Oecologia (2003) 135:304–312
DOI 10.1007/s00442-003-1185-8

COMMUNITY ECOLOGY

Grit Kunert · Wolfgang W. Weisser

The interplay between density- and trait-mediated effects in predator-prey interactions: a case study in aphid wing polymorphism

Received: 1 July 2002 / Accepted: 12 January 2003 / Published online: 27 February 2003

Abstract Natural enemies not only influence prey density but they can also cause the modification of traits in their victims. While such non-lethal effects can be very important for the dynamic and structure of prey populations, little is known about their interaction with the density-mediated effects of natural enemies. We investigated the relationship between predation rate, prey density and trait modification in two aphid-aphid predator interactions. Pea aphids (*Acyrthosiphon pisum*, Harris) have been shown to produce winged dispersal morphs in response to the presence of ladybirds or parasitoid natural enemies. This trait modification influences the ability of aphids to disperse and to colonise new habitats, and hence has a bearing on the population dynamics of the prey. In two experiments we examined wing induction in pea aphids as a function of the rate of predation when hoverfly larvae (*Episyrphus balteatus*) and lacewing larvae (*Chrysoperla carnea*) were allowed to forage in pea aphid colonies. Both hoverfly and lacewing larvae caused a significant increase in the percentage of winged morphs among offspring compared to control treatments, emphasising that wing induction in the presence of natural enemies is a general response in pea aphids. The percentage of winged offspring was, however, dependent on the rate of predation, with a small effect of predation on aphid wing induction at very high and very low predation rates, and a strong response of aphids at medium predation rates. Aphid wing induction was influenced by the interplay between predation rate and the resultant prey density. Our results suggests that density-mediated and trait-mediated effects of natural enemies are closely connected to each other and jointly determine the effect of natural enemies on prey population dynamics.

G. Kunert (✉) · W. W. Weisser
Institute of Ecology, Friedrich-Schiller-University,
Dornburger Strasse 159, 07743, Jena, Germany
e-mail: Grit.Kunert@uni-jena.de
Tel.: +49-3641-949444
Fax: +49-3641-949402

Keywords Induced defence · Wing induction · Density dependence · Chrysopidae · Syrphidae

Introduction

Natural enemies have diverse effects on the behaviour, life history, physiology, and morphology of their victims (Sih 1997; Lima 1998b; Tollrian and Harvell 1998; Nakaoka 2000; de Roos et al. 2002). These non-lethal effects are the result of trait modifications by the prey under the risk of predation and are often termed ‘trait-mediated’ effects (Abrams 1995; Tollrian and Harvell 1998; Peckarsky et al. 2001; Peacor 2002). In contrast to direct predation that immediately changes prey population density, trait-mediated effects modify the interaction between predator and prey with sometimes drastic consequences for both prey and predator population growth (Abrams 1995; Sih 1997; Tollrian and Harvell 1998; Peckarsky et al. 2001; Peacor 2002). For example, under the risk of predation, prey may switch to forage in less productive habitats, resulting in a reduced attack rate of predators and a decreased rate of reproduction in the prey (e.g. Sih 1997; De Meester et al. 1998; Norrdahl and Korpimäki 2000). Some prey adjust life history traits such as the age or size at maturity in the presence of natural enemies, which carry a cost in terms of population growth rate but lower the risk of being eaten by the predator (e.g. Tollrian 1995; Van Buskirk et al. 1997; Peckarsky et al. 2001). In extreme cases of induced morphological or chemical defences, prey can become invulnerable to predation so that predator foraging success virtually declines to zero (e.g. Tollrian and Harvell 1998). Trait-mediated effects of predators may also have consequences for interactions with third species. For example, when the risk of predation results in changes in herbivore behaviour, trophic cascades can occur where not only the predator and prey population, but also the resource levels are affected (Schmitz et al. 2000; Peacor and Werner 2001).

While trait-mediated effects are common in predator-prey interactions, their consequences for the dynamics of natural enemy and victim populations are only beginning to be explored (e.g. Ives and Dobson 1987; Ruxton and Lima 1997; Adler and Grunbaum 1999; Krivan 1998; Kusch 1998; Riessen 1999; Diehl et al. 2000; Norrdahl and Korpimäki 2000). Trait-mediated effects influence the functional response of the predator and trait modifications may themselves be a function of predator attack rate. For example, when prey respond to a direct but unsuccessful attack by the predator (e.g. Tollrian and Harvell 1998), an increase in the rate of attack will increase the proportion of individuals in the prey population with trait modification. On the other hand, predation leads to a decrease in prey density, which may decrease the proportion of responding prey individuals. For example, when signals emitted by attacked prey are the cue for a population to induce defence (Sih et al. 1998), a high rate of predation could lead to a decrease in the concentration of the cue and possibly to a decrease in the response of the population. The consequences of trait-mediated effects for population dynamics will therefore depend on the complex relationship between host density, predator rate of attack, and trait modification.

Aphids are attacked by a wide range of natural enemies that differ greatly in their mode of attack and their effect on aphid numbers (Bänsch 1964; Dixon 1998; Hindayana et al. 2001; Sloggett and Weisser 2002). During the phase of asexual reproduction in these cyclical parthenogenetic organisms, female aphids give birth to genetically identical winged and wingless offspring (Kawada 1987; Dixon 1998). Recently, it was shown that in the presence of natural enemies, pea aphids increase the proportion of winged dispersal morphs among their offspring (Weisser et al. 1999; Dixon and Agarwala 1999; Sloggett and Weisser 2002). Thus, in pea aphids, natural enemy attack not only results in a decrease in prey number, but also in a qualitative change in the composition of the prey population.

