

Host diet affects extinctions and colonizations in a parasitoid metapopulation

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Summary

1. In the Åland islands of SW Finland, the parasitoid *Cotesia melitaearum* (Wilkonson) is a specialist on the Glanville fritillary butterfly, *Melitaea cinxia* (L.), which uses two host plants, *Plantago lanceolata* (L.) and *Veronica spicata* (L.).

2. Extensive survey data on the butterfly and parasitoid populations collected in 1994–97 were used to examine possible associations of parasitoid colonizations and extinctions, with host population isolation, host population size, and host diet (plant species).

3. The likelihoods of parasitoid colonization and host patch occupancy were found to increase with decreasing isolation from other parasitoid populations, increasing host population size and an increasing fraction of host larvae on *V. spicata*. The likelihood of parasitoid population extinction increased with decreasing host population size and decreasing fraction of hosts on *V. spicata*. The pattern of association was exceptional in one area of high-density parasitoid populations as well as during a year of many extinctions but few colonizations.

4. Among host populations occupied by *C. melitaearum*, the fraction of host larval groups parasitized was higher in host populations using the more rare host plant, *V. spicata*. If host larval groups were present on both host plant species within one host population, then the larval groups on *V. spicata* were more likely to be parasitized.

5. The large-scale population dynamics of the parasitoid wasp are influenced by the distribution of the two host plants of the butterfly, by host-plant-dependent parasitoid behaviour and by host butterfly oviposition preference.

6. Possible explanations for the apparent superiority of *V. spicata* for *C. melitaearum* as the host butterfly's host plant are discussed. These include host larval group size, larval web structure, plant spatial aggregation, plant chemistry, and host larval physiology and phenology.

Key-words: *Cotesia melitaearum*, foraging behaviour, tritrophic, population dynamics, population extinction.

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Introduction

Parasitoids of herbivorous insects are attracted to their hosts, the host food plants, the host–host plant complex, and the host plant habitat (Turlings, Tumlinson & Lewis 1990; Vet *et al.* 1990; Vet & Dicke 1992; Steinberg, Dicke & Vet 1993a; Godfray

1994; De Moraes *et al.* 1998). When suitable hosts are found on more than one plant species, parasitoids may not use hosts on all plants with equal facility (Jalali *et al.* 1988; van den Berg, Nyambo & Waage 1990; Godfray 1994; Kester & Barbosa 1994). Such differences in apparent suitability of host plants can result from differential olfactory attraction to the habitat or to the host plant (Steinberg, Dicke & Vet 1993a; Godfray 1994; Benrey, Denno & Kaiser 1997), differences in the ability to find or to get access to the host once near or on the plant (Godfray 1994; Abrahamson & Weis

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1997), and physiological differences among hosts caused by the food plant such as developmental timing or plant chemistry (van den Berg *et al.* 1990; Godfray 1994).

In the Åland islands in SW Finland, the parasitoid wasp *Cotesia melitaeorum* (Hymenoptera: Braconidae) lays eggs in the larvae of the Glanville fritillary butterfly, *Melitaea cinxia* (Lepidoptera: Nymphalidae) (Hanski & Kuussaari 1995; Komonen 1997; Lei *et al.* 1997). While both insects are found in many parts of Europe (Hanski & Kuussaari 1995; Komonen 1997), in Finland the butterfly is confined to the study area (Kuussaari, Nieminen & Hanski 1996), which contains c. 1700 known patches of suitable habitat (dry meadows) with the host plants *Plantago lanceolata* (Plantaginaceae), *Veronica spicata* (Scrophulariaceae), or both (Hanski *et al.* 1995). Each year hundreds of these patches are occupied by *M. cinxia* and, of the latter, about 15% are occupied by *C. melitaeorum*, which is a specialist on *M. cinxia* in the study area (Lei *et al.* 1997).

The two species occur in Åland as assemblages of interacting populations or metapopulations (Hanski *et al.* 1996; Lei & Hanski 1997). The population dynamics of the butterfly are greatly influenced by the area and isolation of suitable habitat patches (Hanski *et al.* 1996; Hanski 1999), and by *C. melitaeorum*, which increases the risk of local host butterfly extinction (Lei & Hanski 1997).

Recent studies have demonstrated that the dynamics of the host butterfly are also influenced by the distribution of the two host plants, due to small-scale evolution of oviposition preference (Kuussaari 1998) and the influence of oviposition preference on the rate of colonization of habitat patches with different relative abundances of the two host plants (I. Hanski & M.C. Singer, unpublished). These results have motivated us to investigate the influence of host diet on parasitoid prevalence in the host populations. Given that the two host plant species have different morphology and biochemistry, and are found in somewhat different microhabitats, it is likely that they are not equally suitable for the parasitoid. Our study indicates that this is indeed the case, and furthermore that the difference in the apparent suitabilities of the two host plants is substantial enough to be reflected in the large-scale spatial dynamics of the parasitoid.

