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Causes and consequences of small population size for a specialist parasitoid wasp

Abstract The parasitoid wasp *Cotesia melitaearum* lives in extremely small extinction-prone populations in the Åland islands of southwest Finland. Intensive observational data from two generations, a laboratory competition experiment, and 8 years of survey data were used to measure the causes, extent and consequences of small population size for this parasitoid. In the spring generations of 1999 and of 2000 we observed 21 out of 23 and 26 populations respectively, ranging in size from 2 to 103 parasitoid cocoons. Within these populations the fraction of individuals surviving to adulthood decreased with increasing parasitoid population size. The largest source of mortality was predation (44%) followed by parasitism (20%) and unknown causes (10%). In the field about 30% of the host butterfly larvae are parasitized by a competing parasitoid, *Hyposoter horticola*. A laboratory competition experiment showed that *C. melitaearum* eggs died when laid in post-diapause host larvae occupied by *H. horticola*. Consequently one-third of the progeny of the over-wintering generation of *C. melitaearum* from the field die as a result of larval competition. The survey of host and parasitoid population dynamics over 8 years showed that extinction of local host butterfly populations occupied by the parasitoid was not associated with current parasitoid population size. Over the same period small parasitoid populations were more likely to become extinct than large populations. However, parasitoid population size was not related to parasitoid extinction when the host also became extinct. These data suggest that the parasitoid populations are kept small through the action of natural enemies and competitors, some of which are density dependent. Local populations are so small that they become extinct frequently and rarely measurably affect the population dynamics of their host. It is likely that this parasitoid persists in Åland because of the spatial asynchrony of local population dynamics.

Keywords *Cotesia melitaearum* · Competition · Extinction · Metapopulation · Predation

Introduction

The intrinsic and extrinsic factors that cause populations to be small and the long-term consequences of small population size are of great interest to ecologists, evolutionary biologists and conservation biologists. Populations may be small because they are declining toward extinction, or they may persist as small populations by continuous replenishment from larger, more stable populations (MacArthur and Wilson 1967). Some small populations may persist in isolation for many generations in spite of there being apparently ample resources to support much larger populations (Cappuccino and Kareiva 1985; Root and Cappuccino 1992; Wissinger et al.1996).

The size of a parasitoid population can be limited by availability of hosts (bottom-up or resource limitation) and by natural enemies (top-down) (Hunter and Price 1992). If a large fraction of individuals in a parasitoid population are killed by natural enemies such as predators and secondary parasitoids, the population cannot persist over many generations because of stochastic processes (MacArthur and Wilson 1967; Hanski 1998). Small populations may also become inviable through negative genetic effects such as inbreeding depression or the loss of genetic variation (Frankham 1995; Saccheri et al. 1998). However, if there is a cluster of host populations within reasonable dispersal distance the parasitoid may persist over time as a network of small extinction-prone populations (Levins 1969).

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In the Åland islands in Finland the specialist parasitoid wasp *Cotesia melitaearum* (Wilkonson) (Hymenoptera: Braconidae) lives in a network of small extinction-prone local populations within a large host metapopulation (Lei and Hanski 1997; van Nouhuys and Hanski 1999). Using observational and experimental data, we analyse the primary sources of mortality of this wasp, which are predation, parasitism and competition, and how they may play a role in controlling parasitoid population size. We then analyse the relationship between parasitoid population size, host population size, and local extinction of the parasitoid and its host using survey data from many populations collected over 8 years.

Materials and methods

Study system

The wasp *C. melitaearum* is a specialist larval parasitoid of Melitaeini butterflies (Lepidoptera: Nymphalidae) (Nixon 1974). In the Åland islands of southwest Finland the host for *C. melitaearum* is the Glanville fritillary butterfly *Melitaea cinxia* (L.) (Lei et al. 1996). The host butterfly lives in sunny dry meadows in semi-independent habitat patch networks (Hanski and Kuussaari 1995; Hanski 1999). *C. melitaearum* occupy only tightly clustered host populations scattered over the networks of host populations (Lei and Hanski 1997; van Nouhuys and Hanski 1999). Within populations the wasps are relatively sedentary (Lei and Camara 1999), and dispersal experiments indicate that movement of more than 500 m between host populations would be rare. This trend is evident in the observed rates of natural colonization of host populations over the last 8 years (S. van Nouhuys and I. Hanski, unpublished work).