Winged morphs differ from wingless morphs in a number of traits, in addition to their ability to colonise new host plants by flight. In many species, winged morphs have a longer developmental time, a lower fecundity and/or a shorter lifespan than wingless morphs (Dixon 1998). As a consequence, an increase in the proportion of winged morphs results in a lower maximum growth rate of the population. In addition, aphid populations often show a metapopulation structure where local populations are connected by dispersal (Addicott 1978; Weisser 2000). Because a change in the proportion of winged morphs has a bearing on the dispersal rate, predator attack also results in consequences at the metapopulation level for population dynamics.

In this paper we investigate the interaction between predation rate, decreasing host density and trait modification in two aphid predator-prey interactions. For both of the predators used in the experiments, hoverfly larvae (Diptera: Syrphidae) and lacewing larvae (Neuroptera: Chrysopidae), the effect on predator presence on aphid wing polyphenism has not previously been investigated. Larvae of hoverflies and lacewings are common natural enemies of aphids and differ in the way they attack aphids (Bänsch 1964; Chambers 1988). Hoverfly larvae, even as first instars, can catch aphids of all sizes by using a secretion which allows them to adhere to their prey (Bänsch 1964). In contrast, lacewing larvae have difficulties in attacking prey that is larger than themselves and generally consume fewer aphids than hoverfly larvae (Hindayana et al. 2001). In this paper, we ask the following questions:

1. Are lacewing and hoverfly larvae similar to predaceous ladybirds and aphid parasitoids in that they also induce dispersal morphs in pea aphids?
2. Is a change in the proportion of winged offspring that is produced dependent on the number of aphids consumed?
3. Does the response of the aphids depend on the type of predator attacking the aphid colony?

Material and methods

Experimental animals and plants

For the experiments the red clone BP of the pea aphid (*Acyrthosiphon pisum*) was used. This clone was originally collected in Bayreuth, Germany, and has been used in a number of previous studies on wing induction (Weisser et al. 1999; Weisser and Braendle 2001). Aphids were reared on and the experiments were conducted on a dwarf variety of the broad bean, *Vicia faba* L. (The Sutton; Nickerson-Zwaan, UK). Individual plants were maintained in 10-cm-diameter pots. In order to prevent the escape of aphids or predators, the plants were caged in air-permeable cellophane bags (18.5 cm×39 cm).

Both hoverfly larvae and lacewing larvae were obtained from a commercial supplier (Katz Biotech Services, Welzheim, Germany). The hoverfly larvae used were reared on broad beans infested with pea aphids. Second instar larvae were taken for experimental work.

The lacewing larvae were also fed with pea aphids, until they reached the second larval stage when they were used for experimentation.

Experimental design

Two experiments, one with each predator, were conducted. The conditions under which the experiments took place were the same for both experiments (16 h light, 8 h dark, 20°C, 75% relative humidity).

For the hoverfly experiment 25 lines of aphids were established, with each line being used for one replicate. A single foundress aphid placed on a bean plant was used to initiate an aphid line. This foundress reproduced over a 2-day period. As the progeny reached the fourth larval or young adult stage, they were transferred separately to new plants to avoid crowding. The progeny were allowed to give birth to several offspring and were then removed. These offspring were also reared until fourth larval or early adult stage and then used for the experiment. For each replicate, offspring of one line, all descendants of a single foundress, were pooled together.

To start the experiment, for each line, 20 aphids were placed together with a second instar predator larva on a bean plant. Identical numbers of aphids from the same line were put on another plant as a control group. Three days later when the aphids had given birth to a number of offspring, the adult aphids of both treatment

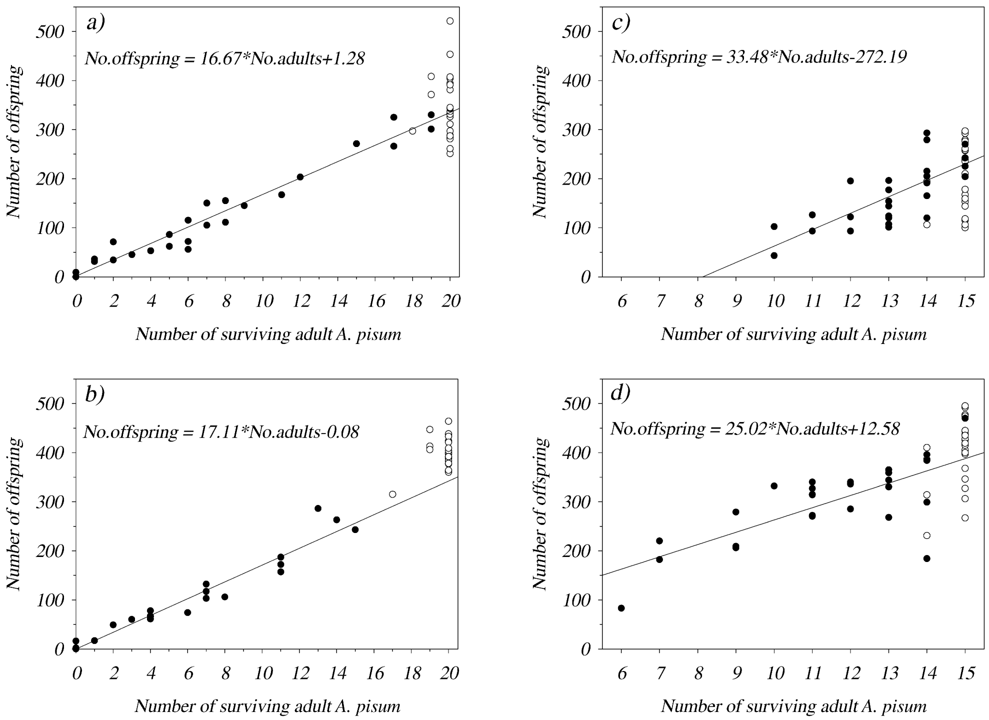

Fig. 1a–d The relationship between the number of surviving adult aphids and the number of surviving offspring following a 3-day exposure to predators (● predator treatment, ○ control). Regression was done with predator treatment only. **a** Hoverfly experiment first period: $P<0.0001$, $R^2=0.95$. **b** Hoverfly experiment second period: $P<0.0001$, $R^2=0.95$. **c** Lacewing experiment first period: $P<0.0001$, $R^2=0.56$. **d** Lacewing experiment second period: $P<0.0001$, $R^2=0.54$