Materials and methods

THE PARASITOID WASP, THE HOST BUTTERFLY, AND THE HOST PLANTS

The wasp *C. melitaeorum* is a specialist larval parasitoid of Melitaeinae butterflies (Nixon 1974). It has been reared from *Melitaea cinxia*, *Mellicta athalia*,

and *Euphydryas aurinia* (Nixon 1974; Porter 1981). While both *M. cinxia* and *M. athalia* are found in the study area, *M. athalia* uses mostly a different habitat (open woodland and forest edges) from *M. cinxia* (dry open meadows), and is at most only an occasional host for *C. melitaeorum* (Lei *et al.* 1997; S. van Nouhuys, personal observation).

Melitaea cinxia lays eggs in large clusters in June and the larvae live gregariously in communal webs until just prior to pupation late in the following spring. From late autumn until early spring the larvae overwinter in a dense silk winter nest (Kuussaari 1998). In the Åland islands, *M. cinxia* is found exclusively on the host plants *Plantago lanceolata* and *Veronica spicata* growing on dry meadows. While *P. lanceolata* is probably the primary host plant over most of the range of *M. cinxia* in Europe (Higgins & Riley 1970; Tolman 1997; Kuussaari 1998), in some localities it has been found to feed monophagously on *V. spicata*, *V. austriaca* ssp. *teuchrium*, and *P. maritima* (Kuussaari 1998).

Cotesia melitaeorum is one of two primary parasitoids of *M. cinxia* in the Åland islands, where it has three generations per year and overwinters within the host larvae (Lei *et al.* 1997). The number of eggs laid in a host larva by a single female wasp varies from one to more than 30 depending on the size of the larva. For details of the parasitoid life cycle see Lei *et al.* (1997). The other primary parasitoid is the specialist ichneumonid *Hyposoter horticola*. It is found in virtually all relatively large host populations (Lei *et al.* 1997; S. van Nouhuys, unpublished data) and is a strong disperser. Within patches occupied by *C. melitaeorum*, *H. horticola* is an inferior competitor and does not noticeably influence the population dynamics of *C. melitaeorum* (Lei & Hanski 1998).

SURVEY DATA

Between 1994 and 1997 the number of host larval groups was counted each autumn in all known potential habitat patches for *M. cinxia* in Åland. Each spring the patches occupied by *M. cinxia* in the previous autumn were revisited, the numbers of host larvae and parasitoid cocoons were counted, and the host plant species used by each larval group was recorded (see Fig. 1, for details of survey methods see Hanski *et al.* 1996). Roughly 50% of the larval groups are found, except in the smallest populations, where recording efficiency is higher, as the presence/absence state of the patches is recorded especially carefully (M. Nieminen & J. Pöyry, unpublished). *Cotesia melitaeorum* emerge from the host larvae soon after diapause in early spring. They are found as cocoons singly or in small clusters in the vicinity of the postdiapause larval groups. While

