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The economics of escape behaviour in the pea aphid, *Acyrthosiphon pisum*

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Summary. Pea aphids have several alternative responses to the detection of alarm pheromone produced by conspecifics. One of these, dropping from the feeding site to the ground, is potentially costly owing to the risk of desiccation-induced mortality on the ground before another host plant can be reached. Both dropping and walking from the feeding site incur a cost due to lost feeding opportunity. The aphids' decision as to which anti-predator tactic to use should be sensitive to the costs of their behaviour. Consequently, aphids should be less likely to drop when the risk of desiccation is higher, and less likely to drop or walk when the lost opportunity cost is higher. We tested these predictions by manipulating climatic severity (temperature and humidity) and host quality, respectively. As predicted, aphids are less likely to drop or walk in response to pheromone when feeding on high quality than on low quality hosts, and less likely to drop when the environment is hot and dry than when it is more benign. The latter is true whether the aphids are feeding on real or simulated leaves. Since all aphids were of the same clone, these results show that individual aphid genotypes possess the ability to adaptively modify their escape behaviour with changes in prevailing conditions. A number of other behavioural observations in the aphid literature may be interpreted in an economic or cost-benefit framework. The approach holds considerable promise for understanding many aspects of the anti-predator behaviour of aphids and other animals.

Key words: Pea aphid – Escape – Cost-benefit analysis

Some animals have available to them several alternative anti-predator tactics. Having encountered a predator, an individual must choose which of these tactics to employ. This decision ought to depend not only upon the potential benefit (i.e., risk reduction) to be gained from the use of a particular tactic, but also on the costs of employing it. The latter include lost opportunity costs (e.g., lost opportunities for mating or feeding; the latter have been reported in caterpillars by Stamp and Bowers 1988) as well as any risk of mortality consequent upon the use of a particular tactic. A more comprehensive treatment of this economic approach to animal escape behaviour is provided by Ydenberg and Dill (1986).

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), is an ideal species in which to test specific hypotheses about the economics of escape behaviour. When an aphid is attacked by a predator it often produces an alarm pheromone (Kislow and Edwards 1972; Nault et al. 1973). The active chemical (trans-β-farnesene; Bowers et al. 1972) is contained in a gummy liquid secreted from the aphid's cornicles, or siphunculi. The secretion may incapacitate the predator's mouthparts, but its major function is probably to dispense the alarm pheromone (Nault and Phelan 1984). When a feeding aphid detects the pheromone produced by a nearby conspecific, it can react in a variety of ways, ranging in intensity from vigorous movements of the legs and antennae (while continuing to feed) to dropping from the plant to the ground below. We will be concerned primarily with walking and/or dropping from the feeding site, since these behaviours have two important potential costs to fitness. Firstly, leaving a suitable feeding site has a cost in lost feeding opportunity. Secondly, dropping results in a substantial risk of mortality from desiccation on the ground; at 42° C (a ground temperature not uncommon in the field), 50% of adult pea aphids become paralysed within 6–7 min (Roitberg and Myers 1979).

We tested the general hypothesis that pea aphids are less likely to employ a particular response to alarm pheromone when the costs of that response are relatively high. They therefore should be less likely to drop or walk away when current feeding opportunities are particularly good (high host quality), and less likely to drop when climatic conditions are severe (high likelihood of desiccation), than when food is of lower quality or cli-

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matic conditions are more benign, respectively. We tested these specific hypotheses by manipulating the costs of the escape responses in three separate experiments.

General methods and materials

All aphids used in these experiments were reared from a single parthenogenic female collected in June, 1984 from vetch (*Vicia* sp.) at Delta (near Vancouver), B.C., Canada. They were reared on broad bean (*Vicia faba*) in the laboratory at 18°–22° C and 55%–75% RH. The colony consisted of the population of aphids on 12–16 plants. As plants deteriorated new ones were put in their place and the aphids were transferred to them. The continual introduction of fresh plants maintained aphids in good condition, as indicated by the absence of winged individuals.

For all experiments, alarm pheromone was produced by removing a single third or fourth instar sister aphid from one of the colony plants and squeezing its head and thorax with fine forceps. Only aphids producing observable droplets from both siphunculi were used as stimuli.