and control were transferred to new plants to prevent overcrowding and early death of the plant and aphids. At this time, hoverfly larvae were replaced by new second instars on the new plant. After 3 further days the remaining adult aphids and the predator were removed from the plants. The number of surviving adult aphids was recorded at the end of each 3-day period and the number of consumed adult aphids was calculated. All pea aphid offspring produced by the adult aphids in the experiment were reared until they reached the fourth instar or adult stage. At this time they were taken off the plants and frozen for later counting and determination of the phenotype. Winged fourth instars from *A. pisum* can easily be differentiated from wingless ones by the presence of wing buds.

For the lacewing experiment the procedure was comparable. But in comparison to the hoverfly experiment 26 lines of aphids were established and to start the experiment, two groups of 15 adult aphids per line were assembled. One group was placed together with a second instar lacewing larva, the second served as a control group. After 3 days all adult aphids and the lacewing larvae were transferred to new plants. Predator larvae were replaced only if the larvae had not eaten any adult aphids.

Statistical analysis

For comparison of means of the predator and control treatments, paired *t*-tests for related samples were used (Sokal and Rohlf 1987), where lines were the unit of replication (indicated by t_{paired}). When lines were not the unit of replication, a simple *t*-test was used. Data was tested for normality and where necessary, a Mann-Whitney rank sum test was used.

Linear regression was utilised to analyse the relationships between the number of surviving adult aphids and the number of offspring. Linear and quadratic regressions were used to investigate the relationship between the number of surviving adults and the percentage of winged offspring produced.

Results are presented as mean±SE in all cases. The software package SigmaStat for Windows version 2.03 was used for all statistical analyses.

Results

Predator activity and offspring production

The number of aphids consumed ranged from five to 20 (mean 14.7±1.0) in the hoverfly experiment and from zero to nine (mean 3.7±0.5) in the lacewing experiment. The number of offspring produced by the target aphids over a 3-day period was linearly correlated with the number of adult aphids surviving until the end of the period (Fig. 1).

For the following three analyses of the hoverfly experiment replicates with fewer than three remaining adult aphids were discarded, because few or no offspring remained. Therefore 19 (first 3-day period) and 16 (second 3-day period) replicates were included in further analyses. In the lacewing experiment at the end of the second period one lacewing larva was dead. Because the length of time the larva survived is not known, we did not remove this replicate. Thus all 26 replicates were used for further analyses.

For both experiments, and in both 3-day periods, the number of offspring was significantly lower in the predator treatment than in the control group (hoverfly experiment period 1, $t_{\mathrm{paired}}=6.79$, $P\leq0.001$, $n=19$; period 2, $t_{\mathrm{paired}}=13.38$, $P\leq0.001$, $n=16$; lacewing experiment period 1, $t_{\mathrm{paired}}=3.24$, $P=0.003$, $n=26$; period 2, $t_{\mathrm{paired}}=5.89$, $P\leq0.001$, $n=26$).

Effect of predation on winged morph production

In the hoverfly experiment, for both 3-day periods, the percentage of winged offspring in the predator treatment

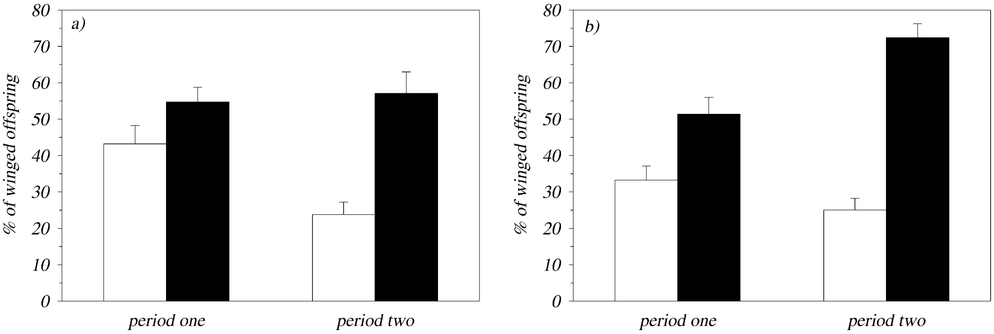

Fig. 2a, b Mean proportion (±SE) of winged offspring of the pea aphid following two 3-day exposure periods to predators. **a** Hoverfly experiment; **b** lacewing experiment. *Filled bars* Predator treatment, *empty bars* control

Table 1 Variables calculated for estimating the effects of selective predation (see text for explanations)