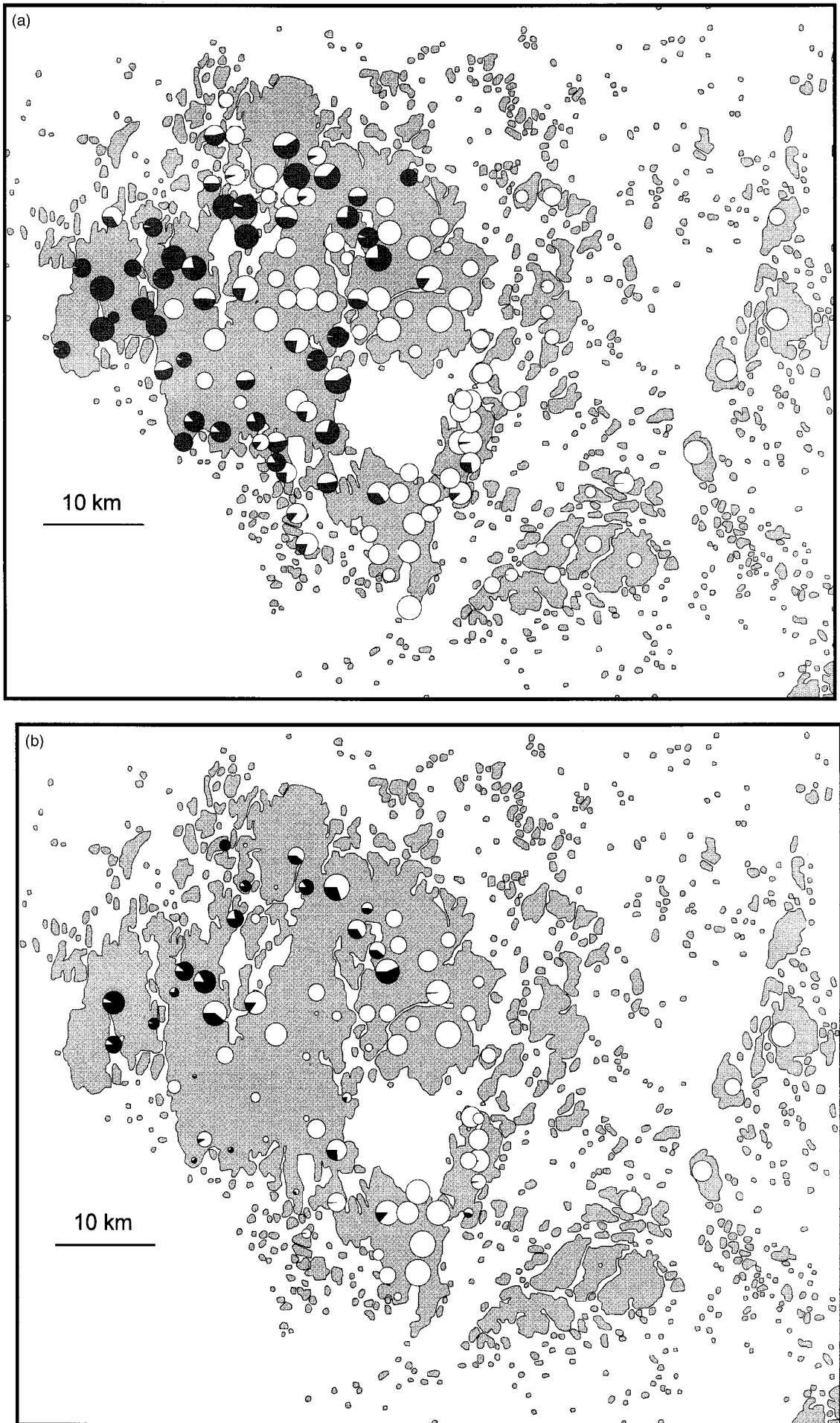


Fig. 1

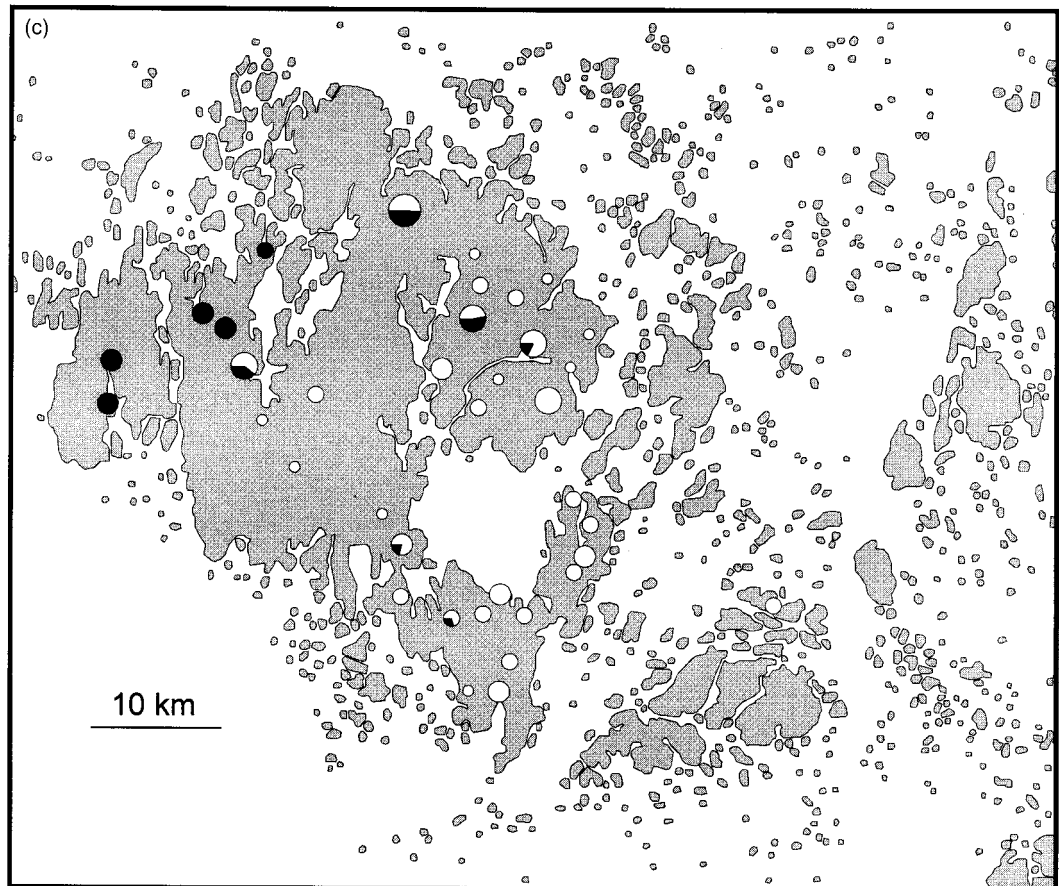


Fig. 1. Spatial distribution of *V. spicata* (black) and *P. lanceolata* (white) availability (a), use by *M. cinxia* (b), and use by *C. melitaeorum* (c). Each pie represents one semi-independent metapopulation (see text). Only those metapopulations in which *C. melitaeorum* was found in 1994–97 are included. Panels a and b are modified from Kuussaari (1998). (a) The colour of the pie diagram represents the relative abundance of each host plant species and the size of the pie is proportional to the logarithm of the habitat area. (b) The colour of the pie diagram represents the fraction of *M. cinxia* larval groups found on each host plant. The size of the pie is proportional to the logarithm of the number of *M. cinxia* larval groups found from 1994 to 1997. (c) The colour of the pie indicates the host plant species used by larvae parasitized by *C. melitaeorum* and the size is proportional to the logarithm of the number of *C. melitaeorum* cocoons found between 1994 and 1997.

the presence or absence of parasitoids in larval groups can be assessed reasonably accurately, the accuracy of counting the number of cocoons or proportion of larvae parasitized depends on the habitat and the movements of the host larval group.

The *c.* 1700 known habitat patches in the $50 \times 70 \text{ km}^2$ area in Åland have been divided into 127 semi-independent patch networks each containing from one to 95 habitat patches (Hanski *et al.* 1996). Patches belong to separate networks if there is at least 1 km of forest or open water, or at least 1.5 km of other unsuitable habitat, between them. There is very little migration between the networks, resulting in relatively independent metapopulation dynamics of *M. cinxia* (Hanski *et al.* 1996). The analyses presented here include only those networks in which at least one host population has been occupied by *C. melitaeorum* at least once during the last 5 years (Fig. 1, panel c). This excludes *M. cinxia* found in

some small networks in eastern and southern Åland containing only *P. lanceolata* as the host plant and located far away from any existing populations of *C. melitaeorum*. It is presumed that the absence of *C. melitaeorum* from small isolated metapopulations of the host butterfly is due to the high rate of parasitoid extinction and low probability of recolonization of isolated host metapopulations (Hanski 1999).

ANALYSIS

The likelihood of a host population being occupied by *C. melitaeorum* and the likelihoods of parasitoid extinction and colonization were estimated using logistic regression. The independent variables include host population size (estimated as number of larval groups), a measure of the isolation of the habitat patch from existing parasitoid populations, and the fraction of host groups found on *V. spicata*

as opposed to *P. lanceolata*. The statistical models presented do not include interactions between the independent variables since none were found to contribute significantly to the model fit.