The host butterfly lays eggs in large clusters in June. Their larvae live gregariously until just prior to pupation in the following spring, spending the winter in silken nests as diapausing larvae (Hanski and Kuussaari 1995; Hanski 1999). The parasitoid usually has three generations during each host generation. Adult wasps lay eggs singly or in pairs into the early-instar larvae in the late summer. These wasps develop and emerge from the third- or fourth-instar host larvae and pupate in the vicinity of the remaining unparasitized host larvae. As adults they lay two to eight eggs in fourth- or fifth-instar larvae just before host diapause. The immature wasps spend the winter in diapause within the host. Soon after the host larvae begin to feed in the spring the parasitoids emerge and pupate. This last generation of adult wasps lay 20–30 eggs in late-instar host larvae (Lei 1997).

There are several other key parasitoids in this system. The solitary ichneumonid, *Hyposoter horticola* is another specialist of Melitaeini butterflies (Lei et al. 1996). It occupies most *M. cinxia* populations in Åland, successfully parasitizing 20–30% of the larvae in each population (Lei 1997; S. van Nouhuys, unpublished work). *C. melitaearum* on the other hand is only found in 10–20% of the host populations during any one year. The two parasitoids compete where they occur in the same host population (Lei and Hanski 1998). Because *C. melitaearum* has three generations during every one generation of *H. horticola* there are opportunities for competitive interactions between several different immature stages of the parasitoids. *Gelis agilis* (and other rarer *Gelis* species) is a wingless solitary generalist parasitoid that commonly parasitizes *C. melitaearum* cocoons (Lei et al. 1996; Schwarz and Shaw 1999), in some cases greatly decreasing *C. melitaearum* population size (Lei and Hanski 1998; van Nouhuys and Hanski 2000).

Study of the fate of *C. melitaearum* cocoons in spring

In the early spring of 1999 and 2000 we searched for cocoons of the third (over-wintering) *C. melitaearum* generation in all host populations known to be occupied by the parasitoid in Åland. Previously occupied host populations and host populations near known *C. melitaearum* populations were also searched. Cocoons identified were then checked every few days and their condition recorded until all of the cocoons had produced wasps, been eaten by predators, died or disappeared. Adult *C. melitaearum* require at most 20 days development time within their cocoons prior to eclosion in the spring (Lei et al. 1996). Cocoons that had been present in the field for more than 20 days were put into individual Eppendorf tubes and taken back to the laboratory where they were examined under a light microscope in order to check for evidence of hyperparasitism, predation or other causes of death. We found 217 cocoons from 23 populations in 1999 (27 April–26 May) and repeatedly visited each cocoon in all but two of the sites. In 2000 (25 April–23 May) 26 populations were found of which the fates of the 365 cocoons from 21 populations were recorded.

We believe that these data represent a large fraction of the cocoons in the entire system on the Åland islands. Each population was searched thoroughly on every visit, and rarely were cocoons found that had previously been overlooked. Many of the populations in 2000 were larger than in 1999 even though the fraction of nests parasitized per population was equal (the mean number of nests parasitized in 1999 was 27% and the mean in 2000 was 29%; a *t*-test puts the probability of these means being equal at $P=0.69$). The difference in population size is due to the number of immature parasitoids emerging from each parasitized larva rather than a large difference in the number of parasitized larvae. In 1999 the mean number of cocoons per parasitized larva was 2.46 ($n=100$ larvae, SD=1.59) and in 2000 3.40 parasitoid cocoons ($n=112$ larvae, SD=2.08) were produced on average from each host larva. These means are significantly different at $P=0.001$.

The fate of the cocoons was classified as: (1) eclosed (an adult *C. melitaearum* wasp emerged); (2) eaten by a predator that chewed through the cocoon and removed the parasitoid pupa; (3) parasitized (psuedohyperparasitized) by the cocoon parasitoid *Gelis* spp.; (4) eaten by a predator that left pin-hole sized holes in the silken cocoon with the dried up remains of *C. melitaearum* pupae inside; (5) died of unknown causes with no visible damage; (6) squashed by human activities; (7) disappeared, possibly taken by predators; and (8) unchecked, due to weather or inaccessibility, or removed from the field early by researchers. These data are summarized in Table 1.