	Hoverfly experiment		Lacewing experiment	
	Period 1	Period 2	Period 1	Period 2
No. offspring control treatment	358.79±14.98	395.25±8.31	200.19±13,08	400.24±13.10
Expected no. offspring predator treatment	266.75±13.04	189.08±22.20	190.07±13.31	329.22±14.19
Expected no. offspring consumed	107.91±17.75	53.33±8.16	24.45±10.12	32.72±14.19
Proportion winged without selective predation	54.71±4.04	57.10±5.90	51.42±4.58	72.43±3.81
Proportion winged assuming selective predation	33.65±5.22	40.79±4.61	46.39±4.96	66.25±4.26
Test for difference in proportion of winged offspring assuming selective predation (control vs. predator treatment)	$t_{paired}=1.55$ $P=0.14$ $n=19$	$t_{paired}=-3.87$ $P=0.002$ $n=16$	$t_{paired}=-2.86$ $P=0.008$ $n=26$	$t_{paired}=-8.79$ $P\leq0.001$ $n=26$

was significantly higher than in the control group (period 1, $t_{paired}=-2.60$, $P=0.018$, $n=19$; period 2, $t_{paired}=-6.17$, $P\leq0.001$, $n=16$; Fig. 2a). The difference between predator treatment and control group became larger in the second period of the experiment (*t*-test on the differences between control and predator treatment within each period, $t=-3.15$, $P=0.003$, $n_{period1}=19$, $n_{period2}=16$). For the control the percentage of winged offspring was significantly lower in the second period of the experiment than in the first period ($t=3.08$, $P=0.004$, $n_{period1}=19$, $n_{period2}=16$). For the predator treatment the proportion of winged offspring was the same in both periods of the experiment ($t=-0.34$, $P=0.735$, $n_{period1}=19$, $n_{period2}=16$).

In the lacewing experiment, for both 3-day periods, the percentage of winged offspring in the predator treatment was significantly higher than in the control group (period 1, $t_{paired}=-3.99$, $P\leq0.001$, $n=26$; period 2, $t_{paired}=-12.48$, $P\leq0.001$, $n=26$; Fig. 2b). The difference between predator treatment and control group became larger in the second period of the experiment ($t_{paired}=-4.93$, $P\leq0.001$, $n=26$). For the control the decrease in the proportion of winged offspring in the second period of the experiment was significant ($t_{paired}=2.97$; $P=0.006$, $n=26$), and the increase in the proportion of winged offspring in the predator treatment in the second period of the experiment was also significant (rank sum test, $T=491$, $P\leq0.001$, $n=26$).

Selective predation as a confounding factor

Predators fed on both aphid larvae and adult aphids. If the predators had selectively fed on apteriform aphid larvae, selective predation might have biased our results by increasing the proportion of winged morphs among offspring in the predator treatment. We tested for this effect by assuming that all offspring consumed by a predator were wingless. The total number of offspring born in the 3-day interval of the predator treatment was calculated by assuming that:

1. Aphids in both the control and the predator treatment produce the same number of offspring per day. This mean number of offspring born to an adult per day (no. offspring/day) was calculated from the control treatment.
2. Adult aphids consumed by the predator were killed after half the period (i.e. 1.5 days) and therefore reproduced for 1.5 days. The expected total number of offspring for the predator treatment could therefore be calculated by the following formula:
   expected no. offspring=(3×no. adults alive+1.5 no. adults killed)×no. offspring/day.

To calculate the number of consumed offspring, we subtracted the observed number of offspring from the expected number (Table 1). In the lacewing experiment, the proportion of winged offspring was still higher than in the predator treatment. In the hoverfly experiment, many more offspring were consumed than in the lacewing experiment, but the predator treatment still showed a significantly higher proportion of winged morph than the control in the second period (Table 1). Only in the first period was the difference no longer significant. Thus, the presence of either lacewing larvae or hoverfly larvae caused pea aphids to produce a higher proportion of

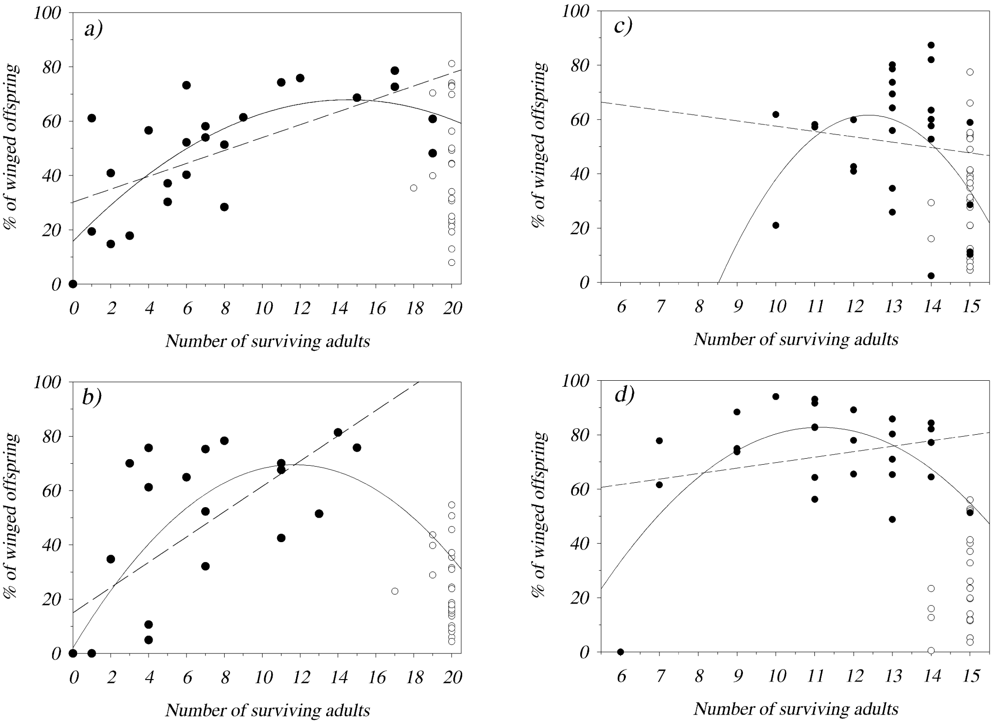

Fig. 3a–d Dependency between surviving adults and the proportion of winged offspring (● predator treatment, ○ control). Regressions were done with predator treatment only. **a** Hoverfly experiment first period, **b** hoverfly experiment second period, **c** lacewing experiment first period, **d** lacewing experiment second period. The linear equation has the form: $y=a\times x+b$. The quadratic equation has the form: $y=d\times x^2+e\times x+f$, where y -is % of winged offspring, and x is no. of surviving adults (see Table 2)

