ORIGINAL ARTICLE

Indirect interaction between butterfly species mediated by a shared pupal parasitoid

Saskya van Nouhuys · Thomas S. Kraft

Abstract Indirect interactions among species can greatly affect their abundances and the structure of the community they live in. Using a field experiment, we tested the hypothesis that congeneric butterfly species interact indirectly through a shared pupal parasitoid. We predicted that symmetrical apparent competition would lead to high parasitism of both species, and the effect would increase with regional butterfly abundance. Instead, parasitism of one host, *Melitaea cinxia*, was reduced in the presence of the second host, *M. athalia*. Parasitism of *M. athalia* did not differ whether or not *M. cinxia* was present. This pattern did not vary with regional butterfly abundance, though overall rate of parasitism did. Details of the experiment suggest that the apparent commensalism occurred because *M. cinxia* pupae are protected by silk tents whereas *M. athalia* are exposed, causing locally foraging parasitoids to favour the more accessible host where the two are present together. The local short-term apparent commensalism favouring *M. cinxia* opposes the landscape scale trend, in which parasitism increases where butterfly density is high. The outcome of this study illustrates short-term apparent commensalism, that host suitability can depend on relative accessibility, and that indirect interactions occurring at different scales may be in opposition.

Keywords Apparent competition · Commensalism · Community · Foraging behaviour · *Melitaea cinxia* · *Pteromalus apum*

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Introduction

Apparent competition and other indirect interactions occurring across spatial and temporal scales are known to have profound effects on abundances of species (Settle and Wilson 1990; Brockhurst et al. 2006; Cronin 2007), and on community structure (Wootton 1994; Bonsall and Hassell 1999; Mitchell et al. 2006; van Veen et al. 2006). These indirect interactions are equally, if not more, important to the ecology of some species than direct interactions such as resource competition and predation. However, indirect interactions may be complex, difficult to identify and conflicting (Holt 1977; Chaneton and Bonsall 2000). The rate of predation or parasitism experienced by a species depends not only on its own susceptibility and density, but also on the availability and relative suitability of other species that share the same enemies. One prey species may draw enemies away from another (as in Settle and Wilson 1990; Heimpel et al. 2003; Cronin 2007), or the combined density of several prey species can either increase or decrease the chance of predation of all individuals (Abrams et al. 1998; Morris et al. 2004; Tack et al. 2011). Over time, the population size of an enemy will depend on the use of combined prey species, and changes in enemy population size may affect each prey species differently.

Taking into account the range of temporal and spatial scales of indirect interactions among prey species that occur in a community, almost any type of interaction can be predicted (Holt and Lawton 1994; Holt and Barfield 2003). At one extreme for instance, as in long-term apparent competition (over multiple generations), vulnerable species may be entirely excluded from a habitat due to an abundant shared natural enemy (Holt 1977; Müller et al. 1999). At the other extreme, the presence of multiple host species in a single habitat patch may lead to an apparent

mutualism if the likelihood of predation of all species is reduced due to an enemy that increases handling time with prey density (as in Hassan 1976). Indirect interactions, especially apparent competition, have been demonstrated at small spatial or temporal scales, and to a lesser extent are reported at larger scales (Settle and Wilson 1990; Östman and Ives 2003; Morris et al. 2005; Hambäck et al. 2006; Whittmer et al. 2007; Oliver et al. 2009).

We present a study of the indirect interaction between two butterfly species, *Melitaea cinxia* (L.) and *Melitaea athalia* (Rottemburg) (Lepidoptera: Nymphalidae), due to a shared pupal parasitoid, *Pteromalus apum* (Retzius) (Hymenoptera: Pteromalidae). These insects are part of a well-studied community in the Åland Islands of SW Finland (Lei et al. 1997; van Nouhuys and Hanski 2005). We used a field experiment repeated over 2 years to test for short-term (within one parasitoid and host generation) apparent competition under the condition that host density increases with the number of host species present. We interpreted the results on their own and in the context of estimates of regional butterfly abundance. Two small laboratory studies were also conducted to confirm the suitability of both host species, and the interval of susceptibility to parasitism.

The outcome of the field experiment should depend primarily on parasitoid behaviour. If *P. apum* adults from the surrounding habitat aggregate in response to local density (Bezemer et al. 2010, but see Lozano et al. 1997) then doubling the local density of hosts by having two rather than one host species in a plot may increase the rate of parasitism. Alternatively, if *P. apum* do not aggregate, then the chance of being parasitized by the resident wasps would decrease as the number of host individuals increased (Heimpel and Casas 2008). Under either condition the effect of the parasitoid on the two species can be asymmetrical, especially if they are not equally suitable. The magnitude and even sign of the effects would depend on the relative suitability of each host species (Hambäck et al. 2006), and the extent to which the presence of one host species modifies the behaviour of the wasp in response to the second host species (Stenberg et al. 2007). Finally, we expect the strength of this indirect interaction to depend on regional abundance of the two butterfly species. That is, the extent to which the density of one host species affects the parasitism of the other will depend on the surrounding density of hosts and the parasitoids (Holt 1977).

