenological matching, have been shown to be greatly changed by the changing weather pattern (Visser & Holleman 2000).

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