

Predator-induced morphological shift in the pea aphid

Wolfgang W. Weisser*, Christian Braendle† and Nicole Minoretti

Zoology Institute, University of Basel, Rheinsprung 9, 4051 Basel, Switzerland

Aphids exhibit a polymorphism whereby individual aphids are either winged or unwinged. The winged dispersal morph is mainly responsible for the colonization of new plants and, in many species, is produced in response to adverse environmental conditions. Aphids are attacked by a wide range of specialized predators and predation has been shown to strongly influence the growth and persistence of aphid colonies. In two experiments, we reared two clones of pea aphid (*Acyrtosiphon pisum*) in the presence and absence of predatory ladybirds (*Coccinella septempunctata* or *Adalia bipunctata*). In both experiments, the presence of a predator enhanced the proportion of winged morphs among the offspring produced by the aphids. The aphid clones differed in their reaction to the presence of a ladybird, suggesting the presence of genetic variation for this trait. A treatment that simulated disturbance caused by predators did not enhance winged offspring production. The experiments indicate that aphids respond to the presence of a predator by producing the dispersal morph which can escape by flight to colonize other plants. In contrast to previous examples of predator-induced defence this shift in prey morphology does not lead to better protection against predator attack, but enables aphids to leave plants when mortality risks are high.

Keywords: induced defence; aphid; ladybird; wing polymorphism; alates

1. INTRODUCTION

Induced structural or chemical defences against natural enemies have been shown for a wide range of plant–herbivore and predator–prey systems (Harvell 1984; Schultz 1988; Harvell 1990; Tollrian & Harvell 1998). Inducible defences are produced in response to stimuli from natural enemies and either deter further predator attack or increase an organism's tolerance to damage (Karban & Baldwin 1997; Tollrian & Harvell 1998). A prerequisite for the evolution of inducible defences is that attacks are spatially or temporally intermittent and can be perceived by a reliable but not fatal cue (Levins 1968; Lloyd 1984; Harvell 1990; Clark & Harvell 1992; Riessen 1992; Frank 1993; Adler & Karban 1994; Astrom & Lundbert 1994; Padilla & Aldolph 1996). Defence against predation is generally assumed to impose costs (Maynard Smith 1972) and theory predicts that inducible defences evolve only if these costs can be saved in times when no protection is necessary (Lively 1986). Among animals, most examples of inducible defences come from aquatic organisms and often involve the development of defensive structures.

Aphid life cycles are complex and typically consist of several asexual generations alternating with a single sexual generation (Moran 1992). During the phase of asexual reproduction, aphids produce a number of different phenotypes, among which are winged (alate) and unwinged (apterous) morphs. The unwinged morphs tend to repro-

duce on the plant where they were born, although dispersal to neighbouring plants occurs (Loxdale *et al.* 1993). In many species, the winged morphs develop in response to deteriorating conditions, i.e. when aphids are crowded or feed on plants of declining quality (Hille Ris Lambers 1966; Dixon 1998). Winged morphs can disperse over great distances to colonize new plants. Because winged morphs have a longer developmental time and a lower fecundity than wingless ones (Dixon & Wratten 1971; Dixon 1972; MacKay & Wellington 1975; Dixon 1998), it is costly for an aphid clone to produce alate aphids. The environmentally determined wing dimorphism enables aphids to save the cost of producing a wing apparatus during times when growing conditions on the host plant are good and dispersal is not advantageous. Aphids are attacked by a wide range of natural enemies, among which are predatory ladybirds (Coleoptera: *Coccinellidae*), hoverfly (Diptera: *Syrphidae*) and lacewing (Neuroptera: *Chrysopidae*) larvae (Dixon 1998). Aphids have evolved a variety of behavioural, morphological and chemical defences against predator attack. Nevertheless, the predation risks of aphid colonies are high, as indicated by predator-exclusion experiments (Way & Banks 1968; Campbell 1978; Frazer *et al.* 1981*a,b*; Dennis & Wratten 1991; Jervis & Kidd 1996). Field studies on aphid–predator interactions show that the number of predators attacking aphid colonies varies both spatially and temporally (Hughes 1963; Kareiva & Odell 1987; Cappuccino 1988; Farrell & Stufkens 1988, 1990; Kfir & Kirsten 1991; Chen & Hopper 1997; Stewart & Walde 1997).

In this paper we test the hypothesis that the presence of predatory ladybirds can induce aphids to produce the

*Author for correspondence (weisser@ubaclu.unibas.ch).

†Present address: Zoology Department, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

winged phenotype. The rationale underlying this hypothesis is that the dispersal morphs are able to leave aphid colonies attacked by a predator and colonize new plants. In two experiments we show that apterous pea aphids (*Acyrtosiphon pisum* Harris) produce the winged dispersal morph in the presence of predatory ladybirds (*Coccinella septempunctata* L. and *Adalia bipunctata* L.). This induced shift in prey morphology in a terrestrial predator–prey system is one of the first examples of an induced morphological response that allows for a more efficient escape from the predator rather than an effective defence.