The association of each mortality source with population size (number of cocoons found in a population) and density (fraction of nests parasitized) was analysed using multiple logistic regression. Year was included in the statistical models as a blocking factor and correlation among individuals within populations was accounted for using the repeated statement in SAS PROC GENMOD (SAS Institute 1998; Allison 1999).

Competition with *H. horticola* within the host larva

We experimentally tested for competition between the late-instar *H. horticola* and the early-instar or egg stage of *C. melitaearum* which occurs within the late-instar host larvae, just prior to pupation. Several hundred host larvae were collected from the field in the spring of 1999. These larvae had been subject to natural parasitism by *H. horticola* in the summer of 1998. A total of 160 larvae were placed randomly in eight cages in groups of 20. All of the larvae in four randomly selected cages were parasitized by *C. melitaearum* in the laboratory while larvae in the other four cages were left untreated. Parasitism of each larva was confirmed by direct observation. A separate group of 80 larvae was parasitized and dissected to confirm that *C. melitaearum* oviposit the same number of eggs in larvae containing *H. horticola* as in unparasitized larvae. The larvae were fed *Plantago lanceolata* leaves and reared in the laboratory under uniform conditions until they became *M. cinxia* pupae, *H. horticola* pupae, or *C. melitaearum* pupae. Five host larvae that died during the experiment were dissected and found not to contain immature parasitoids. All of the parasitoid pupae developed successfully into adult wasps.

Table 1 Fate of cocoons in *Cotesia melitaearum* populations in Åland in spring 1999 and 2000

Site ID	Melitaea cinxia nests (No. parasitized)		Total cocoons		Survive to adulthood		Fraction adult		Eaten by chewing predator		Eaten by piercing predator		Parasitized		Disappeared		Squashed		Unknown cause of death		Unchecked	
	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00
565	29(6)	33(9)	49	31	7	2	0.14	0.07	17	6	5	0	6	5	8	10	0	0	6	5	0	3
576	46(8)	55(13)	21	103	13	15	0.64	0.18	2	13	0	6	1	21	4	19	0	5	1	4	0	20
1653	23(6)	17(a)	27	—	0	—	0.00	—	10	—	7	—	1	—	5	—	0	—	4	—	0	—
1652	9(3)	6(a)	18	—	4	—	0.22	—	4	—	1	—	5	—	0	—	4	—	0	—	0	—
583	38(4)	35(2)	15	5	2	1	0.14	0.20	2	1	3	0	0	2	6	0	1	0	3	1	1	0
1071	15(2)	30(1)	9	8	4	1	0.44	0.13	0	1	0	2	1	4	1	0	0	0	3	0	0	0
601	17(4)	2(0)	9	—	4	—	0.44	—	0	—	0	—	0	—	2	—	0	—	3	—	0	—
606	5(3)	4(0)	9	—	5	—	0.71	—	2	—	0	—	0	—	0	—	0	—	2	—	2	—
21	15(5)	1(0)	9	—	5	—	0.56	—	0	—	0	—	1	—	0	—	0	—	1	—	0	—
562	4(1)	16(2)	8	22	6	5	0.75	0.23	1	1	0	3	0	4	1	9	0	0	2	0	0	0
1648	8(2)	22(2)	7	7	1	1	0.17	0.14	0	1	0	2	3	1	2	2	0	0	0	0	1	0
24	6(3)	1(0)	7	—	3	—	0.43	—	0	—	0	—	1	—	2	—	0	—	1	—	0	—
1051	9(1)	18(3)	6	20	2	3	0.33	0.15	1	1	0	1	1	7	2	5	0	0	0	3	0	0
876	17(1)	8(3)	6	10	2	2	0.33	0.20	3	0	0	0	1	2	0	0	0	0	0	6	0	0
877	11(3)	8(3)	4	17	0	0	0.00	0.00	0	2	1	1	0	3	1	2	2	6	0	3	0	0
875	3(1)	1(0)	4	—	4	—	1.00	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
1640	4(1)	1(0)	4	—	4	—	1.00	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
589	4(2)	a	3	—	2	—	0.67	—	0	—	0	—	0	—	0	—	0	—	1	—	0	—
1221	3(1)	a	2	—	0	—	0.00	—	1	—	0	—	0	—	1	—	0	—	0	—	0	—
1726	10(1)	0(0)	2	—	2	—	1.00	—	0	—	0	—	0	—	1	—	0	—	0	—	0	—
577	4(1)	3(0)	2	—	1	—	0.50	—	0	—	0	—	0	—	1	—	0	—	0	—	0	—
573	9(0)	7(3)	—	32	—	0	—	0.00	—	8	—	2	—	13	—	1	—	6	—	1	—	1
563	3(0)	5(2)	—	27	—	6	—	0.22	—	2	—	2	—	10	—	6	—	0	—	1	—	0
591	5(0)	13(3)	—	23	—	4	—	0.17	—	1	—	3	—	8	—	6	—	0	—	1	—	0
22	15(O)	11(4)	—	14	—	3	—	0.21	—	2	—	2	—	3	—	3	—	0	—	0	—	0
558	2(0)	6(2)	—	12	—	1	—	0.08	—	3	—	2	—	0	—	4	—	2	—	0	—	0
481	4(0)	4(1)	—	11	—	0	—	0.00	—	0	—	6	—	4	—	1	—	0	—	0	—	0
1642	8(0)	6(2)	—	7	—	0	—	0.00	—	1	—	2	—	4	—	0	—	0	—	2	—	0
584	2(0)	6(2)	—	5	—	2	—	0.00	—	2	—	0	—	0	—	0	—	0	—	1	—	1
3772	a	5(1)	—	5	—	2	—	0.40	—	0	—	1	—	0	—	0	—	0	—	0	—	0
570	a	3(1)	—	2	—	0	—	1.00	—	0	—	0	—	1	—	0	—	0	—	1	—	0
550	a	1(1)	—	2	—	0	—	0.00	—	0	—	0	—	0	—	0	—	0	—	0	—	0
1070	12(0)	8(1)	—	2	—	0	—	0.00	—	0	—	0	—	0	—	0	—	2	—	0	—	0
Sum	221	365	221	365	71	48	0.32	0.13	43	46	17	35	21	92	34	68	7	21	24	30	4	25
Fraction of total	1	1	1	1					0.19	0.13	0.08	0.10	0.10	0.25	0.15	0.19	0.03	0.06	0.11	0.08	0.02	0.07