Table 2 Statistics for linear and quadratic regressions and equation parameters in Fig. 3. The linear equation has the form: $y=a\times x+b$. The quadratic equation has the form: $y=d\times x^2+e\times x+f$, where y represents % of winged offspring, and x no. of surviving adults

Period	Regression	R^2	P	a	b	d	e	f
Hoverfly larva experiment								
1	Linear	0.41	0.0008	2.38	30.16			
	Quadratic	0.53	0.0003			–0.25	7.17	15.71
2	Linear	0.49	0.0003	4.66	14.95			
	Quadratic	0.59	0.0002			–0.49	11.55	1.99
Lacewing larva experiment								
1	Linear	0.01	0.55	–1.97	77.15			
	Quadratic	0.18	0.10			–4.12	102.03	–570.76
2	Linear	0.06	0.22	2.02	49.54			
	Quadratic	0.41	0.002			–1.87	41.66	–149.34

winged morphs even if we make the unlikely assumption that all consumed offspring would have developed into wingless adults.

Survival of adult aphids and wing production

In order to test if wing induction was dependent on the number of aphids consumed in the predator treatments of both experiments, the dependency of the percentage of winged offspring on the number of surviving adults was investigated (Fig. 3, Table 2).

In the hoverfly experiment, for both 3-day periods, both the quadratic and the linear regressions were significant. However, the quadratic regressions explained more of the variance of the data than the linear regression (Table 2).

In the lacewing experiment, in the first 3-day period, the number of surviving adult aphids and the percentage of winged offspring were not linearly correlated. The quadratic regression also only explained a low percentage of the variance of the dependent variable and was not significant. In the second period, however, the quadratic regression was significant but again no linear dependency was found (Table 2).

Wing production and predator activity in the previous period

Because the proportion of winged offspring depended on the number of surviving adults, the relationship between the number of surviving adults after the first period and the change in the proportion of winged offspring from the first to the second period was analysed (Fig. 4).

In the hoverfly experiment, when the predatory larvae consumed fewer than 15 adult aphids during the first 3-day period, there was no clear relation between the

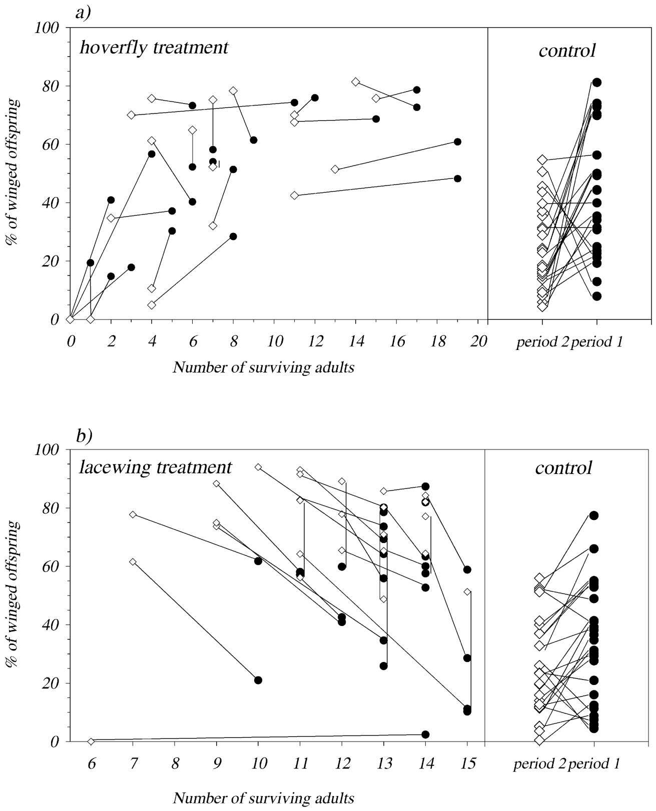

Fig. 4 Relationship between the number of surviving adults in the first 3-day period exposure (●) and the proportion of winged offspring in the second period (◇) of predator exposure. Replicates in the first and second period are joined by a *line*. **a** Hoverfly experiment, **b** lacewing experiment

number of surviving adults after the first period and the change in the proportion of winged offspring from the first to the second period (t_{paired}=–0.11, *P*=0.913, *n*=15). By contrast, if the hoverfly larvae consumed more than 15 adult aphids in the first period, the percentage of winged offspring in the second 3-day period decreased (t_{paired}=3.59, *P*=0.011, *n*=7). For the control group, the percentage of winged offspring in the second period was lower than in the first part of the experiment (t_{paired}=3.34, *P*=0.003, *n*=25), although some replicates showed strong deviations from this trend (Fig. 4a).

In the predator treatment of the lacewing experiment, the percentage of winged offspring increased in nearly all replicates from the first to the second period and the difference was highly significant (t_{paired}=–5.95, *P*≤0.001, *n*=26). However, in the control group the percentage of winged offspring decreased in the second period (t_{paired}=2.97; *P*=0.006, *n*=26; Fig. 4b).