2. METHODS

(a) *Experimental plants and animals*

We used a green clone of pea aphid (SG) originally collected in Sunningdale, England in 1996 and a red clone of pea aphid (BP) originally collected in Bayreuth, Germany in 1997. Aphids were reared on a dwarf form of broad bean, *Vicia faba* L. (variety The Sutton, Nickerson-Zwaan Ltd, Lincolnshire, UK). Adult ladybirds, *C. septempunctata* L. and *A. bipunctata* L., were collected in Switzerland in 1997 and 1998 and bred in the laboratory.

(b) *Experiment 1: C. septempunctata foraging in aphid colonies*

Experimental colonies ($n=30$) were initiated by transferring five adult aphids of the green clone SG from low-density stock cultures (four to five individuals per plant) to 18-day-old bean plants (number of leaves: mean \pm s.e. 7.8 ± 1.3), grown in plastic pots (diameter 10 cm and height 7.4 cm) in a commercial growing medium (TKS[®]2, Floragard VertriebsGmbH, Oldenburg, Germany). Animals were caged by placing an air-permeable transparent cellophane bag over the plants (width 185 mm and length 390 mm; Armin Zeller GmbH, Langenthal, Switzerland). After seven days, colonies consisted of $\bar{x} = 36.7 \pm 12.6$ individuals. At this point, an adult ladybird was released into the cellophane bag in 20 randomly selected replicates. The remaining replicates served as controls. Populations were censused every second day without removing the cellophane bag. Any winged individual (adult alate aphids) that appeared was noted and removed from the colony.

In this experiment, it was not possible to control the number of aphids on the plants precisely. Pea aphids easily drop from the host plant when disturbed (Lowe & Taylor 1964) and a frequent removal of aphids from the plants would have resulted in aphids being regularly interrupted in their feeding activities. On the other hand, aphid populations grow exponentially when undisturbed which can lead to early death of the host plant. To minimize disturbance while at the same time preventing colonies from growing too rapidly, we decided to cull populations if aphid numbers exceeded 150 (on days 4, 6 and 9) or 250 (days 15, 21 and 25). Populations were culled by removing the cellophane bag and gently shaking the plants. Aphids dropping from the plant were removed until the colony size was 100 ± 10 (days 4, 6 and 9) or 200 ± 10 (days 15, 21 and 25) individuals. Because the broad beans showed signs of damage due to aphid feeding after two weeks, we extended the experiment by replacing the original plants on day 15. This was done by cutting the stem of the old plant with a pair of scissors, carefully leaning the plant against a new plant and caging it with a cellophane bag. Within a day, all aphids settled on the new plant. Another transfer took place on day 19. The experiment ended on day 27 after the last count. Rearing of animals and experiment 1 were carried out in

climate chambers (20 ± 1 °C) under long-day conditions (16 L:8 D light intensity 10 000 lux at plant level).

(c) *Experiment 2: A. bipunctata foraging in groups of aphids*

To investigate whether the results found in experiment 1 also hold for other predator–pea aphid clone combinations we performed a second experiment with the two-spot ladybird *A. bipunctata*. The experimental design was chosen so that any confounding effect of aphid density or population culling that may have biased the results of experiment 1 could be avoided. Aphids of the green (SG) and the red (BP) clones were reared at low densities for three generations. First-instar nymphs of the third generation were placed in groups of 30 onto new bean plants. All plants were of the same age and had five to six leaves. Animals were caged with the plants using cellophane bags. The experiment started on day 6 when individuals were just moulting into the adult stage. The experimental procedure is illustrated in figure 1. We established three treatments: (i) ladybird treatment ($n=20$), where a single adult of *A. bipunctata* was placed with the aphids on the plants; (ii) control ($n=10$), where only aphids were caged on the plant; and (iii) disturbance treatment ($n=10$), where only aphids were caged on the plants but plants were dropped twice from a height of 16.5 cm onto a wooden surface three times a day (at 09.00, 13.00 and 17.00). In total, we created 80 groups of adult aphids (two clones \times three treatments with 20 (ladybird treatment) or ten (control and disturbance treatment) replicates per treatment).

The disturbance treatment was designed to simulate the disturbance caused by foraging ladybirds in an aphid colony: pea aphids drop from plants when attacked (e.g. Lowe & Taylor 1964). The disturbance caused in the colony by individuals returning to the feeding site is a possible proximate factor that could lead to an enhancement of the production of winged morphs. We dropped plants by carefully taking the top of the cellophane bag and bringing the plant into position before releasing the bag. Preliminary experiments showed that in colonies of 30 aphids, on average $16.8 \pm 2.9\%$ (clone SG $n=22$) or $19.9 \pm 2.0\%$ (clone BP $n=28$) of the aphids dropped from the plants when such a disturbance was applied. We then observed the number of aphid individuals that had not returned to the host plant at 30 min intervals over the next 4 h after dropping the plant. In the red clone BP, on average 7% of the individuals and in the green clone SG, 10% of the individuals were observed to be off the plant during this period of time. In preliminary experiments where single adults of *A. bipunctata* were caged with a group of 30 pea aphids on plants, on average $17.5 \pm 1.3\%$ ($n=92$ observations) of the individuals of clone SG and $11.7 \pm 1.4\%$ ($n=93$ observations) of the individuals of clone BP were observed not to be on the plant (observations carried out at 30 min intervals over four days). Thus, dropping the plant three times a day at an interval of 4 h over a period of ca. 12 h created a disturbance in the aphid colony that was similar to but not exactly like the disturbance caused by a predatory ladybird.