Materials and methods

The study system

The butterfly *M. cinxia* lives in open meadows, feeding on *Veronica* and *Plantago* (Plantaginaceae), in Europe and temperate Asia. It has declined or become regionally extinct in most of Europe, but is abundant in the Åland Islands of SW Finland where it inhabits a fragmented network of meadows. The biology and population ecology of *M. cinxia* and most of its parasitoids in the Åland Islands are well studied (Kuussaari et al. 1995; Hanski et al. 2004; van Nouhuys and Hanski 2005). In an area of 50 by 70 km there are about 4000 small meadows that are suitable for local butterfly populations (Fig. 1). At any one time *M. cinxia* occupies 300–500 of these meadows. Each

Fig. 1 A map of *Melitaea cinxia* habitat patches in the Åland Islands. *Small light grey spots* indicate patches suitable for *M. cinxia*. The *symbols* indicate the locations of habitat patches used in the experiments both years (*circle*), 2008 (*square*) and 2009 (*triangle*)
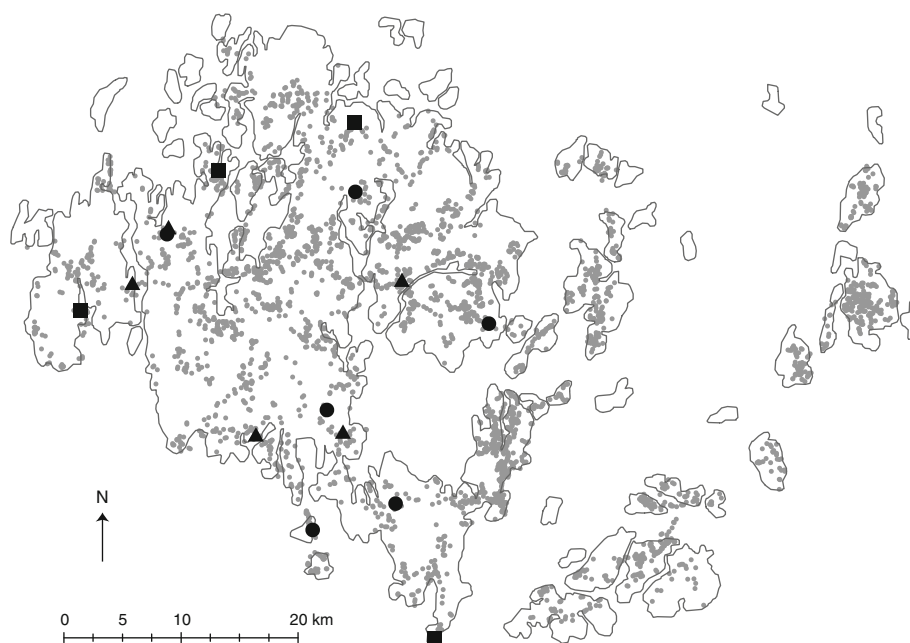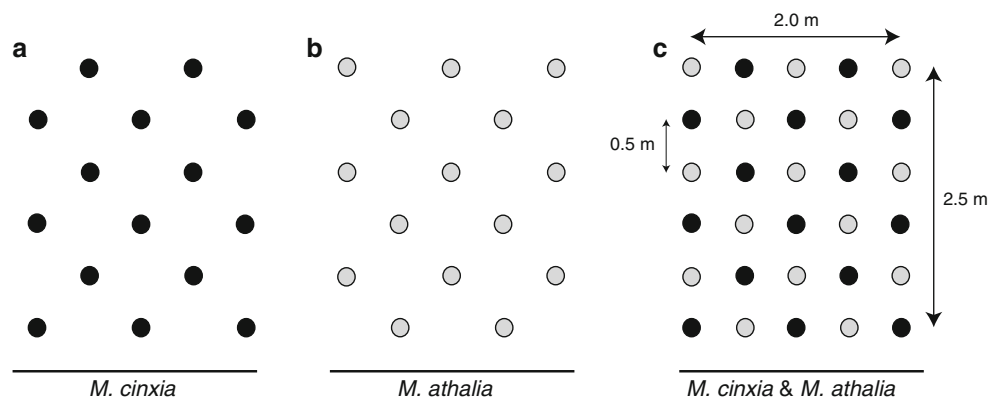
Fig. 2 Design of the experimental plots. The three treatments **a** low density *Melitaea cinxia* (*black circles*), **b** low density *M. athalia* (*grey circles*) and **c** high density plots containing both species (*black* and *grey*) were replicated in 11 (2008) and 10 (2009) habitat patches. Each *circle* represents a potted host plant with a host pupa on it

meadow is surveyed annually, and the number of *M. cinxia* larval nests is counted as part of a long-term study (Nieminen et al. 2004).