Data sets used

Parasitoid colonization and extinction rates were analysed using data pooled over three consecutive time periods: 1994–95, 1995–96 and 1996–97. Turnover between spring censuses in these periods involved 41, 20 and 7 colonizations, and 21, 38 and 26 extinctions, respectively. During the 1994–95 period, five parasitoid extinctions occurred along with the extinction of the host butterfly. These were all in the one high-density network of populations discussed later. Since in this case parasitoid extinction cannot be separated from host butterfly extinction, this network of populations was left out of the logistic model of probability of extinction for 1994–95, as were the six other parasitoid extinctions in the data set that coincided with host butterfly extinctions.

The analysis of host population occupancy for 2 years is included. Spring 1996 is presented as an example of a 'normal' year. Results for spring 1997 are also presented because a relatively large fraction of the parasitoid populations went extinct between 1996 and 1997. It is not helpful to analyse occupancy in all years because the patterns of occupancy are to a large extent correlated between the years.

Not all *C. melitaearum* cocoons are discovered in the spring surveys. It is therefore likely that some low-density wasp populations may have not been detected. However, there is no known bias in the sampling method with respect to any of the explanatory variables used in this study, hence possible missing information about population turnover should not bias the results.

Host population size

The analyses include the host population (measured as the number of larval groups) present in the spring. For the analyses of colonization and extinction we used the number of host larval groups in the spring prior to the population turnover event. The numbers of host larval groups were log-transformed in order to improve the model fit.

Isolation index

Since the probability of host population occupancy, colonization and possibly extinction are likely to be related to the degree of isolation of the patch from existing parasitoid populations, we included an index of isolation in our logistic regression models,

$$S_i = \sum_{j \neq i} \exp[-\alpha d_{ij}] P_j N_j \quad \text{eqn 1}$$

The level of isolation of patch *i*, S_i (smaller values indicate greater isolation, $S_i = 0$ is completely isolated), is thus calculated by taking into account the distances between patch *i* and each of the source patches *j* (d_{ij}) and the size of each source patch, estimated as the number of host larval groups (N_j) (Hanski 1994). All of the host populations occupied by the parasitoid are considered source host populations, hence in the above formula $P_j = 1$ for host populations occupied by the parasitoid, and $P_j = 0$ for other populations. For parameter α we used the value of 1 km^{-1} which is our estimate of the characteristic migration range of the parasitoid (see Lei 1997; Lei & Camara 1999; also S. van Nouhuys, unpublished data). The results of our analyses are not sensitive to the exact value of α .