a Population not observed

C. melitaearum and *M. cinxia* population dynamics
from 1993 to 2000

Each spring *C. melitaearum* populations in Åland were visited to count the number of cocoons and host larval groups. Not all populations were visited each year. Combining data collected over the 8 years there were 215 transitions in which population sizes of the parasitoid and host were reliably assessed over two consecutive spring seasons. We used logistic regression (SAS PROC GENMOD, SAS Institute 1998) to analyse the association between parasitoid and host population sizes during one spring and extinction or persistence of parasitoid population during subsequent spring. The analyses included year as a blocking factor. Host population size was measured as the number of nests. We use the number of nests parasitized as an indicator of parasitoid population size, rather than number of parasitoid cocoons, because we found number of nests parasitized to be more closely associated with the subsequent success of the population (S. van Nouhuys, unpublished work). This is at least partly due to the fact that the presence of cocoons is easier to observe than the actual number of cocoons, and not all nests containing cocoons could be searched equally thoroughly over the entire 8 years.

Population size may affect local extinction of a parasitoid differently when the host population continues to persist than when both populations become extinct simultaneously. We allowed for this distinction between types of extinction by first analysing all 126 parasitoid extinctions and then sub-setting the data. The 27 extinctions that occurred along with host extinctions were excluded in one set, and the 99 parasitoid extinctions that occurred in spite of host persistence were excluded in the other.

The association between extinction of butterfly populations occupied by the parasitoid, and the host and parasitoid population sizes was also analysed using logistic regression. Host population was represented as the number of nests, and parasitoid population size by the number of nests parasitized. Year was again included as a blocking factor.

Results

Mortality of cocoons

The initial number of cocoons per population varied greatly, ranging from 2 to 103 with the mean of 14.