After 72 h (the morning of day 3), adult aphids and predators (ladybird treatment) were removed from the plants and all offspring produced were reared to maturity (offspring ‘days 1–3’). Nine adults of each group were transferred to new bean plants and allowed to reproduce for 36 h (figure 1). After this time they were removed and discarded and their offspring reared to maturity (offspring ‘test day 3’). Another nine adults from each group were also transferred to new plants and continued being

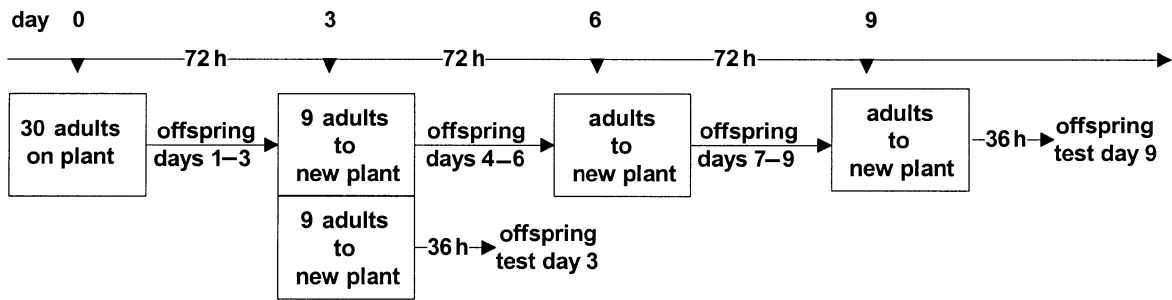


Figure 1. Flow chart of experiment 2 to illustrate the transfer of adult aphids to new plants. Such a line of transfers was established for each of the two clones of pea aphid and each of the treatments (control, ladybird treatment and disturbance treatments). See the text for an explanation.

exposed to the same treatments as before (figure 1). In the ladybird treatment, beetles were also transferred to new plants. The remaining adults from each group were discarded. After another 72 h (day 6), the surviving adults were transferred to new plants where they continued to be exposed to the same treatments as before (figure 1). The offspring produced up to that time were reared until maturity (offspring 'days 4-6'). On day 9, the surviving adults were again transferred to new plants where they were allowed to reproduce for 36 h. The resulting offspring ('test day 9') and the offspring produced until the transfer (offspring 'days 7-9') were reared until maturity. The experiment was carried out in a climate chamber ($21 \pm 3^\circ\text{C}$) under long-day conditions (16 L:8 D and light intensity 10 000 lux at plant level) and the position of each plant in the climate chamber was randomized. Any predator that died was replaced by a new one ($n=2$). The 'tests' were carried out to increase the number of comparisons between the groups of adult aphids.

We determined the percentage of winged morphs for all five groups of offspring (days 1-3, days 4-6, days 7-9, test day 3 and test day 9). Because offspring on a particular plant were produced by several mothers, we treated all offspring on a particular plant as a single independent replicate. Two-way ANOVAs were carried out using SAS version 6.12 (SAS Institute 1989) to analyse arcsine-transformed percentage data with clones and treatments as explanatory variables (fixed effects). The number of offspring on a plant was used as a weight variable.

3. RESULTS

(a) Experiment 1

In 11 out of 20 treatment replicates, the ladybirds consumed the entire aphid population within one week. In the remaining replicates, predation resulted in aphid densities being lower than in the control (figure 2a). Plant quality, if anything, was worse in the control, where more aphids were feeding on the plants. Both crowding and deteriorating host quality should therefore have favoured an earlier production of winged morphs in the control. Winged morphs first appeared, however, in the ladybird treatment, 12 days before the first winged morphs were found in the control (figure 2b; on average, winged morphs appeared after 13.8 ± 1.8 days in the ladybird treatment and after 24.4 ± 0.8 days in the control; U -test $U=4.0$ and $p<0.01$). In the pea aphid an offspring's phenotype is determined before birth (Sutherland 1969) and the development time of winged morphs from birth to adulthood was at least seven days under the experimental conditions (W. W. Weisser and C. Braendle,