The congener *M. athalia* inhabits meadows, clearings and sparse forest, feeding on a range of plants in the families Plantaginaceae and Orobanchaceae (Warren 1987; Wahlberg 1997; Reudler Talsma et al. 2008). This butterfly has also declined throughout Europe (Warren 1992; Schwarzwälder et al. 1997) but is abundant in southern Finland and the Åland Islands (Wahlberg 1997). The distribution and dynamics of *M. athalia* in Åland are not well studied, but based on transect walks in Åland (Schulman 2005; Torri 2007), and yearly visitation, we know that it is present almost everywhere that *M. cinxia* occurs, as well as in some places, such as forest edges, where *M. cinxia* is absent. While the two butterflies feed on some of the same host plant species in Åland (Reudler Talsma et al. 2008), neither is generally limited by food, and they do not compete directly for resources.

Both species of butterflies have one generation per year in the study area. Adults lay eggs in June. The larvae hatch and feed until September and then diapause for the winter. In April they resume feeding as larvae and pupate in May. *Melitaea cinxia* live gregariously as larvae, dispersing to pupate singly in the leaf litter in the vicinity of host plants (Kuussaari et al. 2004). *Melitaea athalia* larvae are solitary after the first few instars, and pupate in the leaf litter (Wahlberg 1997).

The two butterfly species share two generalist pupal parasitoid species, *P. apum* and *Ichneumon graciliconis*, and one more specialized pupal parasitoid *I. cinxiae* (Lei et al. 1997; Shaw et al. 2009). Of these pupal parasitoids *P. apum* is the only one that is abundant in the research system. Though this parasitoid has been recorded mostly from Melitaeini butterflies, it is considered a broad generalist, parasitizing many butterfly species and even pupae of Megachiline bees (Askew and Shaw 1997; Shaw 2002; Shaw et al. 2009). Adult *P. apum* are small (1–2 mm). Like other gregarious *Pteromalus*, a mother will lay multiple

eggs in a single host pupa, and multiple females will successfully parasitize a single host (Askew and Shaw 1997; Dorn and Beckage 2007). Consequently, a brood of 1–110 *P. apum* eclosing from a single host pupa may include both siblings and non-siblings (T.S. Kraft and S. van Nouhuys, unpublished data).

The field experiment

The field experiment was conducted in the summers of 2008 and 2009. There were three treatments: *M. cinxia* pupae alone, *M. athalia* pupae alone, and the two species together (Fig. 2). In each single species treatment, 15 potted plants, each with a single host on it, were placed in a 2.5 × 3 m checkerboard pattern, each pot 1 m apart. In the two species (high density) plots, 15 pots of each species were placed in the grid, so the density was twice as high and the pots were 50 cm apart (Fig. 2). These densities are on par with what is found in the field where the larvae pupate in the vicinity of host plant aggregations. Each set of three treatments was replicated 11 and 10 times in 2008 and 2009 respectively. To include a range of natural regional butterfly densities, the replicates were in habitat patches spread over the Åland Islands (Fig. 1). Within each *M. cinxia* habitat patch three locations of similar host plant density, sun exposure and slope were chosen, at least 25 m apart. One of the three treatments was assigned randomly to each location.

The hosts were placed in the field as last instar larvae rather than as pupae to accommodate parasitoids that use odours associated with feeding or pupation as cues to find the host pupae (Godfray 1994). This also allowed the hosts to pupate in natural locations, which can influence their vulnerability to parasitism. Either *P. lanceolata* or *V. spicata* was used as the host plant in each patch, depending on which plant species was naturally abundant. After a larva was placed on a potted plant in the field, the plant was covered with a coarse mesh cloth that prevented the larvae from escaping, but allowed the parasitoids free access. In 2008 the

mesh covers were left on the pots throughout the experiment. In 2009 the covers were removed after pupation to allow access to the more rare, large *Ichneumon* parasitoids.

The host larvae used in the experiment came from laboratory colonies originating from and maintained in Åland, Finland. The plants were transplanted from natural populations in Åland the previous year. They were maintained outside during the winter, and in a greenhouse during the growing season. Each 25-cm diameter pot was filled with a 1:1 mixture of potting soil and natural coarse gravel to approximate local growing conditions.

