Antipredator responses of aphids to parasitoids change as a function of aphid physiological state

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Under predation risk, prey may prioritize antipredator behaviours and sacrifice feeding. However, energetically constrained animals may choose to sacrifice or change antipredator responses and accept relatively greater risk in order to secure food. In this last case, the antipredator tactics chosen must balance safety and feeding in such a way that costs are minimized and benefits maximized. We studied the antipredator behaviour of pea aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) subjected to different periods of food deprivation, against the parasitoid *Aphidius ervi* (Hymenoptera: Braconidae). As the energetic internal stress of aphids increased, the predominant antipredator response changed from walking away and dropping to kicking behaviour, and parasitization avoidance decreased. Parasitoids did not show preference between food-deprived and nonfood-deprived aphids. Dropping and walking away reduced parasitization from 50 to 33%. These results support the hypothesis that the antipredator behaviour of an aphid changes as a function of internal stress. By performing less costly behaviour such as kicking under energetically constrained conditions, aphids seem to minimize their probability of energy shortfall. Given that aphid antipredator behaviour is a function of nutritional state, its occurrence under natural conditions may match host quality spatial distribution.

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Foraging models predict that under continuous high predation risk, prey are likely to prioritize antipredator behaviours and sacrifice feeding or mating (Lima & Dill 1990; Werner & Anholt 1993; Anholt & Werner 1998; Lima 1998; Lima & Bednekoff 1999). Antipredator behaviour involves direct costs related to its deployment (e.g. allocation to running, jumping, flying), and indirect costs such as lost opportunities for feeding or mating (Abrahams & Dill 1989; Grand & Dill 1997). The antipredator behaviour chosen must balance safety and feeding in such a way that costs are minimized and benefits maximized (Stephens & Krebs 1986; Tollrian & Harvell 1999). The manipulation of the physiological (energetic) state of the test animal, such as by submitting it to periods of food deprivation, has been useful to estimate the energetic cost of different antipredator behaviours, thus contributing to the understanding of the antipredator decision-making process (see review by Lima

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1998). For instance, many empirical studies have shown that energetically constrained animals sacrifice or shift antipredator responses and accept relatively greater risks in order to obtain food (Cartar 1991; Lima 1998), but little is known about the decision rules these animals use to choose among a range of antipredatory options.

Aphids display a number of antipredator behaviours in response to predators and parasitoids. They may be short-term responses such as: (1) releasing an alarm pheromone (*trans*-β-farnesene), which is contained in a gummy liquid droplet secreted from the aphid's cornicles, that alerts conspecifics and alters predator foraging (Bowers et al. 1972; Nault et al. 1976); (2) shaking the body vigorously while kicking at the parasitoid with the hind legs (Dixon 1958); (3) walking away from the threatened feeding site (Dill et al. 1990); (4) dropping off the plant to avoid exposure (Dill et al. 1990; Chau & Mackauer 1997); (5) clustering together to reduce predation risk by dilution effect (Turchin & Kareiva 1989); and (6) selecting host plants and microhabitats free of predators (Hopkins & Dixon 1997). Antipredator responses may also be long-term responses such as: (7) ingesting toxic allelochemicals having deterrent or toxic effects on predators (Szentesi & Wink 1991); (8) enhancing the production of winged

morphs, which may eventually avoid predators (Weisser et al. 1999); and (9) enhancing the production of soldiers, which may eventually defend the colony (Aoki et al. 1998; Foster & Rhoden 1998). Among these tactics, dropping behaviour is one of the most studied aphid antipredator responses (Bowers et al. 1977; Roitberg & Myers 1978; Dill et al. 1990; Stadler et al. 1994; Andrade & Roitberg 1995; Chau & Mackauer 1997; Losey & Denno 1998a, b).

The antipredator behaviour of the pea aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), is one of the best understood. Laboratory experiments established that alarmed pea aphids are less likely to walk away from and drop off high-quality plants than poor-quality plants, and are also less likely to do so when climatic conditions are severe (i.e. hot and dry environments), suggesting that aphids display escape behaviours that minimize lost feeding opportunities and desiccation-induced mortality (Dill et al. 1990). Another study showed that recently moulted, adult-stage pea aphids drop off and walk away from high-quality plants more frequently than do older aphids, and they are also more likely to relocate to a new host plant after dropping, suggesting that the age-dependent physiological state affects antipredator decisions (Stadler et al. 1994). Adult pea aphids are more prone to perform dropping behaviour than those at younger stages (Gerling et al. 1990; Chau & Mackauer 1997), regardless of the presence or absence of foliar-foraging predators (Losey & Denno 1998a).