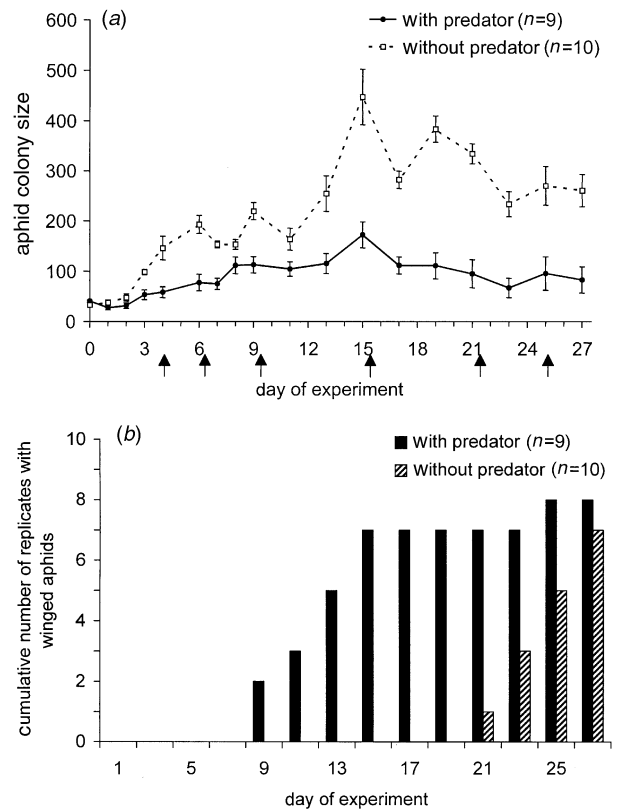


Figure 2. The effect of the predatory ladybird *C. septempunctata* on aphid population density and the occurrence of winged aphids in experiment 1. (a) Number (mean \pm s.e.) of aphids on plants with and without ladybirds (b) Cumulative number of replicates in which at least one winged aphid was found up to the census date. Days when colonies were culled are marked by arrows.

unpublished data). This implies that, in some replicates of the ladybird treatment, aphids must have responded to the presence of ladybirds within the first three days after the predators were introduced (figure 2).

In the ladybird treatment, replicates were culled 1.8 ± 0.5 times (minimum zero (two replicates) and maximum four (one replicate)), while in the control, replicates were culled 4.0 ± 0.6 times (minimum one (one replicate) and maximum six (two replicates)). There was no relationship between the number of times a replicate was culled and the day of first appearance of winged morphs (treatment $n=8$, $r_s=0.12$ and $p=0.78$ and control $n=7$, $r_s=0.09$ and $p=0.98$). We also tested the

hypothesis that the earlier appearance of winged morphs in the ladybird treatment is due to a population size effect on our ability to detect a winged morph. For each day at which alate aphids were recorded in any of the replicates we noted down the population density of all replicates on this day. For each replicate we also noted down whether or not we had found winged morphs. A logistical regression (procedure Genmod; SAS Institute Inc. 1993) showed that in the ladybird treatment there was a significant positive relationship between aphid population density and the presence of winged morphs ($n=84$, d.f. = 1, $\chi^2=6.85$ and $p=0.009$), whereas in the control the relationship was negative but not significant ($n=99$, d.f. = 1, $\chi^2=2.798$ and $p=0.09$).

(b) *Experiment 2*

The two clones differed significantly in the proportions of winged morphs among their offspring (table 1; figure 3*a,b*). The red clone BP always produced a higher proportion of winged offspring than the green clone SG. In most of the comparisons, a higher proportion of winged offspring was found in the ladybird treatment (figure 3*a,b*; table 1). For the offspring of days 1–3 and days 4–6 a significant interaction between clone and treatment was found (table 1), indicating the presence of genetic variation in the response to the different treatments. The disturbance treatment had no effect on the green clone. In the red clone, the disturbance treatment resulted in a highest percentage of winged forms in two out of the five comparisons. The mean percentage of winged offspring produced declined towards the end of the experiment (days 6–9 and test day 9). Due to ladybird predation, the number of adults that were transferred to new plants and the number of offspring produced were lower in the ladybird treatment (table 1).

When all offspring from a particular group of adults were pooled, the mean percentages of winged morphs among the offspring of the green clone SG were $2.1 \pm 1.2\%$ for the control ($n=10$), $23.7 \pm 3.4\%$ for the ladybird treatment ($n=20$) and $1.8 \pm 0.7\%$ for the disturbance treatment ($n=10$). In the red clone BP, the means were $49.2 \pm 4.7\%$ for the control ($n=10$), $67.9 \pm 2.3\%$ for the ladybird treatment ($n=20$) and $54.7 \pm 2.3\%$ for the disturbance treatment ($n=10$). In a two-way ANOVA, the effects of clone ($F_{1,74}=4257.8$ and $p=0.0001$), treatment ($F_{2,74}=381.9$ and $p=0.0001$) and the interaction ($F_{2,74}=66.2$ and $p=0.0004$) were all highly significant.