The plots were set out in May, synchronously with the natural host populations. In 2008 the plots were placed in the field over 10 days, and each plot was left out for 12 days. In 2009 they were set up over 8 days, and each plot was left out for 14–18 days, depending on the speed at which the larvae pupated in different local microclimates. This interval was chosen to allow for pupation in the first few days and include the entire period of vulnerability of the host pupae. The vulnerable interval of the pupa was confirmed in a laboratory experiment (see below). In 2009 we recorded the location of each pupa (hanging from plant or debris, attached to the inside or outside edge of the pot, or net), if the pupa was surrounded by a silken tent or exposed, and if the silk tent was torn by removal of the mesh cover.

The pupae were next brought into the lab and kept individually in mesh-topped cups at ambient laboratory temperature until adult butterflies or parasitoids eclosed. Pupae from which nothing emerged were dissected and scored as containing dead parasitoid(s), a dead butterfly or a dead butterfly pupa. The pupae that died as a result of predation or for some unknown reason were excluded from the analysis of rate of parasitism.

The parasitoids were identified to species, counted, and the sex of each was determined. Using a taxonomic key (Askew and Shaw 1997) there was still some ambiguity about the morphologically similar *P. apum* and *P. puparum*, both of which have been reported from *M. cinxia* in Åland previously (Lei et al. 1997). We sent a representative sample of the range of morphologies to Askew who identified them as entirely *P. apum*.

Post facto comparison of parasitism of M. cinxia with and without silk tents

To test the idea that silken tents around *M. cinxia* (Fig. 3) could protect them from parasitism by *P. apum*, we compared parasitism of *M. cinxia* with and without silk tents. This was possible because we inadvertently partially destroyed the silk tents of just under half the *M. cinxia* while removing the mesh covers from the pots in 2009. Data from 2008 were not used because that year we did not

Fig. 3 Photograph of a silk tent surrounding a *Melitaea cinxia* pupa. The thin silk tent (marked in the center by the letter *A*) is built just before pupation. The pupa is hanging in the centre of the tent, attached to the underside of a leaf

remove the mesh covers over the plants so none of the silk tents were disturbed.

Regional and local abundances of butterflies

To detect an association of the surrounding butterfly density with rate of parasitism we estimated the regional densities of butterflies around each study site. Due to constraints of the butterfly biology and available information this was done differently for the two butterfly species. For *M. cinxia* we categorized each region on a scale of 0–4 based on the number of nests in the surrounding habitat patch network in fall 2008 (as measured during an annual *M. cinxia* survey, Nieminen et al. 2004). At level 0 there were no *M. cinxia* in the surrounding landscape, and at level 4 there was the highest density in the surrounding habitat patches. For *M. athalia*, we categorized each region on a scale of 1–4 qualitatively based on observation during the adult flight season and previous transect walks (Schulman 2005; Torri 2007). No region was designated as entirely lacking *M. athalia*.

For *M. cinxia* we also estimated the abundance on a smaller local scale, as the number of *M. cinxia* larval nests in the habitat patch used for each study site, counted in the autumns of 2007 (for the 2008 experiment) and 2008 (for the 2009 experiment). We did not estimate the local *M. athalia* abundance at the scale of individual patches because the larvae are inconspicuous, making their density impossible to assess. The adult *M. athalia* abundance is also difficult to compare among patches because the flight period is long and the density is low at any one time (see Torri 2007).

Laboratory experiments

We conducted two small laboratory experiments in July 2009 to quantify the effects of host pupal age on parasitism, and to compare the suitability of the two host species under laboratory conditions. The *P. apum* used for these experiments were those that emerged from the field experiment in 2009. Upon eclosion they were mated and fed honey-water (1:3) absorbed into cotton wool, and kept at room temperature until needed. The host pupae were from the same origin as described above, but were kept as larvae in diapause for two extra weeks in the spring to delay their development.

Under laboratory conditions both *M. cinxia* and *M. athalia* remain as pupae for about 12 days. In the field, development time ranges from 10 to 20 days, depending on temperature. Individual female parasitoids were placed in 9-cm Petri dishes with individual *M. cinxia* pupae aged 0 days (still soft, less than 12 h after pupation), to 7 days. Each pupa age was replicated 6–8 times over 2 weeks. We did not include older pupae because starting on the eighth day, though *P. apum* appear to attempt to parasitize, the butterfly is quite well developed and we have never seen successful parasitism (S. van Nouhuys, personal observation).

In a second laboratory experiment we compared the performance of *P. apum* on the two host species. Three to seven day old mated *P. apum* females were placed individually in a 9-cm petri dish with a single 4-day-old *M. cinxia* or *M. athalia* pupa for 24 h under ambient laboratory conditions. This was replicated 30 times for *M. cinxia* and 17 times for *M. athalia* in July 2009.