Aphid behavioural responses to the pheromone were characterized as belonging to one of four categories: "agitate" (raising and lowering of the legs and vigorous waving of the antennae, but without withdrawal of the stylet), "walk" (removal of the stylet and movement from the feeding position), "drop" (removal of the stylet followed by dropping from the feeding surface), and "no response". Our "agitate" is similar to "waggle" or "jerk" of Nault and Phelan (1984), and "walk" includes Roitberg and Myers' (1979) two categories of "run" and "back up". In all experiments a proportion of aphids failed to respond . This could be due to failure of the squeezed aphid to produce a biologically active product, failure of the chemical to reach the feeding aphid because of uncontrolled variation in presentation method or air currents in the laboratory, or a decision by the feeding aphid to ignore the pheromone; we did not attempt to separate these possibilities experimentally.

Experiment 1

Methods

Trials were conducted August and September 1984, under three different environmental conditions: cool-moist, ambient, and hot-dry (Table 1). Cool-moist and hot-dry environments were set up in controlled environment rooms, and varied minimally during the experiment; the ambient room varied to a greater extent with prevailing weather conditions. All three test areas were lit by fluorescent tubes, providing 230 lx. Lights in all environments were on between 0600 and 2100 hours.

Between two and six bean plants were kept in each test area for the duration of the trials. Plants were placed on a tray, in front of a green cardboard wall. As older plants deteriorated they were replaced; this occurred more frequently in the hot-dry environment (over the test period 12, 13, and 18 plants were used in the cool, ambient and hot environments, respectively). All plants were greenhouse-germinated and 12–35 cm tall. New plants were taken from the greenhouse to the controlled environment rooms and infested with approximately 15 adult aphids. Tests were run on third and fourth instar larvae and adults of subsequent generations. We made no attempt to control aphid inter-plant movement or crowding, because plants deteriorated and were removed before populations on individual plants became too large.

Table 1. Conditions in the three environments used in Experiment 1. Temperatures were measured on each experimental day; humidities were measured at intervals throughout the experimental period

Environment	Temperature (°C)			Humidity (%RH)		
	Mean	(*n*)	Range	Mean	(*n*)	Range
Cool-Moist	13.2	(11)	12.5–14.5	71.7	(6)	69–75
Ambient	19.7	(11)	18.0–21.5	62.9	(5)	56–76
Hot-dry	28.0	(11)	None	48.8	(6)	44–55

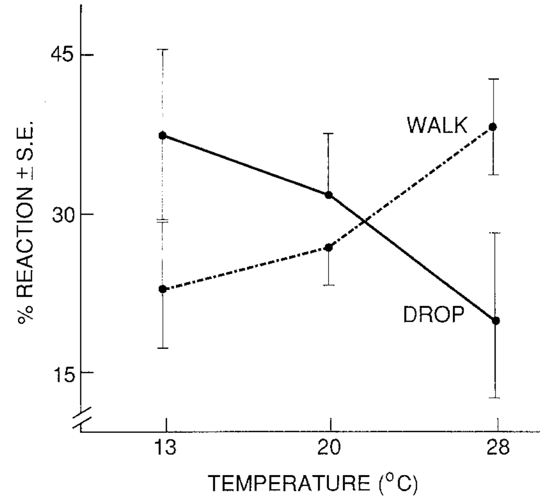

Fig. 1. The results of Experiment 1, showing the weighted mean proportion (±SE) of aphids dropping and walking at each temperature. Although the likelihood of responding to pheromone remains constant, pea aphids are less likely to drop and more likely to walk as temperature increases. The values shown are back-calculated from the arcsin square root transformed proportions dropping and walking on each day at each temperature ($N=11$ at 13° and 20°; $N=10$ at 28°)

The pheromone-producing aphid (see General Methods) was placed head first into a micropipette, which was then waved slowly for 30 s under a single arbitrarily chosen leaf harbouring a group of aphids, as close as possible to the aphids without actually touching them (about 1 cm in this and subsequent experiments). Responses were recorded only for feeding adult aphids; these were categorized broadly as "walk", "drop", and "no response" ("no response" included "agitate", which we did not treat as a distinct response type at this stage). Trials were carried out until approximately 300 aphids had been tested in each environment (this required 10–11 test days); the actual numbers were 311, 281, and 328 aphids in the cool, ambient, and hot environments, respectively. To determine the effect of temperature, we carried out separate weighted least squares regressions on the percentage drop and percentage walk data, treating each test day as an independent observation. Percentages were arcsin square root transformed to normalize the distributions. The transformed values for a particular test day-temperature combination were weighted according to the number of aphids tested.