4. DISCUSSION

The results show that the presence of a predatory ladybird can induce pea aphids to produce winged offspring. Before we discuss the implication of this result we will address possible confounding factors in experiment 1. As pointed out above, our experimental design allowed us to control for the two main environmental factors previously known to induce the production of winged offspring in aphids, crowding and bad plant quality. Both of these factors led to the expectation of an earlier appearance of winged morphs in the control. Thus, the experimental design was conservative with respect to the known factors for wing induction. Another potential confounding factor is the culling of the populations, which might have biased

the results. Because replicates in the control were growing faster due to the absence of predators, a larger number of individuals were removed from these colonies. These individuals could have been those that would have produced winged offspring in the control had they not been removed from the experimental colony. However, culling is unlikely to have interfered with the production of winged individuals in the control because (i) there were always adult aphids left in the colonies that could have produced winged offspring, (ii) the frequency of culling was not very high, so that even the adults taken out are likely to have reproduced for several days prior to culling, (iii) culling also affected populations in the ladybird treatment which nevertheless produced winged offspring and (iv) there was no relationship between the number of times a replicate was culled and the day of first appearance of alate aphids. Because densities in the control were higher than in the ladybird treatment, there might also have been a detection problem such that winged morphs were more likely to be overlooked in larger populations, i.e. in the control. Such an effect could have contributed to the difference in the time of appearance of winged morphs between the treatment and control. For the control, the logistic regression analysis revealed a negative relationship between the probability that we encountered a winged morph in a population at a particular sampling date and aphid density. However, this relationship was not significant and winged morphs are easy to recognize even in large aphid populations so it is extremely unlikely that we should have overlooked winged individuals in the larger control populations for several days. Importantly, because of the time delay of at least seven days between the birth of a nymph and its final moult into an adult winged aphid when it would have been recorded in the experiment, the first replicates in the ladybird treatment must have started producing winged individuals before the first culling took place on day 4.

In experiment 2, the presence of another species of ladybird also resulted in an increase in winged offspring production. The response of the green clone was stronger than the response of the red clone, possibly because of a higher 'background' level of wing production in the red clone. Clones of pea aphids are known to differ in their propensity to produce winged offspring (e.g. Sutherland 1969; Lamb & MacKay 1979) and colonies of clone BP are rarely observed to be free of winged adults in culture (C. Braendle and W. W. Weisser, unpublished data). Our results indicate that there is genetic variation in the propensity of producing winged forms in the pea aphid and also with respect to the response to predators. The percentage of winged forms among the offspring declined as the experiment progressed (figure 3). Several mutually non-exclusive hypotheses could explain this result. First, in the ladybird treatment aphids may have received fewer wing-inducing stimuli as the experiment progressed. This seems unlikely as the predators were still feeding in the colonies and the decline was observed in all treatments. Second, there may have been an effect of aphid age in the response. Studies by MacKay & Wellington (1977) and MacKay & Lamb (1979) suggest that, in the pea aphid, the production of winged offspring is influenced by aphid age. Third, the plants to which aphids were transferred later in the experiments might have been of a better

Table 1. Results of experiment 2 with *A. bipunctata* and two clones of pea aphid

(Statistical analysis was performed using generalized linear model procedure (SAS Institute 1989). Dependent variable: arcsine-transformed percentages of winged forms among offspring. The number of offspring was used as the weight variable. *n* plants gives the number of replicates used in the analysis, *n* offspring is the number of offspring produced by the *n* adults that were transferred to the plants. Numbers are means \pm s.e. See figure 1 and §2 for explanations.)

source of offspring		green clone SG			red clone BP			main effect clone	main effect treatment	interaction clone \times treatment
		<i>n</i> plants	<i>n</i> offspring	<i>n</i> adults	<i>n</i> plants	<i>n</i> offspring	<i>n</i> adults			
days 1–3	control	9 ^a	206.8 \pm 22.1	30.0 \pm 0	9 ^a	200.7 \pm 28.7	30.0 \pm 0	$F_{1,72} = 381.3$ $p = 0.0001$	$F_{2,72} = 21.4$ $p = 0.0001$	$F_{2,72} = 12.1$ $p = 0.0001$
	ladybird	20	149.7 \pm 19.5	30.0 \pm 0	20	126.4 \pm 12.8	30.0 \pm 0			
	disturbance	10	173.2 \pm 28.4	30.0 \pm 0	10	169.2 \pm 17.9	30.0 \pm 0			
test day 3	control	10	129.3 \pm 5.4	9.0 \pm 0	8	124.3 \pm 8.2	9.0 \pm 0	$F_{1,72} = 284.0$ $p = 0.0001$	$F_{2,72} = 26.6$ $p = 0.0001$	$F_{2,72} = 0.8$ $p = 0.461$
	ladybird	20	124.9 \pm 4.7	9.0 \pm 0	20	117.3 \pm 9.3	9.0 \pm 0			
	disturbance	10	130.5 \pm 3.8	9.0 \pm 0	10	113.3 \pm 8.3	9.0 \pm 0			
days 4–6	control	10	165.6 \pm 15.5	9.0 \pm 0	9	135.3 \pm 20.2	9.0 \pm 0	$F_{1,72} = 298.8$ $p = 0.0001$	$F_{2,72} = 10.9$ $p = 0.0001$	$F_{2,72} = 7.4$ $p = 0.001$
	ladybird	20	54.3 \pm 9.3	9.0 \pm 0	20	56.3 \pm 8.0	9.0 \pm 0			
	disturbance	9	182.0 \pm 7.5	9.0 \pm 0	10	146.1 \pm 13.5	9.0 \pm 0			
days 7–9	control	10	168.6 \pm 10.0	8.2 \pm 0.3	9	146.3 \pm 18.3	8.0 \pm 0.5	$F_{1,65} = 229.6$ $p = 0.0001$	$F_{2,65} = 7.4$ $p = 0.001$	$F_{2,65} = 0.9$ $p = 0.423$
	ladybird	13	53.3 \pm 14.9	4.5 \pm 0.5	19	62.7 \pm 13.9	5.3 \pm 0.5			
	disturbance	10	200.0 \pm 16.1	8.5 \pm 0.3	10	191.2 \pm 11.0	8.4 \pm 0.2			
test day 9	control	9	108.6 \pm 5.2	7.2 \pm 0.2	10	108.6 \pm 12.9	7.4 \pm 0.5	$F_{1,61} = 27.6$ $p = 0.0001$	$F_{2,61} = 2.1$ $p = 0.13$	$F_{2,61} = 0.3$ $p = 0.748$
	ladybird	13	48.6 \pm 11.3	3.5 \pm 0.6	15	64.6 \pm 11.5	3.5 \pm 0.6			
	disturbance	10	118.1 \pm 8.3	8.0 \pm 0.4	10	96.2 \pm 12.5	7.3 \pm 0.5			