Survival of cocoons also varied between populations, ranging from 0 to 100% with mean of 31%. Of the 557 cocoons where fates were observed, *C. melitaearum* successfully eclosed from 21% of cocoons ($n=119$), whereas 79% ($n=438$) of cocoons failed to develop into adult wasps. We did not record the fate of the remaining 29 cocoons from seven different populations (Table 1) so they were excluded from the analysis of mortality.

In 1999 67% of cocoons died (Table 1). The largest source of mortality was predation by predators that opened up the cocoons to remove the developing parasitoids (chewing predators, 20%), followed by removal of entire cocoons by predator(s) (disappeared, 16%), death due to unknown causes (unknown death, 11%) parasitism by *Gelis* spp. (parasitized, 9%), and predation by piercing predators (piercing predators, 8%). The fraction of cocoons surviving to adulthood was much lower in 2000 (86% died). The primary sources of mortality also differed between years. In 2000, the largest single mortality factor was parasitism (27%) followed closely by disappearance (20%) and then predation by chewers (14%) (Table 1).

Mortality increased with increasing population size, such that the odds of dying were 80% higher in the largest population than in the smallest populations (Table 2, total mortality odds ratio=1.80). The association between population size and each source of mortality separately varied. Mortality due to chewing predators increased with population size, as did removal of cocoons (Table 2). Parasitism by *Gelis* spp. increased with cocoon density (fraction of host nests parasitized) rather than absolute number (Table 2). Mortality due both to piercing predators and unknown sources was independent of parasitoid population size.

Table 2 Multiple logistic regression analysis of the population size and density with cocoon mortality in spring 1999 and 2000. Coefficients and test statistics in *bold* are statistically significant

Model df=551 (n=555 cocoons)	Deviance	χ^{2a}	$P>\chi^2$	Number of cocoons				Cocoon density			
				Coefficient	Odds ratio	Z^b	$P>Z$	Coefficient	Odds ratio	Z^b	$P>Z$
Total mortality	**537.45**	**39**	**0.005**	**30.59**	**1.80**	**1.991**	**0.046**	–0.07		0.359	0.720
Mortality due to chewing predators	**475.83**	**37**	**0.005**	**0.40**	**1.49**	**2.149**	**0.032**	–0.02		0.193	0.846
Mortality due to piercing predators	343.89	2	0.500	0.03		0.129	0.897	0.01		0.048	0.961
Disappearance	**521.87**	**11**	**0.010**	**0.31**	**1.36**	**2.387**	**0.017**	–0.24		–1.230	0.219
Mortality due to parasitism	**551**	**35**	**0.005**	0.05		–0.378	0.705	**0.16**	**1.17**	**2.432**	**0.015**
Unknown cause of death	352	6	0.100	–0.19		0.984	0.324	–0.22		–1.571	0.116

[a] Test statistic for the goodness of fit of the overall logistic regression model
[b] Test statistic for the individual coefficient in the logistic regression model

Table 3 Results of competition between *C. melitaearum* and *Hyposoter horticola* in post-diapause host larvae. Each cage initially contained 20 larvae sampled from a population of *M. cinxia* after parasitism by *H. horticola* in the field. Eggs were laid by *C. melit-* *aearum* in each of the larvae in the four treatment cages. Host larvae in the untreated cages became *M. cinxia* or *H. horticola* pupae. Host larvae in the treated cages became *M. cinxia* or *H. horticola* pupae, or yielded clusters of *C. melitaearum* cocoons

Cage	Treatment	*M. cinxia* pupae	*H. horticola* pupae	*C. melitaearum* pupae clusters	Dead *M. cinxia*
1	*Cotesia*	3	3	13 larvae	1
2		14	5	0	0
3	*Cotesia*	2	3	14 larvae	1
4		19	0	0	1
5	*Cotesia*	0	4	16 larvae	0
6		15	3	0	2
7	*Cotesia*	7	3	10 larvae	0
8		18	2	0	0