Results and discussion

The warmer the room in which the tests were conducted, the less likely the aphids were to drop in response to alarm pheromone (Fig. 1). The overall percent response to pheromone remained roughly constant (62.5%, 60.4%, and 61.4% at the low, medium, and high temperatures, respectively), but temperature had a significant influence on the likelihood of the aphids both dropping ($t=-2.17$, $p=0.04$) and walking ($t=2.74$, $p=0.01$).

While these results are in accordance with our predictions, there are two potential problems that limit our interpretation of these data. First, because the data were collected and analyzed by day and treatment only (i.e., aphids from all plants within each treatment-day were lumped) differences in crowding (i.e., group size within leaves) may have confounded our results. Second, there could be a confounding effect of food quality. If, for any reason, the aphids found the bean plants in the hot-dry room to provide higher quality food than those in the cooler rooms, then the results could be explained by a lost opportunity cost hypothesis. The next two experiments were designed to clearly separate the effects of climate, food quality, and variation among groups of aphids on aphid escape behaviour.

Experiment 2: Climatic Effects

To eliminate the possibility that the results of Experiment 1 were due to varying host quality, we developed artificial leaves (food sachets), whose quality could be precisely controlled, and repeated the previous experiment in two controlled environments (cool-moist and hot-dry).

Methods

These experiments were carried out inside a single walk-in environmental chamber. A portable humidifier in the chamber allowed us to maintain elevated humidity levels. Humidity could not be experimentally reduced, however, and varied somewhat with ambient conditions in the hot-dry environment (Table 2). Fluorescent tubes provided 1400 lx, between 0600 and 2100 hours daily. The experiments were carried out in blocks of 4–5 days with each climate, separated by several days to re-set and stabilize the chamber.

The artificial diet used was based on the results of Mittler and Dadd (1964) and Mittler (1967) concerning food preference in the peach aphid (*Myzus persicae*). The main dietary component was sucrose (20% weight to final volume of solution). Six amino acids (asparagine, leucine, isoleucine, phenylalanine, methionine, and tryptophan) were mixed in equal amounts and added to form 1% of the solution (weight to final volume). The actual (wt./wt.) percentages of sucrose and amino acids were 19 and 0.95%, respectively. Food stocks were heated into solution in 0.02 M Tris buffered double distilled water. When cooled, one drop of green food colouring was added per 50 ml of solution to simulate plant leaf coloration; aphids (including *A. pisum*) have been reported to be attracted to yellow and green solutions (Cartier and Auclair 1964; Herger 1975). The pH was then adjusted to 7.6 using 10% NaOH; adults prefer this pH, which is optimal for growth and reproduction (Auclair 1965). Preliminary cafeteria-type experiments showed clearly that this food type was acceptable to the pea aphids and preferred by them to other solutions with which it was paired. We found, as have other workers (e.g. Mittler and Dadd 1964; Srivastava and Auclair 1974), that amino acids act as phagostimulants only when sucrose is present.

Table 2. Environmental conditions in Experiment 2. Temperatures and humidities were measured on each experimental day. Evaporation rate was measured with a Piche tube (10.6 cm^2 evaporative area), for 21–24 h, beginning on experimental day 6 (1 cool-moist and 4 hot-dry trials had already been completed)

Environment		Temperature (°C)	Humidity (%RH)	Evaporation (ml/h)
Cool-Moist	Mean	19.3	46.4	0.18
	Range	18.6–20.8	39.9–49.0	0.09–0.25
	s.d.	0.57	2.70	0.06
	n	10	10	9
Hot-dry	Mean	28.5	26.2	0.62
	Range	26.9–29.9	9.3–39.2	0.25–0.73
	s.d.	0.84	11.67	0.26
	n	10	10	6