Fraction of host larval groups on *V. spicata*

In order to address the possible effect of host plant species used by the butterfly on parasitoid host population occupancy, extinctions, and colonizations, the fraction of host groups on *V. spicata* in each host population was included in the statistical model. The fraction ranged from 0 when all host groups were found on *P. lanceolata* to 1 when all host groups were found on *V. spicata*.

Analysis of host group size and host plant species

The presence of parasitoids in individual host larval groups was analysed with respect to host group size and host plant species using logistic regression. The number of host larvae per group was log-transformed to improve the model fit. Year was included in the model because there was variation in parasitism between years and previous results suggest that the influence of host group size on parasitism varies depending on weather conditions (Lei 1997).

Results

HOST DIET AND PARASITISM IN THE METAPOPOPULATION

Most of the habitat patches suitable for *M. cinxia* in the study area have only *P. lanceolata* as the host plant, and most of the larval groups in the entire metapopulation are therefore on *P. lanceolata* (Table 1, Fig. 1 panels a and b). However, due to female butterfly oviposition preference and geographical distribution of the host plants, there are more host larval groups on *V. spicata* than expected from its abundance in the study area (Kuussaari 1998).

Each year at least 9–19% of the *M. cinxia* populations were occupied by *C. melitaearum* (Table 1,

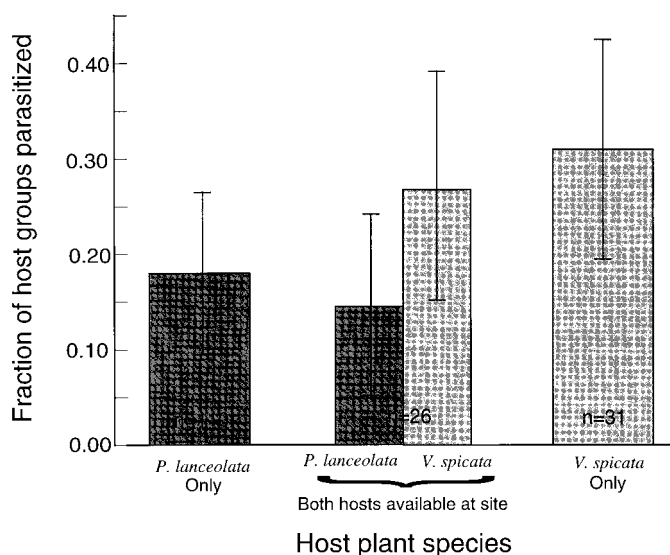


Fig. 2. The mean (SE) fraction of *M. cinxia* larval groups parasitized in habitat patches with a different composition of larval groups on the two host plants, *V. spicata* and *P. lanceolata*. *n* is the number of host populations of each type. The data are pooled for 1994–97. The differences between host plant species are significant at $P < 0.001$ in an ANOVA including host population size both using pooled data and when each year is analysed separately.

Fig. 1, panels b and c). A higher fraction of host populations using *V. spicata* were parasitized compared to the fraction of host populations using *P. lanceolata* (Table 1, statistically significant difference in each year at $P < 0.0001$). Thus, the incidence of parasitism in host populations feeding on *V. spicata* is greater than is expected from the abundance of *V. spicata* feeding butterfly populations.

HOST DIET AND PARASITISM WITHIN LOCAL POPULATIONS

Among the host populations occupied by *C. melitaearum*, fewer larval groups were parasitized in populations in which larvae used only *P. lanceolata* than in populations in which larvae used only *V. spicata* (Fig. 2; pooled over all years, mean in *P. lanceolata* patches = 18%, mean in *V. spicata* patches

= 31%, $n = 141$, $t = 3.04$, $P < 0.001$. The difference is also significant within single years).

Most host populations fed only on one of the two host plant species, but in some populations host larval groups were found on both host plants (Fig. 1, panel b). In these cases, in which an individual wasp had a choice, the fraction of larval groups parasitized on *V. spicata* tended to be higher than expected given the fraction of host larval groups on *V. spicata* (Fig. 2). Pooled over all years, the fraction of larval groups parasitized that were using *P. lanceolata* (on average 15%) is lower than the fraction of larval groups parasitized that were using *V. spicata* (on average 28%; $n = 26$, $t = 2.04$, $P = 0.046$).