^a One group of offspring was lost after adults had already been transferred to new plants on day 3.

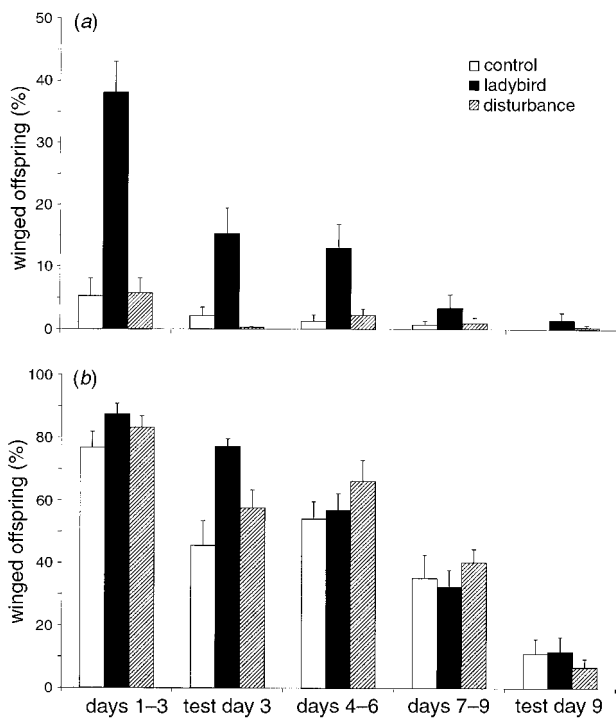


Figure 3. Proportion of winged offspring produced by aphids in experiment 2 with *A. bipunctata*. The results of the statistical analysis are given in table 1. (a) Green clone SG and (b) red clone BP.

quality than the plants to which aphids were transferred early in the experiment, even though they appeared to be very similar. To distinguish between these hypotheses an experiment could be carried out where plant quality, aphid age and exposure times to a stimulus are carefully controlled. Importantly, for the tests carried out on days 3 and 9 in experiment 2, aphids were transferred to new plants where they were no longer exposed to the predator while producing offspring. This could also have contributed to the decline in winged offspring production in the ladybird treatment.

Several possibilities exist concerning the proximal cue that induces aphids to produce winged offspring in the presence of predators. In experiment 2 we tested for one possibility, i.e. the disturbance caused by a foraging predator. Under this hypothesis, aphids do not perceive the predator directly, but react to the increased disturbance in the colony caused by individuals that return to feeding sites after dropping off the host plant. The results do not provide strong support for this hypothesis. The green clone did not respond to this treatment at all, while the red clone produced most winged offspring in the disturbance treatment in only two instances. Although we tried to mimic the rates of dislodgement caused by predators, it is very possible that the type of disturbance caused by predators differs from the disturbance imposed on aphids by our experimental procedure.

In the laboratory, single adults of *C. septempunctata* have been shown to consume more than 50 aphids per day and relative densities of more than two ladybirds per 100 pea aphids have been reported from the field (Hodek & Honek 1996). Other predators such as predatory gallmidges or syrphid fly larvae can also eradicate aphid colonies within a few days (Markkula *et al.* 1979; Chambers 1988; Nijveldt

1988). That predators can cause the extinction of aphid colonies is also supported by the observation that more than half of the replicates in the ladybird treatment in experiment 1 were consumed entirely by the beetles within one week. This raises a question about the effectiveness of a strategy of producing dispersing offspring. Because the time lag between the appearance of a predator and escape of winged offspring will be at least one aphid generation (i.e. at least one week under field conditions), many aphid colonies will have become extinct before their offspring can escape from the plants. However, if predator attack results in the extinction of a colony, the production of winged offspring may be the only chance of a clone escaping predation. An inducible response could be selected for if there is a non-zero chance that at least some of the offspring survive until wings have developed. Thus, it is conceivable that the effectiveness of the strategy varies with the voracity of the predator that attacks the aphid colony. It may also vary with the size of the aphid colony at the time of the attack because larger colonies are likely to persist for longer than smaller colonies. The next step, therefore, is to obtain quantitative data from field studies to determine how times to extinction of aphids in the field depend on colony size and the type of predator that attacks the aphid colony.