Table 4 Multiple logistic regression analysis of persistence of populations from one spring to the following spring by: (a) host populations occupied by parasitoids; (b) parasitoid populations; (c) parasitoid populations when the host populations persist, and (d) parasitoid populations when extinctions of both the host and parasitoid occur together

	df	Deviance	χ^2	$P>\chi^2$	Coefficient.	χ^2	$P>\chi^2$	Odds ratio
(a) Butterfly populations	215	140.23	24.63	0.005				
Year	6					11.437	0.758	
Log(host nests parasitized)	1				0.710	0.194	0.659	
Log(host nests)	1				0.234	6.100	0.013	2.034
(b) Parasitoid populations	206	247.97	43.68	0.005				
Year	6					14.552	0.024	
Log(host nests parasitized)	1				0.817	8.010	0.004	2.263
Log(host nests)	1				0.275	1.967	0.161	
(c) Parasitoids without host extinctions	179	224.88	35.21	0.005				
Year	6					13.492	0.036	
Log(host nests parasitized)	1				0.885	8.665	0.003	2.422
Log(host nests)	1				0.138	0.475	0.491	
(d) Parasitoid with host extinctions	107	92.02	33.86	0.005				
Year	6					12.049	0.061	
Log(host nests parasitized)	1				0.403	0.466	0.495	
Log(host nests)	1				1.010	7.520	0.006	3.007

Mortality due to competition among immature parasitoids

Parasitism by *C. melitaearum* did not reduce the number of *H. horticola* emerging from host larvae (Table 3). A χ^2-test puts the probability of the number of *H. horticola* emerging from the treated and untreated cages being equal at *P*=0.49. If both parasitoid species were equally likely to be successful a mean of 1.62 *H. horticola* would emerge from each of the treated cages. A power test shows that the observed mean of 3.25 can be distinguished from the null-hypothesis mean of 1.62 at the 0.05 level of statistical significance. We conclude that *H. horticola* is the superior competitor when *C. melitaearum* oviposit into late-instar host larvae parasitized by *H. horticola* from the previous summer.

Patterns of parasitoid and host population dynamics

12% of host butterfly populations occupied by *C. melitaearum* between 1993 and 2000 became extinct. We tested the hypothesis that the survival of parasitoid-occupied host populations would be related to parasitoid and host population sizes using logistic regression. The host populations that survived tended to be large and their survival was unrelated to parasitoid population size (Table 4, model a).

A much larger fraction of the parasitoid populations became extinct (59%). Not surprisingly, the odds of population survival were 126% higher in the largest populations than in the smallest (Table 4, model b). In this overall analysis there was no significant association between the survival of parasitoid populations and the host population size (Table 4, model b). In 27 of the 126 parasitoid extinctions the host also became extinct. Because these extinctions were possibly unrelated to the presence

of the parasitoid we excluded them from the second analysis and found the same result as for the first (Table 4, model c). However, it is also possible that parasitoids contributed to the extinction of host populations, so the third analysis included only simultaneous extinctions. In this case we found parasitoid survival to be related only to host population size. The odds of parasitoid survival were 200% higher in the largest host population than in the smallest, independent of the parasitoid population size (Table 4, model d).

Discussion

What causes *C. melitaearum* populations to be small?

Population size can be limited by the availability of resources, by the action of natural enemies and by environmental factors such as weather. Persistence of populations under these constraints is affected by the reproductive capacity of a species and can be influenced by dispersal.

A female *C. melitaearum* can easily lay several hundred eggs in her life time in the laboratory (W.T. Tay and S. van Nouhuys, unpublished work), and in the spring (third) generation one individual can potentially lay hundreds of eggs in the field if she emerges before most of the host larvae have pupated (S. van Nouhuys and G.C. Lei, unpublished work). However, this is not usually the case, and during two generations in each year individual wasps are relatively sedentary and probably successfully parasitize only a few larvae, laying one to three eggs in each (Lei 1997). Thus, the number of eggs developing to pupation is frequently small.

Predation

A large fraction of cocoons were preyed upon, either by predators that chew through cocoon cases to get to the immature wasp or by insects that make pinprick-size holes in the cocoons (perhaps predatory Hemiptera). The second highest mortality factor we measured was disappearance (Table 1, 18%). We believe that disappearance is primarily due to removal of cocoons by predators. In most cases cocoons are sheltered and affixed to a surface with silk, making it unlikely that they would blow or roll away. Lei and Hanski (1997) found removal of cocoons by the ant *Tetramorium caespitum* to be an important density-dependent source of mortality. If we count disappearance as mortality due to predation, then 44% of the cocoons are eaten by predators. Mortality due to chewing predators and disappearance increased with increasing population size (Table 2). This suggests that though the predators are likely to be generalists, they play a role in regulating parasitoid population size.