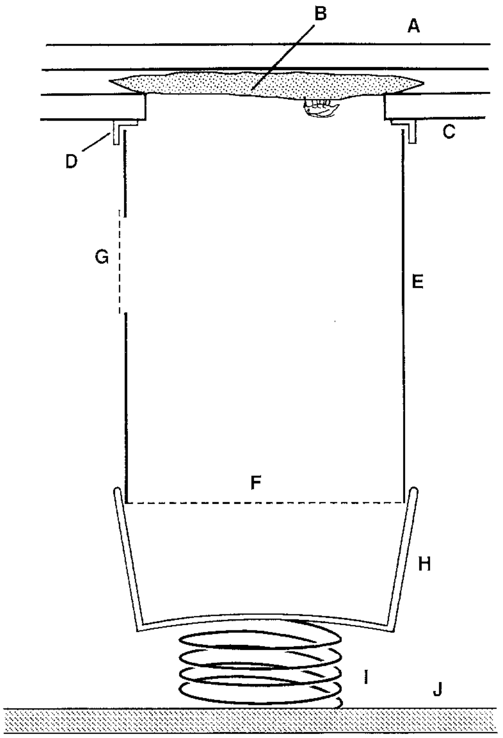

Fig. 2. Schematic cross-section of one of the feeding cells used in Experiments 2 and 3. Four of these comprised a test chamber. *A*, clear plexiglass pane; *B*, parafilm sachet filled with food solution; *C*, opaque chamber roof; *D*, docking ring; *E*, acetate sleeve; *F*, mesh bottom; *G*, air vent; *H*, plastic dish; *I*, spring wire; and *J*, chamber floor. The artificial stems to aid the aphids in reaching the food are not shown in this section

Food sachets similar to those used by Auclair (1965) were formed from bilayered Parafilm™ cut into 9 cm diameter circles. The upper and lower layers were fused by applying two heat seals perpendicular to one another across the middle of each sachet, dividing each sachet into equal quadrants. The circumference was heat sealed after 2–2.5 ml of food solution had been added to each quadrant. Food and food sachets were prepared daily.

Plexiglass test chambers were used to hold sachets and aphids. Each chamber contained four isolated cells (Fig. 2), evenly spaced. These cells were composed of a 9 cm high by 8 cm diameter acetate sleeve with a mesh bottom, inserted into a 4 cm deep plastic dish. Each acetate sleeve contained a small air vent halfway up, and 4 green tubes (0.8 cm diameter) running up the inside wall to simulate plant stems. The plastic dishes had coiled wires glued to their bottoms, which spring loaded them into docking rings located on the underside of the chamber roof; the docking rings were simply the plastic dish lids with their tops removed. The chambers each had four 7 cm diameter holes under which docking rings were centered. Food sachets were placed over these holes and a pane of clear plexiglass held them down tightly against the chamber roof.

Fifteen aphids (apterous adults) were placed into each cell and trapped there by resetting the sleeve into the docking ring. They reached the underside of the food sachets by climbing up the artificial stems or the acetate wall. The aphids (180 per test day, in 3 test chambers) were left in the cells for 23 h before testing, which was carried out between 0900 and 1100 hours, on 10 days for each climatic condition. Tests were conducted on a single cell at

Table 3. The effect of climate on pea aphid escape behaviour (Experiment 2). Values shown are the percentages of aphids (of all those tested) which responded in each fashion. The *t*-test reported in the text was carried out on the percent drop data for individual cells

Response	Climate	
	Hot-Dry	Cool-Moist
Drop	1.1	13.3
Walk	2.9	7.1
Agitate	16.8	15.2
None	79.3	64.4
N	666	1052

a time. To accomplish this, the spring was compressed, the dish and sleeve removed, and a note made of the positions of all feeding aphids on the underside of the sachet. A pheromone-producing aphid from the stock culture was held by forceps and waved slowly about the underside of the sachet, as close as possible to the feeding aphids (individuals or groups), for 15 s. When two or more isolated groups or individuals were present on the same sachet each was tested with a separate pheromone preparation. The occasional aphid that showed any agitation prior to testing (e.g., in response to removal of the sleeve) was not tested. Responses were scored in all four categories described under "General Methods". Responses for each cell tested were then further categorized as "drop" and "no drop". The percent "drop" was then arcsin square root transformed and the treatment groups compared using a two sample *t*-test with unequal variances. A total of 666 aphids (113 cells) was tested in the hot-dry climate, and 1052 (118 cells) in the cool-moist one, between 18 October and 5 December 1985.

Results and discussion

The results (Table 3) provide strong support for the hypothesis that aphid escape responses represent economic decisions. As predicted, aphids in the hot-dry environment almost never dropped from plants in response to alarm pheromone (0.07% ± 0.01 SE), whereas the drop response in the cool-moist environment was much more frequent (5.33% ± 0.12 SE). This effect was confirmed by the *t*-test on the data for individual cells ($t = 6.62$; $p < 0.001$; df = 136). In control experiments we could find no response to the waving forceps alone, so responses were to some component of the stimulus aphid.