For both laboratory experiments we recorded date of parasitism, identity of wasp (including the host species from which it came), host pupal weight (at day 0), eclosion of wasps or butterflies, rate of development to adulthood, number of progeny *P. apum* (brood size), and the sex of each *P. apum*.

Statistical analyses

Field experiment

We evaluated the association of the binomial response variable *parasitized* with three explanatory variables, and the interactions among them, using the statistical package R (R Development Core Team 2011), and generalized linear mixed models (GLMMs) from the package glmmML (Broström and Holmberg 2011). We modelled parasitism (0/1 response) using a binomial error distribution and a logit link function. As determined by the design of the experiment, the main factors of interest in both years were the categorical variables *host density* (high or low), *host*

species (*M. athalia* or *M. cinxia*), and the interaction of host density with host species. *Habitat patch* (Fig. 1) was included as a random categorical blocking factor to account for unmeasured differences between habitat patches, such as surrounding habitat, and small-scale temperature and rainfall differences. The continuous variable *date placed* was included to account for variation associated with when larvae were placed in the field over a 10 day period. Finally, the binomial models were tested for overdispersion and the distribution of the residuals was evaluated. Data from 2008 and 2009 were originally analyzed in a single statistical model but were ultimately separated so that ecologically important factors would not need to be interpreted as part of complicated three way interactions involving year.

Silk tents around *M. cinxia* in 2009

The effect of silk tent removal on parasitism of *M. cinxia* was examined using the 2009 *M. cinxia* data, using GLMMs implemented in R (Broström and Holmberg 2011; R Development Core Team 2011). We modelled parasitism (0/1) using a binomial error distribution and a logit link function. The main factors were the categorical variables *host density* (high or low), *silk tent* (present or absent), and the interaction of *host density* with *silk tent*. As above, *habitat patch* was included as a random categorical blocking factor, and *date placed* was included as a continuous variable. The model was tested for overdispersion and the distribution of the residuals was evaluated.

Regional and local butterfly abundance

To test the association of surrounding butterfly density with rate of parasitism we performed a logistic regression using JMP (SAS Institute 2010), with regional abundance [on a scale of 0 (1) to 4] of *M. cinxia* and *M. athalia*, or local (patch) *M. cinxia* population size (number of nests) as ordered categorical explanatory variables. We did not include habitat patch in the model because abundance varied directly with habitat patch so the two factors were confounding. As above, the model included *host density*, *host species* (*M. athalia* or *M. cinxia*), *date placed* and the interaction of host density with host species. This statistical model included both years, with *year* as a categorical factor along with the interaction of year with host density and species.

Laboratory experiments on pupa age and species

For both experiments we analyzed rate of successful parasitism (0/1) using logistic regression in JMP (SAS Institute 2010), with *date*, *pupa weight* and *pupa age* (or

Table 1 Generalized linear mixed model analysis of parasitism of *M. cinxia* and *M. athalia* pupae by the parasitoid *P. apum* in 2008 and 2009

Variable	2008[a]		2009[b]	
	Coefficient (SE)	*z* value	Coefficient (SE)	*z* value
Intercept	1.13 (0.75)	1.51 ns	0.35 (0.85)	0.41 ns
Species (*M. cinxia*)	−1.65 (0.38)	4.30***	0.54 (0.31)	1.72 ns
Density (low)	−0.12 (0.33)	0.37 ns	0.04 (0.32)	0.13 ns
Date placed	−0.15 (0.12)	1.33 ns	−0.15 (0.13)	1.16 ns
Species × density (*M. cinxia*, low)	1.19 (0.52)	2.28*	−0.76 (0.46)	1.67 ns

Patch is included in the model as a random variable

Significance level *** ≤ 0.001; * ≤ 0.05

[a] Residual deviance: 402 on 353 *df*

[b] Residual deviance: 479 on 393 *df*

species) and *wasp origin* (host species in which it developed) as factors. We analyzed the brood size and rate of development using ANOVA and the same factors.

Results

Pupation site

Both butterfly species generally pupated just above the soil, suspended from a silk patch attached to the underside of a low host plant leaf, dead leaf, or piece of debris. Some were attached to the inside or outside edge of the pot, or pupated on the net surrounding the plant. *Melitaea cinxia* pupae were almost all hanging suspended in the center of a tent formed from a thin silk web (Fig. 3), whereas *M. athalia* were all exposed with no silk around them. The presence of the silk tent around *M. cinxia* was not known before this study.