The number of host larvae per group in the spring was greater on average on *V. spicata* than on *P. lanceolata*. For example, in host populations occupied by *C. melitaearum* in spring 1997 the mean host

Table 1. The occupancy of habitat patches by the host butterfly *Melitaea cinxia* and the parasitoid *Cotesia melitaearum* in 4 years

	1994	1995	1996	1997
Host populations	401	385	299	331
Host populations on <i>P. lanceolata</i>	354	334	201	243
Host populations on <i>V. spicata</i>	33	36	86	70
Host populations using both plant species *	14	15	12	18
Host populations parasitized	42	73	49	31
Fraction of host populations parasitized	0.10	0.19	0.16	0.09
Host populations on <i>P. lanceolata</i> parasitized	28	55	35	12
Fraction of host populations on <i>P. lanceolata</i> parasitized	0.08	0.16	0.16	0.05
Host populations on <i>V. spicata</i> parasitized	10	15	13	18
Fraction of host populations on <i>V. spicata</i> parasitized	0.30	0.42	0.15	0.26

* at least 10% of the hosts found on each plant species

Table 2. Multiple logistic regression model of factors affecting host group occupancy by *Cotesia melitaearum*. Data include only host groups from populations in which parasitoids were present and the host plant species and the number of host larvae per group were recorded each spring from 1994 to 1997 (1450 larval groups from 132 populations)

Predictor variable	Coefficient	Walds	χ^2	P
Constant	-0.68	2.7	0.09	
Year	-0.16	5.58	0.02	
Host plant species	0.67	17.50	0.00	
Log (no. larvae per group)	0.50	45.70	0.00	

The fit of the model is significant at $P < 0.001$ and each variable included improves the fit of the model significantly. The table lists the statistical significances of the coefficients.

group size on *V. spicata* was 26.2, whereas the mean group size on *P. lanceolata* was 16.5 ($t = 3.7$, $P < 0.001$, $N = 221$). Logistic regression analysis including both host plant species and larval group size indicated that the likelihood of host larval group parasitism is influenced by both. Large host groups, especially if they were on *V. spicata*, were more likely to be parasitized than small host groups, especially if they were on *P. lanceolata* (Table 2).

EXTINCTION-COLONIZATION DYNAMICS OF THE PARASITOID

The colonization of host populations was most likely to happen when the host populations were large, close to existing *C. melitaearum* populations, and when the fraction of host larval groups on *V. spicata* was high (Table 3). Extinction of a parasitoid population was especially likely to happen when the host population was small and had few or no larval groups on *V. spicata* (Table 4). The isolation of the population from other parasitoid populations was

Table 3. Multiple logistic regression model of factors affecting *Cotesia melitaearum* colonization. A colonization occurs when cocoons are absent in a particular spring and present in the subsequent spring. Colonization events between 94 and 95, 95 and 96, and 96 and 97 are included

Predictor variable	Coefficient	Walds	χ^2	P
Constant	-4.03	76.59	0.00	
Fraction of host groups on <i>V. spicata</i>	1.08	6.4	0.01	
Isolation from <i>C. melitaearum</i> populations	0.98	10.51	0.00	
Log (no. of host groups)	1.2	31.80	0.00	

$n = 349$. The fit of the model is significant at $P < 0.001$ and each variable included improves the fit of the model significantly. The table lists the statistical significances of the coefficients.

Table 4. Multiple logistic regression model of factors affecting *Cotesia melitaearum* extinction. An extinction occurs when cocoons are present in one spring and are absent in the subsequent spring. Extinction events between 94 and 95, 95 and 96, and 96 and 97 are included

Predictor variable	Coefficient	Walds	χ^2	P
Constant	2.08	19.17	0.00	
Fraction of host groups on <i>V. spicata</i>	-1.59	10.69	0.00	
Isolation from <i>C. melitaearum</i> populations	-0.05	0.08	0.70	
Log (# of host groups)	-1.31	32.69	0.00	

$n = 196$. The model is significant at $P < 0.001$. Removal of the variable Isolation does not change the overall fit of the model or the other coefficients. The table lists the statistical significances of the coefficients.

not found to influence the likelihood of extinction (we return to this result in the discussion by describing an exceptional situation in one region during one year). As expected based on the patterns of parasitoid colonization and extinction, a high probability of host population occupancy by the parasitoid is associated with large host population size, low isolation, and a large fraction of host groups on *V. spicata* (Table 5).

Discussion

The distribution of a parasitoid is constrained by the range of the host insects and their host plants. Within the geographical host range the population dynamics of a parasitoid is influenced by weather conditions and other environmental factors, the spatial distribution and quality of suitable habitat, and by host dynamics. Within a host population the success of a parasitoid is influenced by microhabitat and host availability as well as by individual parasitoid behaviour, which includes dispersal and within-patch foraging activity. These influences are well known. The less familiar result described in this paper is that within-patch foraging behaviour of a parasitoid wasp influences its regional population dynamics. In particular, the extinction-colonization dynamics of the parasitoid *C. melitaearum* is influenced by the distribution of the two host plants used by the host larvae through host plant-dependent parasitoid behaviour.