Thus, the aphid–predator system seems to fulfil a number of requirements for the evolution of inducible defences (Tollrian & Harvell 1998). Predator attack is spatially and temporally intermittent and the possession of wings is costly for an aphid clone. Predator impact can be considerable and the presence of a predator in an aphid colony is a clear indication to an aphid of an enhanced risk of being eaten. Open questions remain concerning the effectiveness of the response in the field and about the exact nature of the cue that aphids use to switch to the production of winged offspring.

The finding that a predator induces the production of winged offspring in aphids indicates that adaptive changes in the morphology of prey need not be limited to defensive structures. In the pea aphid, the induced change in offspring morphology allows for predator avoidance behaviour. The induced winged morphs can disperse by flight and thereby reduce the risk of being eaten on the plant. Examples of adaptive changes in animal morphology have so far been largely confined to aquatic predator–prey systems. Our findings emphasize that they also exist in terrestrial systems.

We thank Tony Dixon, Dieter Ebert, Jukka Jokela, Tad Kawecki, Tom Little, Jürg Spring, Bernhard Stadler, Steve Stearns, Ralph Tollrian and Wolfgang Völkl for critically reading previous versions of this manuscript. Wolfgang Völkl and Beat Reber provided aphids and ladybirds, respectively. Helpful comments from two anonymous referees are gratefully acknowledged. This study was supported by the Roche Research Foundation, the Novartis Stiftung and grant no. 3100-053852.98 of the Swiss Nationalfond to W.W.W.

REFERENCES

- Adler, F. R. & Karban, R. 1994 Defended fortresses or moving targets? Another model of inducible defences inspired by military metaphors. *Am. Nat.* **144**, 813–832.
 Astrom, M. & Lundbert, P. 1994 Plant defence and stochastic risk of herbivory. *Evol. Ecol.* **8**, 288–298.