Association of parasitism with host density and species

Overall, parasitism varied from 0 to 100% (mean 40%) among treatment plots and patches, and was slightly higher in 2009 than in 2008. In 2008 parasitism of *M. athalia* was higher than *M. cinxia* ($z = 4.30$, $P < 0.0001$; Table 1). This was mainly due to low parasitism of *M. cinxia* in the high density treatments (species × density interaction, $z = 2.28$, $P < 0.05$; Table 1; Fig. 4a). In 2009, there was not an effect of host species or density on parasitism (Table 1; Fig. 4b).

Effects of silk tents

Parasitism of *M. cinxia* pupae with broken silk tents was significantly higher than parasitism of those with intact silk
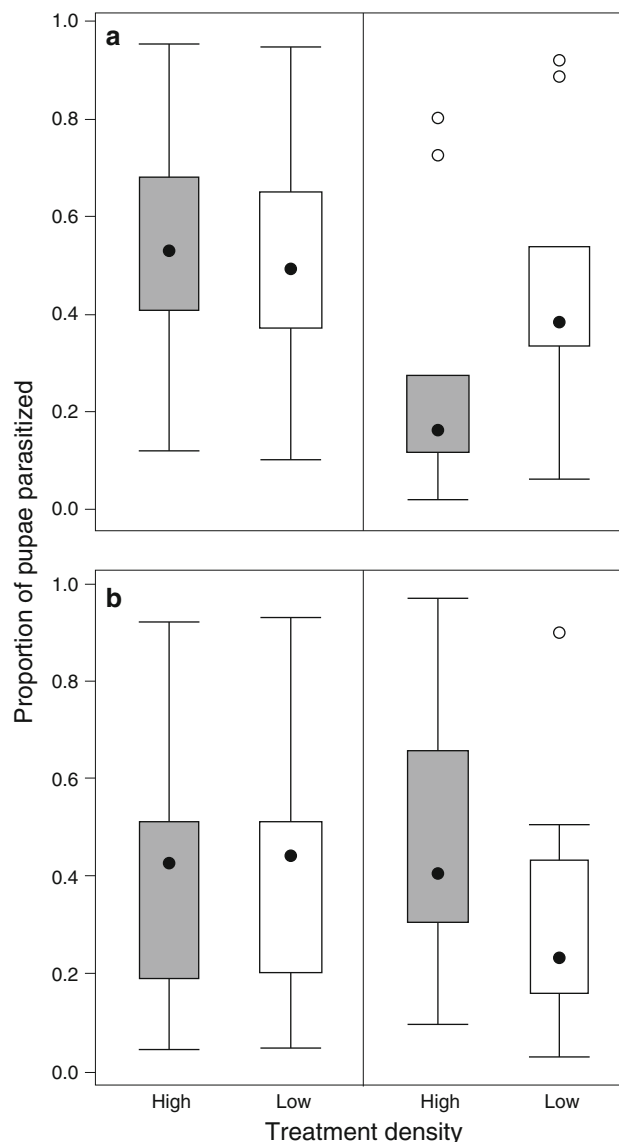

Fig. 4 Plot of rate of parasitism of *Melitaea athalia* (*grey rectangles*) and *Melitaea cinxia* (*white rectangles*) at low (single species) and high (both species together) densities in 2008 (**a**) and 2009 (**b**). *Black dots* represent the median fraction of pupae parasitized. The lower and upper limits of rectangles represent the first and third quartiles, *error bars* represent 1.5 times the interquartile range, and *open dots* represent outliers (values beyond the *bars*). See Table 1 for statistical analysis

tents (Table 2; Fig. 5). 55% of the exposed *M. cinxia* were parasitized whereas only 23% of the *M. cinxia* pupae in silk were parasitized. This contrast was greater in the high than in the low density plots (Table 2; Fig. 5).

Rate of parasitism and surrounding butterfly abundance

Overall, the rate of parasitism increased at least twofold with regional abundances of both *M. cinxia* (likelihood

Table 2 Generalized liner mixed model analysis of parasitism of *M. cinxia* by *P. apum* in 2009, testing the effect of the silk tents

Variable	Coefficient (SE)	z value
Intercept	2.30 (0.82)	2.82**
Silk tent (yes)	−2.27 (0.54)	4.24***
Host density (low)	−1.54 (0.48)	3.23***
Date placed	−0.44 (0.19)	2.39*
Silk tent × density (yes, low)	2.06 (0.74)	2.80**