Three factors may confound the results: uncontrollable differences in aggregation size (cf. results of Montgomery and Nault (1978) for peach aphids), and temperature/humidity effects on either pheromone transmission or the likelihood of falling from the sachet by accident. Although the modal aphid was in a group of 9 in the cool-moist treatment and only 5 in the hot-dry treatment (where there were fewer aphids feeding overall), there was no obvious effect of feeding group size on the likelihood of dropping. For example, in the cool-moist treatment 12.1% and 14.1% of the aphids dropped when tested in group sizes of 1–8 and 10–15, respectively. It is highly unlikely that any effect of climate on transmission of the pheromone could have confounded the results, as evaporation was greater in the hot-dry climate (Table 2) and the pheromone should have been even more likely to reach the aphids there. Wiener and Capinera (1979) invoke this mechanism to explain their observation that high humidity suppresses the response to alarm pheromone analog in the greenbug, *Schizaphis graminum*. These authors also claim that greenbugs become unresponsive at high temperatures and low humidities, but in neither case do their data reveal a significant effect.

An increased likelihood of accidental falling from the sachet at the low temperature also seems quite unlikely, since dropping was almost always an immediate response to the pheromone; aphids were seldom observed to fall while they were walking.

Experiment 3: Food Quality Effects

Here we test the hypothesis that aphids should be less willing to leave feeding sites (by walking or dropping) when food quality at that site is high. Our rationale for this hypothesis is based upon evidence that aphids often do not rediscover those sites which they have left (Niku 1975; Roitberg et al. 1979), and may not find another plant (or leaf) of equivalent quality. Even if an equally good feeding site is eventually found, the time spent away from the food can result in a measurable decrease in the production of young (Roitberg et al. 1979).

Methods

All trials were carried out in the same walk-in environmental room used in Experiment 2. Temperature averaged 21.7° C (1 measurement per experimental day; $n = 15$; range 20.8°–22.7° C), and relative humidity 51% ($n = 15$; range 46.5%–57.7%), approximating the cool-moist condition in the previous experiment. The aphids in this experiment were allowed to feed on either the standard food solution (see Experiment 2) or a 50% dilution of it (i.e., a 10% sucrose and 0.5% amino acid mixture). The diluted food was much less preferred by the pea aphids. In a series of experiments run in the same chamber prior to Experiment 3, groups of aphids were allowed to move freely for 16–18 h between sachet quadrants filled with either the standard or the dilute solution, and their final positions recorded. The aphids preferred the full strength food by a ratio of about 2:1 (64% of 330 aphids chose the standard food in a total of 15 trials).

Test chambers and cells were identical to those of Experiment 2, as was the testing procedure, with the following exceptions. Six cells containing each food type (in all four quadrants), were set up on each test day. Each of the three chambers contained four cells (two of each food type in diagonally opposite corners); these cells were alternated between positions daily to avoid any positional bias. Adult aphids were given 16–18 h to feed, and tested between 0930 and 1100 hours. The person testing the aphids with pheromone did not know the identity of the solution on which the aphids fed. As was the case for Experiment 2, the pheromone producers came from the stock culture on bean plants, so differential stimuli can be ruled out when interpreting the results. Data were collected on 513 and 420 individuals on the concentrated and dilute diets, respectively, on 15 test days (i.e., 90 cells each) between 17 February and 13 March 1986. Proportions of aphids walking and dropping in each cell were added together to create the category "left the feeding site"; all others "remained". These proportions were arcsin square root transformed and the treatment groups compared using a two sample *t*-test with unequal variances.

Results and discussion

As predicted, the aphids were less likely to respond to the alarm pheromone in any way, and in particular by leaving their feeding sites (Table 4), when feeding on the richer solution (means of 18.0% ± 0.20 SE and 9.34% ± 0.11 SE for the high and low quality foods, respectively); this was confirmed by the *t*-test on the data for individual cells ($t = 2.31$; $p < 0.05$; $df = 166$). This was true for both sub-categories, walking and dropping, though the difference was greatest for walking. The aphids may have walked less because of the risk of losing their footing and dropping inadvertently, even though this possibility seems remote (see Discussion of Experiment 2). It is more likely that walking, like dropping, incurs a lost opportunity cost. In fact, potential feeding sites, within plants, can vary significantly in quality as a result of age, position, and somatic mutation (Whitham et al. 1984).