In this study only data on cocoon predation have been presented. Mortality of immature parasitoids due to predation of host larvae has not been measured and is likely to play an important role, as is predation of adult parasitoids.

Parasitism

The number of cocoons parasitized by the generalist cocoon parasitoid *Gelis* spp. (mostly *G. agilis*) varied between populations from none to 57% with a mean of 16% (Table 1). In 2000 parasitism was the largest single source of mortality. It is likely that the fraction of cocoons parasitized was actually greater because some of the cocoons eaten by predators were probably parasitized. While parasitism did not increase with *C. melitaearum* population size it did increase with cocoon density (fraction of host nests parasitized (Table 2). Lei and Hanski (1997) also found that *G. agilis* aggregate at large clusters of *C. melitaearum* cocoons. This is not surprising because *G. agilis* is a wingless extreme generalist (Schwarz and Shaw 1999). While local density is not necessarily related population size, cocoons in large populations are likely to be close together. Van Nouhuys and Hanski (2000) experimentally tested the impact of adding a large number of suitable host cocoons (*Cotesia glomerata*) on subsequent generations of *C. melitaearum*. They found that when an abundance of hosts for *Gelis* spp. was added to *C. melitaearum* populations, the treated populations declined by the next year relative to the untreated populations.

Competition

Hyposoter horticola is an extremely abundant parasitoid of *M. cinxia* in the Åland islands. The laboratory competition experiment shows that *C. melitaearum* eggs oviposited into the late-instar host larvae parasitized by *H. horticola* do not survive to emergence from the host. This was expected because *H. horticola* larvae are large in the spring (S. van Nouhuys, personal observation) and have been in the host for more than 10 months, and so they are likely to be able to physically or physiologically suppress *C. melitaearum* (Quicke 1997). Because adult *C. melitaearum* do not seem to distinguish between unparasitized hosts and those parasitized by *H. horticola*, potentially 30% of the spring generation of *C. meli-tae-arum* (the progeny of the generation presented in Table 1) may be killed prior to pupation. The late spring generation of *C. melitaearum* can greatly influence their adult population size because many host larvae can be parasitized and up to 30 wasps emerge from one host larva (Lei 1997) which is an order of magnitude more than during the other two *C. melitaearum* generations each year.

It is important to note that Lei and Hanski (1998) found that in the field host populations occupied by both parasitoids, fewer *H. horticola* pupated from host larvae in nests containing *C. melitaearum* than from nests containing only *H. horticola*. Therefore, the sum of the outcomes of the three intervals of competition is that *C. melitaearum* is the superior competitor within host larvae in spite of being the inferior competitor during the important late spring generation.

Resource limitation

The survey data from 1993 to 1999 suggest that *C. melitaearum* rarely reaches the point at which it is limited by the size of the host population, because the survival of *C. melitaearum* populations was found to be independent of host population size as long as the host population itself persisted (Table 4, model b).

Typically only a fraction of the host larval groups in a host population are parasitized, and within each larval nest only a fraction of larvae are parasitized (Lei 1997). It is possible that larvae that appear to us to be available to the parasitoid are not, either due to the poor searching ability of the adult parasitoid (Hubbard and Cook 1978; Waage 1983; Ives et al. 1999), or because of defensive behavior or physiological resistance of the host larvae to parasitism (Godfray 1994; Quicke 1997). However, we do not believe that these factors alone account for the low number of host larvae successfully parasitized within a population. In the field *C. melitaearum* adults successfully move between larval groups (Lei and Camara 1999), and the defensive behavior of caterpillars has not been found to deter *C. melitaearum* (Lei 1997). Parasitism of late-instar larvae in the laboratory is almost always successful suggesting insignificant physiological defense against parasitism by *C. melitaearum* (Table 3). Parasitism of early-instar larvae may indeed be thwarted by host physiological defenses, but the extent of such defense is presently unknown.