Patch is included in the model as a random variable

Significance level *** ≤0.001; ** ≤0.01; * ≤0.05

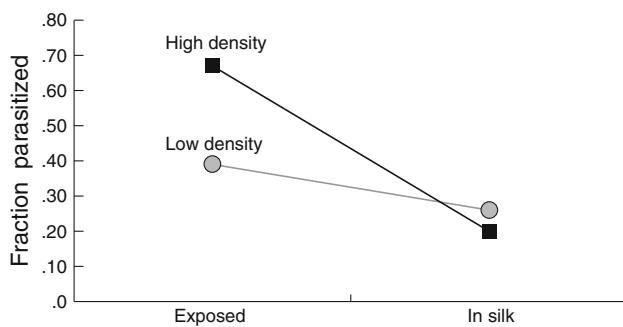Residual deviance: 194 on 188 *df*

Fig. 5 The fraction of *Melitaea cinxia* pupae parasitized in 2009 that were exposed ($n = 106$ pupae) versus enclosed in a silken tent ($n = 93$ pupae) in high density (*black squares*) and low density (*grey circles*) plots. See Table 2 for statistical analysis

ratio $\chi^2_{4df} = 24.55$, $P < 0.0001$) and *M. athalia* (likelihood ratio $\chi^2_{3df} = 15.23$, $P < 0.0016$). The effect differed between years and species (three way interaction likelihood ratio $\chi^2_{year \times abundanceA \times species, 3df} = 11.77$, $P < 0.01$; likelihood ratio $\chi^2_{year \times abundanceA \times species, 4df} = 31.87$, $P < 0.0001$), but not systematically. Parasitism rate was not associated with the number of *M. cinxia* nests in the local habitat patch (likelihood ratio $\chi^2_{1df} = 0.78$, $P = 0.37$).

Laboratory experiment on host pupa age

Pteromalus apum probed and appeared to parasitize all of the *M. cinxia* pupae. Pupae were susceptible to parasitism from the day of pupation through day 6. None of the 7 day old pupae were successfully parasitized (likelihood ratio $\chi^2_{1df} = 6.67$, $P < 0.01$; Fig. 6), and instead yielded healthy butterflies. Successful parasitism (0/1) was independent of pupa weight and the origin of the mother (from *M. cinxia* or *M. athalia*), and varied significantly among days (likelihood ratio $\chi^2_{weight, 1df} = 0.14$, $P = 0.71$; $\chi^2_{origin, 1df} = 1.54$, $P = 0.21$; $\chi^2_{date, 9df} = 17.94$, $P < 0.0358$). Brood size ranged from 1 to 38 (mean 21, SD 9.52) and was independent
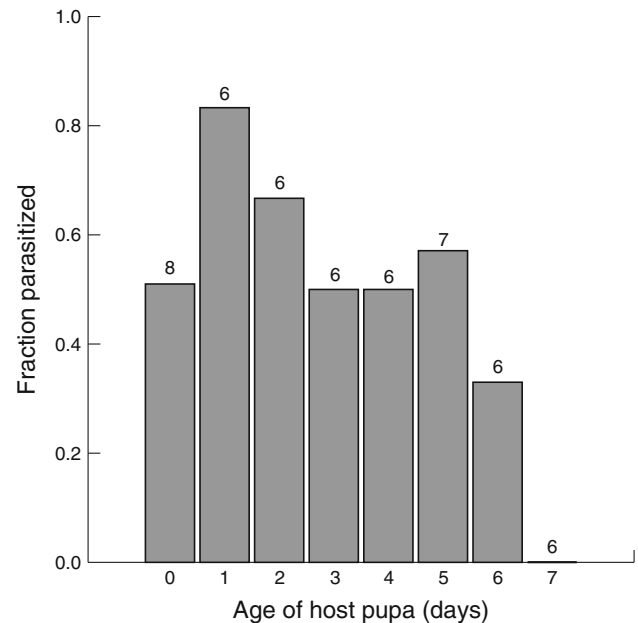
Fig. 6 The fraction of *Melitaea cinxia* pupae parasitized at ages 0 through 7 days by *Pteromalus apum* in the laboratory experiment. The *number* in *each bar* indicates the number of trials. No 7 day old pupae were successfully parasitized

of host age and weight ($F_{age, 1df} = 0.38$, $P > 0.54$; $F_{wt, 1df} = 9.02$, $P = 0.62$). Development time was consistently about 18 days (mean = 17.64, SD = 1.60) and was also independent of host age and weight ($F_{age, 1df} = 1.27$, $P = 0.33$; $F_{wt, 1df} = 01$, $P = 0.91$).

Laboratory experiment on host species

Pteromalus apum successfully parasitized about the same fraction of *M. cinxia* and *M. athalia* pupae (88 and 87% respectively) ($\chi^2_{species, 1df} = 1.04$, $P = 0.31$) and the brood sizes were equal on the two hosts with a mean of 43 (SD 34) in *M. cinxia* and 44 (SD 21) in *M. athalia* ($F_{species, 1df} = 0.003$, $P = 0.96$).