Discussion

The results presented here clearly demonstrate that the presence of both lacewing larvae and hoverfly larvae can induce pea aphids to produce a higher proportion of winged offspring. Because wing induction has also been shown for pea aphids exposed to predatory ladybirds (Weisser et al. 1999; Dixon and Agarwala 1999), and parasitoids (Sloggett and Weisser 2002), wing induction appears a universal response by pea aphid to the presence of natural enemies. Our results also suggest, however, that this trait-mediated effect interacts with the density-mediated effects of the natural enemies of aphids. The percentage of winged morphs among the offspring produced by aphids depended not only on the rate of predation, but also on the resulting prey density and predator species.

One potential confounding factor is selective predation. If predator larvae had selectively fed on apteriform aphid larvae, this would have inflated the proportion of winged morphs among offspring in the predator treatment. A possible reason for such a preference could be that wingless morphs develop faster than winged morphs and for a given age apteriform aphid larvae are larger (e.g. Dixon 1998). Thus, preying on apteriform aphid larvae might be more profitable for a predator. However, in pea aphids the difference in size is small for the first and second instar, and only in the third instar do differences become apparent. At 20°C, aphids will moult into third instars after 2–3 days (G. Kunert, unpublished data). Because in our experiments adult aphids and predators were transferred or taken off the plants after 3-day intervals, only offspring born on the very first day of an interval had moulted into a third instar before the end of the period. Thus, only a small fraction of the offspring would have suffered from selective predation. In addition, size-selective predation is very unlikely for hoverfly larvae, because of their way of catching prey. If a hoverfly larva comes into contact with an aphid, it will glue itself onto the prey by using an adhesive secretion and there is no size selectivity (Gries 1986). Size-selective predation of third-instar larvae is therefore only conceivable for lacewing larvae. Our estimate for the effects of selective predation on our results showed that even if all consumed aphids were wingless, the difference between the control and predator treatments would still be significant, in three out of the four intervals analysed. It is important to keep in mind that in this calculation we clearly overestimated the number of wingless offspring. Thus, not all of the consumed aphids would have been wingless. In addition, we overestimated the number of expected offspring. First, the killed adult aphids were probably consumed at the beginning of the 3-day period when few offspring were present on the plant rather than after the 1.5 days we assumed. Second, if the predatory larvae consumed adult aphids, they probably consumed fewer offspring. Thus, selective predation cannot explain the increase in winged morph production in the presence of predators.

With respect to known wing-induction factors, crowding and poor plant quality (Sutherland 1969a, 1969b), the experiments were conservative: the number of adult aphids and therefore the number of offspring were higher in the control than in the predator treatment. As a result of higher aphid numbers, crowding was higher and plant quality lower in the control replicates. Thus, although crowding and plant quality should have favoured a higher production of winged morphs in the control groups, the percentage of winged offspring was significantly higher in the treatment groups. This difference between predator and control treatments increased in the second period of both experiments, because the percentages of winged offspring declined in the control. This decrease in the second period could be caused by an increase in aphid age (MacKay and Wellington 1977; MacKay and Lamb 1979). In the predator treatment, the percentage of winged offspring was either unchanged (hoverfly experiment) or increased (lacewing experiment, Fig. 2). Because of the decrease in the percentage of winged offspring in the control, both an unchanged or an increasing proportion of winged offspring in the predator replicates represents an overall increase relative to the control, suggesting that the effect of the predator overcompensated for any effect of aphid age. An increased proportion of winged offspring in the predator treatment may be due to a delayed response by aphids to the presence of a predator. In the pea aphid, morph determination occurs maternally and offspring are determined some time before their birth (Sutherland 1969a, 1969b). Thus, in the first period of the predator treatments, two types of offspring were born: first those which were determined before the predator was introduced and then, after a certain time, progeny influenced by parental exposure to the predator.

Wing induction was strongly dependent on the number of aphids consumed (Fig. 3). Interestingly, in all cases, a quadratic regression explained more of the variance than a linear regression, suggesting that the effect of the predator was low when very few or a great many aphids were consumed, and highest when an intermediate number of aphids was consumed. This pattern was most pronounced in period 2 of the lacewing experiment (Fig. 3d). In the hoverfly experiment the quadratic regression also explained more of the variance than the linear regression, although this pattern was not as clear as in the lacewing experiment (Fig. 3a, b). It is likely that this is due to the small number of replicates with little predation in the hoverfly experiment.

For both predators, the proportion of winged offspring first increased with an increase in the number of surviving adult aphids, i.e. a decrease in the number of aphids consumed (Fig. 3). Wing induction was lowest when only very few aphids survived. The exact mechanism by which natural enemies induce aphids to produce winged offspring is still unclear (Sloggett and Weisser 2003). One possibility is that the effect of the predator is based on disturbance caused in the aphid colony (Sloggett and Weisser 2003). A number of different types of predator disturbance may be envisaged. Aphids often drop from a plant to escape from natural enemies (Dixon 1998). When returning to the plant, these aphids will encounter other aphids, such that both returning individuals and those still on the plant will experience tactile stimuli similar to those caused by crowding ("pseudo-crowding", Sloggett and Weisser 2002). Increased concentrations of an alarm pheromone, released by attacked aphids, could also cause disturbance (Clegg and Barlow 1982; Montgomery and Nault 1977; Wohlers 1981). The disturbance hypothesis would be consistent with the results of our experiment: fewer aphids surviving in a replicate, the more time a predator probably needed to catch a prey and, thus, fewer aphids were consumed per unit time. Thus, as the number of surviving aphids decreased, the number of tactile stimuli between individuals probably also decreased as would have the amount of alarm pheromone released.