- Campbell, C. A. M. 1978 Regulation of the damson-hop aphid (*Phorodon humili* Schrank) on hops (*Humulus lupulus* L.) by predators. *J. Horticult. Sci.* **53**, 235–242.
- Cappuccino, N. 1988 Spatial patterns of goldenrod aphids and the response of enemies to patch density. *Oecologia* **76**, 607–610.
- Chambers, R. J. 1988 Syrphidae. In *Aphids, their biology, natural enemies and control*, vol. B (ed. A. K. Minks & P. Harrewijn), pp. 259–270. Amsterdam: Elsevier.
- Chen, K. & Hopper, K. R. 1997 *Diuraphis noxia* (Homoptera: Aphididae) population dynamics and impact of natural enemies in the Montpellier region of southern France. *Environ. Entomol.* **26**, 866–875.
- Clark, C. W. & Harvell, C. D. 1992 Inducible defences and the allocation of resources: a minimalist model. *Am. Nat.* **139**, 521–539.
- Dennis, P. & Wratten, S. D. 1991 Field manipulation of populations of individual staphylinid species in cereals and their impact on aphid populations. *Ecol. Entomol.* **16**, 17–24.
- Dixon, A. F. G. 1972 Fecundity of brachyperous and macropterous alatae in *Drepanosiphum dixonii* (Callaphididae, Aphididae). *Entomol. Exp. Appl.* **15**, 335–340.
- Dixon, A. F. G. 1998 *Aphid ecology*. London: Chapman & Hall.
- Dixon, A. F. G. & Wratten, S. D. 1971 Laboratory studies on aggregation, size and fecundity in the black bean aphid, *Aphis fabae* Scop. *Bull. Entomol. Res.* **61**, 97–111.
- Farrell, J. A. & Stufkens, M. W. 1988 Abundance of the rose-grain aphid, *Metopolophium dirhodum*, on barley in Canterbury, New Zealand, 1984–87. *NZ J. Zool.* **15**, 499–505.
- Farrell, J. A. & Stufkens, M. W. 1990 The impact of *Aphidius rhopalosiphii* (Hymenoptera: Aphidiidae) on populations of the rose grain aphid (*Metopolophium dirhodum*) (Homoptera: Aphididae) on cereals in Canterbury, New Zealand. *Bull. Entomol. Res.* **80**, 377–383.
- Frank, S. A. 1993 A model of inducible defence. *Evolution* **47**, 325–327.
- Frazer, B. D., Gilbert, N., Ivers, P. M. & Raworth, D. A. 1981a Predator reproduction and the overall predator–prey relationship. *Can. Entomol.* **113**, 1015–1024.
- Frazer, B. D., Gilbert, N., Nealis, V. & Raworth, D. A. 1981b Control of aphid density by a complex of predators. *Can. Entomol.* **113**, 1035–1041.
- Harvell, C. D. 1984 Predator-induced defence in a marine Bryozoan. *Science* **224**, 1357–1359.
- Harvell, C. D. 1990 The ecology and evolution of inducible defences. *Q. Rev. Biol.* **65**, 323–340.
- Hille Ris Lambers, D. 1966 Polymorphism in aphididae. *A. Rev. Entomol.* **11**, 47–78.
- Hodek, I. & Honek, A. 1996 *Ecology of Coccinellidae*. Dordrecht: Kluwer Academic Publishers.
- Hughes, R. D. 1963 Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *J. Anim. Ecol.* **32**, 393–424.
- Jervis, M. A. & Kidd, N. A. C. (ed.) 1996 *Insect natural enemies*. London: Chapman & Hall.
- Karban, R. & Baldwin, I. T. 1997 *Induced responses to herbivory*. University of Chicago Press.
- Kareiva, P. M. & Odell, G. 1987 Swarms of predators exhibit ‘preytaxis’ if individual predators use area-restricted search. *Am. Nat.* **130**, 233–270.
- Kfir, R. & Kirsten, F. 1991 Seasonal abundance of *Cinara cronartii* (Homoptera: Aphididae) and the effect of an introduced parasite, *Pauesia* sp. (Hymenoptera: Aphidiidae). *J. Econ. Entomol.* **84**, 76–82.
- Lamb, R. J. & MacKay, P. A. 1979 Variability in migration tendency within and among natural populations of the pea aphid, *Acyrtosiphon pisum*. *Oecologia* **39**, 289–299.
- Levins, R. 1968 *Evolution in changing environments*. Princeton University Press.
- Lively, C. M. 1986 Canalization versus developmental conversion in a spatially variable environment. *Am. Nat.* **128**, 561–572.
- Lloyd, D. G. 1984 Variation strategies of plants in heterogeneous environments. *Biol. J. Linn. Soc.* **21**, 357–385.
- Lowe, H. J. B. & Taylor, L. R. 1964 Population parameters, wing production, and behaviour in red and green *Acyrtosiphon pisum* (Harris). *Entomol. Exp. Appl.* **7**, 287–295.
- Loxdale, H. D., Hardie, J., Halbert, S., Footitt, R., Kidd, N. A. C. & Carter, C. I. 1993 The relative importance of short- and long-range movement of flying aphids. *Biol. Rev.* **68**, 291–311.
- MacKay, P. A. & Lamb, R. J. 1979 Migratory tendency in aging populations of the pea aphid, *Acyrtosiphon pisum*. *Oecologia* **39**, 301–308.
- MacKay, P. A. & Wellington, W. G. 1975 A comparison of the reproductive patterns of apterous and alate virginoparous *Acyrtosiphon pisum* (Homoptera: Aphididae). *Can. Entomol.* **107**, 1161–1166.
- MacKay, P. A. & Wellington, W. G. 1977 Maternal age as a source of variation in the ability of an aphid to produce dispersing forms. *Res. Popul. Ecol.* **18**, 195–209.
- Markkula, M., Tiittanen, K., Hämäläinen, M. & Forsberg, A. 1979 The aphid midge *Aphidoletes aphidimyza* (Diptera, Cecidomyiidae) and its use in biological control of aphids. *Ann. Entomol. Fennici* **45**, 89–98.
- Maynard Smith, J. 1972 *Evolution and the theory of games*. New York: Cambridge University Press.
- Moran, N. A. 1992 The evolution of aphid life-cycles. *A. Rev. Entomol.* **37**, 321–348.
- Nijveldt, W. 1988 Cecidomyiidae. In *Aphids, their biology, natural enemies and control*, vol. B (ed. A. K. Minks & P. Harrewijn), pp. 271–277. Amsterdam: Elsevier.
- Padilla, D. K. & Aldolph, S. C. 1996 Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol.* **10**, 105–117.
- Riessen, H. P. 1992 Cost–benefit model for the induction of an anti-predator defence. *Am. Nat.* **140**, 349–362.
- SAS Institute 1989 *SAS/STAT user's guide: basics. Version 6.04*. Cary, NC: SAS Institute Inc.
- SAS Institute 1993 *SAS technical report P-243, SAS/STAT software: the Genmod procedure, release 6.09*. Cary, NC: SAS Institute Inc.
- Schultz, J. C. 1988 Plant responses induced by herbivores. *Trends Ecol. Evol.* **3**, 45–49.
- Stewart, H. C. & Walde, S. J. 1997 The dynamics of *Aphis pomi* De Geer (Homoptera: Aphididae) and its predator, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae), on apple in Nova Scotia. *Can. Entomol.* **129**, 627–636.
- Sutherland, O. R. W. 1969 The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrtosiphon pisum*. *J. Insect Physiol.* **15**, 1385–1410.
- Tollrian, R. & Harvell, C. D. (ed.) 1998 *The ecology and evolution of inducible defences*. Princeton University Press.
- Way, M. J. & Banks, C. J. 1968 Population studies on the active stages of the black bean aphid, *Aphis fabae* Scop., on its winter host *Evonymus europaeus* L. *Appl. Biol.* **62**, 177–197.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