Discussion

Insects that share the same natural enemies potentially influence each other's abundances by either increasing or decreasing parasitism or predation (Settle and Wilson 1990; Bonsall and Hassell 1999; van Veen et al. 2006). The strength and even direction of an indirect interaction depend on the mechanisms of the interaction, as well as the scale (spatial and temporal) at which it is being observed (Holt 1977). We address the local short term indirect interaction between two butterfly species due to a shared pupal parasitoid and speculate about the contrast between local and regional scale indirect interactions.

Parasitism in the experimental plots

The overall rate of parasitism of host pupae was unrelated to host density, suggesting that *P. apum* forage locally (within plots) (as suggested by Hassan 1976), rather than recruiting from the surroundings in response to density. This type of behaviour is characteristic of both type II and type III functional response (Holling 1959a). However, in 2008 parasitism of *M. cinxia* was reduced in the high density plot while parasitism of *M. athalia* did not change with density. That is, the proximity of *M. athalia* pupae reduced parasitism of *M. cinxia* pupae by about 30%. This could come about if parasitism of *M. cinxia* is negatively density dependent regardless of which species causes the increased density. Alternatively, the decrease of parasitism of *M. cinxia* could be a specific response to the increase of *M. athalia* due to differences in host suitability or parasitoid preference.

In the second year (2009), parasitism was unrelated to host species or density, and there was no interaction. The environmental conditions (temperature and plot locations) were quite similar in the 2 years, and the only obvious difference between the years was a procedural change. We believe that this difference provides strong evidence for a mechanism that could cause *M. cinxia* to be parasitized at a lower rate in the presence of *M. athalia*. In the first year the silk tents around *M. cinxia* pupae remained intact throughout the experiment. In the second year, we inadvertently destroyed just under half of the silk tents of *M. cinxia* during removal of the mesh cover over the pots. Later, we found that many more of the exposed *M. cinxia* pupae were parasitized than were the pupae in intact tents (Fig. 5). The destroyed tents were those that were partially attached to the mesh net or were torn when removal of the net top caused the plant to move in a way that tore the delicate silk. If we assume that the destroyed tents were a representative sample of all of the tents then it is likely that the silk tent protects *M. cinxia* against parasitism by *P. apum*.

The pattern of apparent commensalism (+, 0) favouring *M. cinxia*, rather than apparent competition (−, −), occurred even though the two host species were equally suitable under simplified laboratory conditions in 2008. The pattern was absent when half the silken tents surrounding *M. cinxia* pupae was removed in 2009. We suggest that where the two species of pupae are presented together, a parasitoid that forages locally ends up using the more accessible host (*M. athalia*) over the less accessible host (*M. cinxia*). The wasps may either encounter or choose *M. athalia* more readily than *M. cinxia* pupae, or the handling time of *M. athalia* pupae may simply be lower than that of *M. cinxia*. Where *M. cinxia* is presented alone, locally foraging parasitoids behave differently, spending greater effort to parasitize the less accessible host.

Regional scale

Regionally, at the scale of a landscape, the occurrence of multiple host butterfly species that do not interact directly (compete for resources) should increase the abundance of *P. apum* above what it would be if there were a single host species present because the combined host species would provide a large and reliable resource. If *M. cinxia* and *M. athalia* are primary hosts of *P. apum*, then where their density is high we expect the density of the gregariously developing *P. apum* to be high. This should lead to a high rate of parasitism simply due to the population level numerical response of the parasitoid over time, as described by Holling (1959b) and many others. However, the same pattern would also exist if the densities of the two *Melitaea* were simply indicative of overall regional butterfly (host) density, which may indeed be the case.

We found that parasitism tended to be high where either butterfly species was regionally abundant, but was unrelated to the size of natural *M. cinxia* populations at the local patch scale. Thus at a small scale (within a treatment plot or single habitat patch) *M. cinxia* benefits from the co-occurrence of *M. athalia* because individual foraging parasitoids are drawn away from *M. cinxia* (Fig. 4a). On the landscape scale however, the relationship differs because parasitism of *M. cinxia* increases with regional butterfly density.

In Åland, *M. cinxia* lives as a metapopulation made up of many small populations in a fragmented habitat. Reduction in local population sizes, caused by something such as pupal parasitism, increases the frequency of stochastic local extinctions, leading to sparseness and reduced stability of the entire metapopulation (Hanski 1998). For *M. cinxia* the large scale negative effects of sharing a parasitoid with a co-occurring butterfly may be partially mitigated at a local scale by the behavioural response of foraging parasitoids in the presence of more accessible host pupae. While the mechanisms of conflicting roles of indirect interaction are specific to this research system, the notion that indirect interactions occurring at different scales can be conflicting is general, and potentially important in many communities.

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