The disturbance hypothesis would also be consistent with the quadratic dependence of the proportion of winged offspring on the number of surviving aphids. To the right of the maximum point of the curve (high numbers of surviving adults), no or only few adult aphids were consumed by predators. This suggests that in those replicates the lacewing larvae were not very active and thus the effect caused by the predator was not very high. Cases where no adult aphids were consumed form extreme examples of this. Assuming that the predator was not active at all, the regression curve should pass through the mean value of the control data points. However, in most of the cases the curve passes the control data points above their means (Fig. 3). Thus, there was a predator effect even though no adult aphids were consumed. It is likely that in these replicates predators only consumed offspring, which is supported by the fact that the average number of offspring in the lacewing larva treatment (first period) is lower than the average number of offspring of the same lines of the control treatment (mean difference 25.75±21.22). But there is also the possibility that the predator effect does not require the consumption of aphids.

To test the hypothesis that both the rate of predation and the resulting aphid density are important for the strength of the aphid response, the development of each replicate was analysed (Fig. 4). In the predator treatment of the hoverfly experiment (Fig. 4a), as a consequence of the small number of adults surviving after period 1, a decrease in wing production occurred. In agreement with the hypothesis, in those replicates where the number of surviving adults was high, such a reduction of the proportion of winged offspring did not occur. In the lacewing experiment (Fig. 4b), the percentage of winged offspring increased from period 1 to period 2 in most cases. However, in the lacewing larva treatment there was no replicate where more than ten aphids were consumed, hence a decrease in the response was not expected according to the hypothesis. Taken together, the temporal changes in winged morph production in the different replicates are consistent with the hypothesis that it is the interaction between the predation rate and the resulting prey density that determines wing induction in pea aphids, mediated by the level of disturbance caused in an aphid colony.

The two predator species not only differed in the number of prey they consumed, but also in their foraging mode. Whereas a hoverfly larva can catch an aphid independent of its size, for a lacewing larva, especially in the first two instars, it is more difficult to catch adult aphids, which are larger than themselves. As a consequence, lacewing larvae often fail to subdue an aphid they attack and thus need more attempts per successful catch than hoverfly larvae (G. Kunert, personal observation). This difference in foraging mode has consequences for aphid wing induction. Under the pseudo-crowding hypothesis the level of wing induction should therefore be higher for a lacewing larva than for hoverfly larvae. Even though the aphid densities used in the experiments differed and do not allow a direct comparison, it appears that the proportion of winged offspring is generally higher in the lacewing experiment, in particular in period 2 (Fig. 3).

In the ecology of predator-prey interactions little is known about the interaction of lethal and nonlethal effects (Lima 1998a). While Lima's (1998b) review concentrated on behavioural modifications under the risk of predation, this conclusion is probably also true for the multitude of trait modifications that are not behaviourally mediated, such as induced morphological defences, physiological changes in the prey, or life history adjustments (Abrams 1995; Tollrian and Harvell 1998; Nakaoka 2000; Peckarsky et al. 2001; Peacor 2002). Our results show that trait-mediated effects can be strongly dependent on the density-mediated effects of natural enemies. Wing induction in pea aphids in the presence of predatory hoverfly and lacewing larvae depended on the way in which predation reduced prey density. If the rate of predation was high such that predators strongly reduced prey density, trait-mediated effects were weak and a low percentage of aphids developed a winged phenotype. If predation rate was lower and more prey survived, trait modification was more important than density reduction. Thus, the results of our experiments demonstrate that the relative importance of trait-mediated versus density-mediated effects of natural enemies may depend on the interaction between the rate of predation and prey density.

What do these results imply for the population dynamics of aphid-aphid predator interactions? As pointed out by Lima (1998b), it is difficult to infer population-level effects from studies carried out on a small spatial scale such as single plants. Nevertheless, some population-level consequences of trait modifications in aphids are easily envisaged even though they need to be tested in population-scale experiments. For example, because winged morphs have a longer developmental time and a lower fecundity than wingless morphs, an increase in the proportion of winged morphs among the offspring implies a lower maximum growth rate of the local aphid population, even when the winged individuals remain in the colony. A second population-level effect is an increase in the rate of dispersal, that is likely to follow the increase in the proportion of winged morphs in the population. One can predict that this would lead to a higher rate of colonisation of empty habitat and increased immigration into existing populations. How these effects modify the dynamics and stability of the predator-prey interaction remains to be investigated.

Acknowledgements We are very grateful to John Sloggett for elucidating discussions and for his comments to the manuscript. We would also like to thank Katz Biotech Services for donating *E. balteatus* and *C. carnea*, and Ingrid Jakobi for technical assistance. The study was supported by the state of Thuringia, Germany, under the grant scheme Graduiertenstipendium.

References

Abrams PA (1995) Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. Am Nat 146:112–134

Addicott JF (1978) The population dynamics of aphids on fireweed: a comparison of local populations and metapopulations. Can J Zool 56:2554–2564

Adler FR, Grunbaum D (1999) Evolution of forager responses to inducible defenses. In: Tollrian R, Harvell CD (eds) The ecology and evolution of inducible defenses. Princeton University Press, Princeton, N.J., pp 259–285

Bänsch R (1964) Vergleichende Untersuchungen zur Biologie und zum Beutefangverhalten aphidivorer Coccinelliden, Chrysopiden und Syrphiden. Zool Jb Syst 91:271–340

Chambers RJ (1988) Syrphidae. In: Minks AK, Harrewijn P (eds) Aphids, their biology, natural enemies and control, vol B. Elsevier, Amsterdam, pp 259–270