If host availability limits parasitoid population size we would likely have detected a negative impact of the parasitoid on the host population. This has occurred in the Åland islands when the host populations were large and close together (Lei and Hanski 1997; van Nouhuys and Hanski 1999). However, for the majority of parasitoid-occupied populations no great impact on the host has been observed (Table 4 model a, see also van Nouhuys and Hanski 1999). The analyses presented here do not address possible delayed density dependence in the parasitoid or host population dynamics.

Unfavorable weather

Cool or rainy weather can reduce the amount of time an adult parasitoid spends searching for hosts (Juillet 1964; Godfray 1994) and increase the development time of para-sitoids and hosts (Porter 1983; Gould and Elkinton 1990; Godfray 1994), which may lead to small populations. Some mortality of parasitoids is also due to weather events that kill both parasitized and unparasitized host larvae. For example, between 16 and 50% of the host larval groups present in the autumn die during the winter (S. van Nouhuys, M.C. Singer and M. Nieminen, unpublished work).

Weather does occasionally directly kill parasitoids. For example, in the spring of 1999 we observed one *C. melitaearum* larva attempting to slowly spin its cocoon during a cold rainy afternoon (6°C). At our next visit we found the dead, dried-out larva in a partially completed cocoon. We do not believe that this is a common event because we found no other partially formed cocoons, though it is possible that poorly formed cocoons were eaten by predators before we found them.

In summary, *C. melitaearum* successfully parasitizes relatively few hosts in the field considering its potential fecundity. A large fraction of the immature wasps are then killed via larval competition, predation, parasitism, unknown causes, and weather, leaving the population small and prone to local extinction. Mortality of cocoons was greater in the larger populations, suggesting that mortality, especially that due to predation and parasitism, is density dependent. In contrast to the likely density-dependent population limitation by natural enemies, we have not found evidence of *C. melitaearum* being limited by host population size (resource limitation) under most conditions. *C. melitaearum* thus appears to be kept at small enough population sizes by "top-down" factors to make within-population resource limitation nearly insignificant.

What are the consequences of small population size?

Small populations are likely to go extinct via environmental and demographic stochasticity. The extinction probability of small parasitoid populations is elevated because, especially in the spring generation, there is only a small window of opportunity for the adult wasp to parasitize the host. If few nests are previously parasitized there is a small range of adult emergence times, which would increase the likelihood of the parasitoid missing the vulnerable stages of the host (S. van Nouhuys and G.C. Lei, unpublished work).

Extinction risk is also increased by the reproductive and genetic consequences of there being only a few individuals present. The frequency of sib mating, not mating at all and mating late in life increases with decreasing population size. This, in combination with low gene flow due to the geographical isolation of populations, leads to low genetic diversity, and may cause inbreeding depression (Falconer 1989; Lande 1995; Antolin 1999). Haplodiploidy enables unmated *C. melitaearum* females to produce male offspring so their genes can persist to the subsequent generation. However, in small isolated populations the male offspring are likely to have only siblings or close relatives to mate with, or no mates at all. The gravity of this situation will depend on how well adapted *C. melitaearum* is to sib-mating (Godfray and Hardy 1993; Quicke 1997), an issue that is poorly understood at present.

Metapopulation structure and regional persistence

Some sources of mortality, such as competition with *H. horticola*, are not likely to vary spatially or between populations. *H. horticola* is consistently abundant in all

of the host populations occupied by *C. melitaearum*. Other sources of mortality are spatially and temporally variable. Examination of Table 1 suggests that predation and parasitism differ between host populations, and within the same population over two consecutive years. This, in combination with spatial variation in weather, host population dynamics, and limited dispersal probably allows for local parasitoid population sizes to increase and decrease somewhat independently. Spatially asynchronous population dynamics throughout the region can allow *C. melitaearum* to exist in one location while in another area it becomes extinct. However, if the host populations were to become more fragmented, the distance parasitoids would have to travel in order to colonize other host populations would increase, causing the rate of successful colonizations to decrease.

The small number of *C. melitaearum* populations relative to the number of host populations in the Åland islands leads one to ask whether *C. melitaearum* is moving toward extinction or if it is rare at equilibrium. Over the last 7 years the number of *C. melitaearum* populations has on average declined, but not monotonically. The number of host populations has also declined on average. It is impossible to say whether this is part of the normal fluctuations of population sizes or whether both species are declining.

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