EXTINCTION-COLONIZATION DYNAMICS AND PATCH OCCUPANCY

The colonization success and occupancy of host populations by a parasitoid is expected to be positively influenced by the size of the host population. The colonization probability is also expected to increase with decreasing isolation from other host

Table 5. Multiple logistic regression models of factors affecting host population occupancy by *Cotesia melitaearum*

	Predictor variable	Coefficient	Walds χ^2	P
Spring 1996	Constant	-4.27	70.90	0.00
	Fraction of host groups on <i>V. spicata</i>	1.60	9.35	0.00
	Isolation from <i>C. melitaearum</i> populations	1.14	11.70	0.00
	Log (no. of host groups spring 1996)	1.40	39.53	0.00
Spring 1997	Constant	-4.09	50.56	0.00
	Fraction of host groups on <i>V. spicata</i>	1.58	7.43	0.01
	Isolation from <i>C. melitaearum</i> populations	0.08	0.03	0.87
	Log (no. of host groups spring 1997)	3.4	27.81	0.00

The fit of the models are statistically significant at $P < 0.001$. The table lists the statistical significances of the coefficients. Removal of the variable Isolation from the 1997 statistical model does not change the overall fit of the model or the other coefficients.

populations occupied by the parasitoid. Our data support these expectations. Additionally, we found that food plant species used by the host insect influences parasitoid colonization and host population occupancy, apparently because *V. spicata* is for some reason a better host plant of the host insect for *C. melitaearum* than is *P. lanceolata*, and because there is sufficient variation of host plant species composition among host populations. Notice that *V. spicata* is the more rare of the two host plants.

Extinction of *C. melitaearum* populations is less likely in large host populations and where there is a large fraction of host larval groups on *V. spicata*. We did not find that more isolated populations would be more likely to go extinct than less isolated populations. An effect of isolation would be expected if within a year extinction is often followed by isolation-dependent recolonization. In spite of three opportunities for colonization per year, as the wasp has three generations per host generation (Lei *et al.* 1997), we did not detect an effect of isolation on extinction.

In 1994, 1995 and 1996, the more isolated host populations had lower probabilities of parasitoid occupancy (Table 5 shows the results for 1996). In contrast, in 1997 no such isolation effect was detected (Table 5). Lack of isolation effect in 1997 is possibly due to a large fraction of the parasitoid populations going extinct between 1996 and 1997, and only a few new populations being established. As extinctions are not influenced by isolation, regional patterns of occupancy following a wave of extinctions are not expected to be strongly influenced by isolation.

In general, over the 4 years the local parasitoid population sizes seemed to be so small that they did not greatly increase the extinction risk of the host populations. However, in 1994 and 1995 there were many extinctions of both the parasitoid and the host populations in one intensively studied habitat patch network, which was also densely occupied by parasitoids

(Lei 1997; Lei & Hanski 1998). Interestingly, in this case there was a statistically significant positive association between the probability of parasitoid extinction and both parasitoid population size and connectivity (large S_i values). In other words, parasitoid populations that were large and close together in the spring of 1994 were more likely to go extinct than small isolated populations in the same network. Parasitoid extinctions in this case were associated with striking declines in host population sizes, themselves largely due to the impact of previous parasitism (Lei & Hanski 1997). Thus, where the host populations happen to be large and situated close to each other, the interaction between the host and the parasitoid is strong and may amplify extinction-colonization dynamics. Another factor that may cause *C. melitaearum* populations to collapse is density-dependent hyperparasitism by the ichneumonid *Gelis agilis* (Lei & Hanski 1997).

WHY SHOULD *C. MELITAERUM* BE MORE SUCCESSFUL USING HOSTS ON *V. SPICATA* THAN ON *P. LANCEOLATA*?

The survey data that we have used in this paper allow us to analyse the pattern of parasitoid host population occupancy and levels of parasitism within populations, but these data do not shed much light on the processes leading to the observed patterns. Some possible causes for the more successful use of host larvae on *V. spicata* than on *P. lanceolata* include the following factors.

Host group size

The rate of parasitism of gregarious lepidopteran larvae may be influenced by host larval group size (Stamp 1981). While larger larval groups are more likely to be parasitized than smaller groups, and on average there are larger groups on *V. spicata* than on *P. lanceolata*, our results indicate that the high frequency of parasitism on *V. spicata* cannot be

explained simply by host group size. Even when host group size is taken into account, larval groups on *V. spicata* are more likely to be parasitized than host groups on *P. lanceolata* (Table 2). However, further research is necessary because our estimate of group size in the spring may be biased by dissimilar larval behaviour on the two host plants, and the number of larvae per group on the two host plants in the summer and autumn is unknown.