Clegg JM, Barlow CA (1982) Escape behaviour of the pea aphid *Acyrthosiphon pisum* (Harris) in response to alarm pheromone and vibration. Can J Zool 60:2245–2252

Diehl S, Cooper SD, Kratz KW, Nisbet RM, Roll SK, Wiseman SW, Jenkins TM (2000) Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. Am Nat 156:293–313

Dixon AFG (1998) Aphid ecology. Chapman and Hall, London

Dixon AFG, Agarwala BK (1999) Ladybird-induced life history changes in aphids. Proc R Soc Lond B 266:1549–1553

Gries G (1986) Zum Beutefangverhalten der Schwebfliegenlarve *Syrphus balteatus* Deg. (Diptera, Syrphidae). J Appl Entomol 102:309–313

Hindayana D, Meyhöfer R, Scholz D, Hans-Michael Poehling H-M (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. Biol Contr 20:236–246

Ives AR, Dobson AP (1987) Antipredator behaviour and the population dynamics of simple predator-prey systems. Am Nat 130:431–447

Kawada K (1987) Polymorphism and morph determination. In: Minks AK, Harrewijn P (eds) Aphids, their biology, natural enemies and control, vol A., Elsevier, Amsterdam, pp 299–314

Krivan V (1998) Effects of optimal antipredator behavior of prey on predator-prey dynamics: the role of refuges. Theor Pop Biol 53:131–142

Kusch J (1998) Long-term effects of inducible defense. Ecoscience 5:1–7

Lima SL (1998a) Nonlethal effects in the ecology of predator-prey interactions – what are the ecological effects of anti-predator decision-making? BioScience 48:25–34

Lima SL (1998b) Stress and decision making under the risk of predation: recent development from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290

MacKay PA, Lamb RJ (1979) Migratory tendency in aging populations of the Pea Aphid, *Acyrthosiphon pisum*. Oecologia 39:301–308

MacKay PA, Wellington WG (1977) Maternal age as a source of variation in the ability of an aphid to produce dispersing forms. Res Popul Ecol 18:195–209

Meester L de, Dawidowicz P, van Gool E, Loose C (1998) Ecology and evolution of predator-induced behavior of zooplankton:

depth selection behavior and diel vertical migration. In: Tollrian R, Harvell CD (eds) The ecology and evolution of inducible defenses. Princeton University Press, Princeton, N.J., pp 160–176

Montgomery ME, Nault LR (1977) Comparative response of aphids to the alarm pheromone, (E)-ß- farnesene. Entomol Exp Appl 22:236–242

Nakaoka M (2000) Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. Ecology 81:1031–1045

Norrdahl K, Korpimäki E (2000) The impact of predation risk from small mustelids on prey populations. Mammal Rev 30:147–156

Peacor SD (2002) Positive effect of predators on prey growth rate through induced modifications of prey behaviour. Ecol Lett 5:77–85

Peacor SD, Werner EE (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. Proc Natl Acad Sci USA 98:3904–3908

Peckarsky BL, Taylor BW, McIntosh AR, McPeek MA, Lytle DA (2001) Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82:740–757

Riessen HP (1999) Chaoborus predation and delayed reproduction in *Daphnia*: a demographic modeling approach. Evol Ecol 13:339–363

Roos AM de, Leonardsson K, Persson L, Mittelbach GG (2002) Ontogenetic niche shifts and flexible behavior in size-structured populations. Ecol Monogr 72:271–292

Ruxton GD, Lima SL (1997) Predator-induced breeding suppression and its consequences for predator-prey population dynamics. Proc R Soc Lond B 264:409–415

Schmitz OJ, Hamback PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. Am Nat 155:141–153

Sih A (1997) To hide or not to hide? Refuge use in a fluctuating environment. Trees 12:375–376

Sih A, Enlund G, Wooster D (1998) Emergent impacts of multiple predators on prey. Trees 13:350–355

Sloggett JJ, Weisser WW (2002) Parasitoids induce production of the dispersal morph in the pae aphid, *Acyrthosiphon pisum*. Oikos 98:323–333

Sloggett JJ, Weisser WW (2003) A general mechanism for predator- and parasitoid-induced dispersal in the pea aphid, *Acyrthosiphon pisum* (Harris). Proceedings of the 6th International Symposium on Aphids, in press

Sokal RR, Rohlf FJ (1987) Introduction to biostatistics, 2nd edn. Freeman, New York

Sutherland ORW (1969a) The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. J Insect Physiol 15:1385–1410

Sutherland ORW (1969b) The role of the host plant in the production of winged forms by two strains of the pea aphid *Acyrthosiphon pisum*. J Insect Physiol 15:2179–2201

Tollrian R (1995) Predator-induced morphological defenses – costs, life-history shifts, and maternal effects in *Daphnia pulex*. Ecology 76:1691–1705

Tollrian R, Harvell CD (1998) The ecology and evolution of inducible defences. Princeton University Press, Princeton, N.J.

Van Buskirk J, McCollum SA, Werner EE (1997) Natural selection for environmentally induced phenotypes in tadpoles. Evolution 51:1983–1992

Weisser WW (2000) Metapopulation dynamics in an aphid-parasitoid system. Entomol Exp Appl 97:83–92

Weisser WW, Braendle C (2001) Body colour and genetic variation in winged morph production in the pea aphid. Entomol Exp Appl 99:217–223

Weisser WW, Braendle C, Minoretti N (1999) Predator-induced morphological shift in the pea aphid. Proc R Soc Lond B 266:1175–1182

Wohlers P (1981) Effects of the alarm pheromone (E)- ß- farnesene on dispersal behaviour of the pea aphid *Acyrthosiphon pisum*. Entomol Exp Appl 29:117–124