Table 4. The effect of food quality on pea aphid escape behaviour (Experiment 3). Values shown are the percentages of aphids (of all those tested) which responded in each fashion. The *t*-test reported in the text was carried out on the percent "leave site" data for individual cells

Response		Food Quality			
		High		Low	
Drop	Leave site	3.1	14.2	4.5	26.2
Walk		11.1		21.7	
Agitate		14.2		20.5	
None		71.5		53.3	
N		513		420	

The failure of more aphids to respond on the high quality food might be attributed to an inability to withdraw their stylets from the sachet when actively feeding. We ruled out this possibility by touching aphids feeding on the concentrated food source with ladybird beetles (*Coccinella californica* Mannerheim). In virtually every case aphids dropped from their sachet after being contacted by a beetle (304 of 337 individuals tested).

General discussion

The cost/benefit or economic approach to anti-predator behaviour adopted in this paper predicts very well how aphids respond to threat of predation. This approach has also proven useful in understanding escape behaviour in other insects, for example how escape behaviour in waterstriders varied with lost feeding opportunity costs (Ydenberg and Dill 1986) and with group size, which influences the benefits of flight (Dill and Ydenberg 1987). The concept has also been applied to animals as diverse as squirrels and cichlid fishes (Dill and Houtman 1989; Dill 1990). The present paper extends the analysis for the first time to aspects of escape behaviour other than flight initiation distance, and demonstrates the generality of the underlying theory.

We used a single clone of aphids in our experiments. The fact that the type of escape behaviour employed depended upon such environmental variables as food quality, temperature and humidity suggests that individual aphids (or genotypes) can vary their escape behaviour in an adaptive way. However, it is clear from the work of Roitberg and Myers (1978, 1979) that genetic differences between pea aphid populations in their anti-predator behaviour also exist: aphid populations from a hot-dry environment (Kamloops, B.C.) are less likely to drop from plants than are those from a more moderate environment (Vancouver), even when tested under the same conditions. The present results incidentally confirm Roitberg and Myers' (1978) original interpretaton of their findings; differences between populations are not due to differences in the amount or activity of the alarm pheromone produced (contrary to the suggestion of Clegg and Barlow 1982).

Not all aphids responded in the same manner to alarm pheromone even when feeding within a particular aggregation. Given that all of the individuals were from the same clone, one might have expected identical responses to the stimulus. There are several reasons why this might not be so. Firstly, the aphids varied in age and possibly physiological conditon. Recent work on feeding and oviposition by insects suggests that their behaviour can be very sensitive to both conditions (e.g. Houston et al. 1988). Secondly, alarm pheromone probably did not reach all individuals at identical concentrations. Finally, there may be heritable differences among clone mates. Bunting and van Emden (1980) and others have shown that there may exist considerable heritable variation in physiological abilities within aphid clones. Any or all of the above may have contributed to the variation we observed.

A number of observations of aphid escape behaviour by other authors can be interpreted within an economic framework, the sometimes quite different interpretations of the original authors notwithstanding: (1) Vibration and pheromone together produce a stronger response in pea aphids than either stimulus alone (Roitberg and Myers 1978); (2) as the distance to a pheromone source increases, peach aphids are more likely to walk and less likely to drop (Montgomery and Nault 1977b); (3) Pea aphids are more likely to drop in response to a more dangerous coccinellid beetle than a less dangerous syrphid larva (Brodsky and Barlow 1986); (4) Pea aphids are less responsive to pheromone when feeding on leaves than on stems, where they are more likely to be touched by a passing predator (Clegg and Barlow 1982); (5) Nymphs (less-likely to regain a food plant than are adults) are less likely to drop than the latter (Roitberg and Myers 1978; Montgomery and Nault 1978); (6) Alate aphids (able to quickly regain plants by flying) are more sensitive to pheromone than are apterae (Nault et al. 1973); (7) Species which live in grasses are more likely to drop than those inhabiting trees (Montgomery and Nault 1977a); (8) Pea aphid clones that live on pond plants are less likely to drop than are morphs from other host plants (Müller 1983). The first four observations suggest that aphids are sensitive to the benefits of their escape behaviour (i.e., to the risk of predation), and the remainder that they are sensitive to the costs of escape as well. Taken together with the results of our experiments they provide convincing support for the notion that aphid anti-predator behaviour is determined in an economic fashion.

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