Web structure

The communal webs of gregarious lepidopteran larvae are often thought to serve as defence structures against predation and parasitism (Stamp 1982; Godfray 1994). *Melitaea cinxia* larvae build differently shaped webs on *V. spicata* than on *P. lanceolata* (S. van Nouhuys, personal observation). The communal webs on *P. lanceolata* tend to be more compact than the webs on *V. spicata*, which may influence the accessibility of host larvae to the summer and autumn generations of the wasp (the larvae are relatively dispersed in the spring). The web structure may be an important factor for *C. melitaeorum*, since individual female wasps often tend to prediapause larval groups for several days but successfully parasitize only a small fraction of the larvae available (Lei & Camara 1999).

Plant spatial aggregation

Host plants growing close together may provide a larger target for foraging female wasps that are attracted to host plants. Plant aggregation may also result in the aggregation of host larval groups and increase the efficiency of parasitoid movement from one host group to another. Lei & Hanski (1998) found that *C. melitaeorum* tend to parasitize aggregated host larval groups more than isolated host groups within a habitat patch. Analysis of the distribution of host larval groups in 22 habitat patches occupied by parasitoids in spring 1997 and 1998 suggests that host larval groups are less isolated from each other in patches in which hosts use *V. spicata* than in patches in which they use *P. lanceolata* (S. van Nouhuys, unpublished data).

Plant chemistry

Parasitoid wasps use primarily olfactory cues to locate hosts (Turlings *et al.* 1990). The volatile chemical mixtures produced by the two host plants in the presence of herbivores are likely to be at least somewhat different hence not equally attractive to *C. melitaeorum*. Possibly *V. spicata* is more attractive than *P. lanceolata*.

The two host plant species share some characteristic iridoid glycoside secondary chemicals (Bowers

1980, 1983; Lei & Camara 1999; M.D. Camara, unpublished data) that are known to influence butterfly (Bowers 1983) and may influence parasitoid attraction. Interestingly, Lei & Camara (1999) found in laboratory studies that *C. melitaeorum* parasitized host larvae that had fed on *P. lanceolata* more readily than they parasitized larvae fed with *V. spicata*. While this is counter to what is expected given the observed pattern of parasitism in the field, it is important to note that the laboratory study was done using individual larvae removed from the web and host plant, which themselves are important cues for foraging parasitoids (Vet & Dicke 1992; Godfray 1994). It also may be that the volatile chemicals produced by herbivore infested *V. spicata* are more attractive long-distance cues than those produced by *P. lanceolata*, but once the host larval group is located by the wasp non-volatile cues and the accessibility of host larvae may become important. Thus, the laboratory test may have addressed only one component of a complex foraging behaviour.

Larval physiology and phenology

The quality of a host insect may depend on the host plant species on which it feeds (Greenblat & Barbosa 1981; Lawrence 1990; Steinberg, Prag & Rosen 1993b; Gauld & Gaston 1994; Godfray 1994). For example, host plant species may influence host larval growth rate, the ultimate size of the larvae and their immune response to parasitism. While Lei & Camara (1999) found that an equal number of cocoons emerged from host larvae fed each of the host plants in the laboratory, in the field slow-growing larvae may be available for parasitism for longer while larger-sized larvae may allow for larger clutch size of parasitoids.

While both host plants of *M. cinxia* grow on dry meadows, they do not grow in exactly the same microhabitat. Microclimatic conditions may differ between the microhabitats used by *V. spicata* and *P. lanceolata*, which could influence the larval growth rate and synchrony with parasitoid phenology.

BUTTERFLY HOST PLANT PREFERENCE

Recent studies have found evidence for small-scale evolution of oviposition preference in the host butterfly *M. cinxia* in Åland (Kuussaari 1998). Oviposition preference reflects a geographical gradient in host plant availability (Fig. 1, panels a and b), but in addition to this the butterflies generally prefer *V. spicata*. This evolution or maintenance of oviposition preference occurs in spite of *V. spicata* being the rarer host, a higher risk of parasitism on *V. spicata*, and there being no apparent difference in larval fitness on the two host plants (M. Kuussaari,

personal communication). Currently, the cause of selection on butterfly preference toward *V. spicata* is unknown.

Conclusion

In this study we found that the large-scale population dynamics of a specialist parasitoid wasp are dependent on the food plant species of the host butterfly, host population size, and isolation from other parasitoid populations. By using data collected over several years from many populations within an area where the metapopulation dynamics of the host butterfly are well studied, we were able to demonstrate not only the operation of factors that influence specialist parasitoid metapopulation dynamics, but also variation in the effects of these factors between years and between parts of the entire host metapopulation that differed in relative host food plant abundance. By measuring parasitism in relation to food plant use by the host butterfly both within and among populations we were able to show that the distribution of host plants within the study region affects, via behaviour of individual wasps (a small-scale process), the large-scale metapopulation dynamics of the parasitoid.

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