To understand better the antipredator decision-making process, and allow us to predict which antipredator alternatives an aphid would choose when facing different internal or external conditions, we used a cost–benefit approach based on manipulating the internal (energetic) state of the aphid. Here, we report on the effect of physiological state, as modified by submitting pea aphids of similar age (wingless adults) to periods of food deprivation, on the frequency of antipredator behaviours. We tested the hypothesis that aphid antipredator behaviour changes as a function of internal stress. In particular, since food deprivation stresses the energy budget, we predicted that, as stress increases, aphids should minimize the probability of energy shortfall by performing less costly (both direct cost and lost opportunity cost) antipredator behaviours, while unconstrained individuals should have enough energetic scope to perform more costly alternatives. We tested these predictions in laboratory experiments with the pea aphid, and its main parasitoid in Chile, *Aphidius ervi* Haliday (Hymenoptera: Braconidae).

METHODS

Insects

The pea aphid, *A. pisum*, is a Palaearctic aphid of nearly world-wide distribution, and one of the largest aphid species (about 4 mm long). It usually infests legumes and related species (Blackman & Eastop 1984). *Aphidius ervi* is a solitary endoparasitoid (laying eggs within the host

body) of European origin, now also showing nearly world-wide distribution. It attacks many aphid species and has been introduced in many countries to control crop aphids. Parasitoids usually locate aphids using chemical cues from the aphids (e.g. sex and aggregation pheromones) and from the host plant (e.g. plant volatiles), and then rapidly try to oviposit on the aphid (Godfray 1994). After successful oviposition, parasitoid development occurs through several stages within the aphid body, lasting about 2 weeks, after which an adult parasitoid emerges from the dead host. Aphid antipredator behaviours may prevent oviposition.

We collected aphids and parasitoids for the stock colony from alfalfa fields at Instituto Nacional de Investigaciones Agropecuarias (INIA) at La Platina, Santiago, Chile, and reared the parasitoids on pea aphids, and the aphids on broad beans (*Vicia faba* L.).

Effect of Food Deprivation on Aphid Survival

We first determined the effect of food deprivation time on survival in order to choose a suitable period of food deprivation for experiments studying its effect on antipredator behaviours and parasitoid attacks (i.e. a period reflecting an escape decision rather than a physiological limitation). We placed 20 wingless 7-day adult individuals of *A. pisum* obtained after reproductive synchronization on wet filter paper inside petri dishes in a culture chamber at 20 °C and 50% RH. We recorded the number of surviving individuals every 8 h for 84 h, and replicated this procedure four times.

Effect of Food Deprivation on Antipredator Behaviour

Once the effect of food deprivation time on survival had been documented, we established food deprivation treatments. We food-deprived groups of wingless adult individuals of *A. pisum* from the culture stock by placing them on wet filter paper inside petri dishes in a culture chamber at 20 °C and 50% RH, for 24 and 48 h. The control (nonfood-deprived wingless adults) came directly from the stock culture without being placed in petri dishes to maximize sustained food ingestion. We then transferred individual aphids with a paint brush to the surface of an alfalfa leaf (*Medicago sativa* L.) placed inside each petri dish (4–cm diameter). After an adaptation period of 5 min, all aphids settled on the leaves and began performing probing behaviours. Thereafter, we introduced one CO_2-anaesthetized mated female of the parasitoid, and videotaped aphid behaviour. We stopped recording 3 min after the first contact between the aphid and the parasitoid. We replicated this experiment at least 14 times per treatment. In each replicate we replaced all components (aphid, parasitoid, alfalfa leaf and petri dish) to avoid pseudoreplication of data.

We analysed aphid behaviour using the software The Observer 3.0 (Noldus). For aphids, we assessed the

Table 1. Behaviours displayed by the aphid *Acyrthosiphon pisum* subjected to 0, 24 or 48 h of food deprivation and then confronted with the parasitoid *Aphidius ervi*: univariate effect of each behavioural variable on overall MANOVA

Behaviour	MS effect	MS error	$F_{2, 53}$	P
Walking away time	8727.190	1898.852	4.596	0.014
Nonfeeding time	13 143.141	3277.079	4.011	0.024
Feeding time	42 822.422	4248.253	10.080	0.000
Number of kicks	26.877	47.805	0.562	0.573
Number of droppings	0.364	0.074	4.939	0.011

number of kicks and drops, and cumulative time walking away, feeding and not feeding. Under our conditions dropping behaviour consisted in a short jump of the aphid away from the feeding site, usually separating the aphid from the leaf. Under natural conditions, gravity helps the aphid fall off the plant and escape from the parasitoid during the dropping behaviour. We determined the occurrence of feeding by the perpendicular position of the aphid rostrum relative to the plant surface and the slow movement of antennae, usually laid back on the aphid dorsum (Hardie et al. 1992; Powell et al. 1993). We considered that aphids were not feeding when their proboscis was not perpendicular to the leaf epidermis and the antennae were performing rapid movements. We determined nonfeeding time by subtracting feeding, walking and dropping times from total time. For parasitoids, we assessed the number of contacts with the aphids via antennation and oviposition.

Because antipredator behaviours were correlated, we compared behavioural differences between treatments using one-way multivariate analysis (MANOVA). We used log (X+1) transformed variables when the data violated the assumptions for normality or homoscedasticity.

Effect of Food Deprivation on Parasitoid Attacks

Because food deprivation of aphids could have affected parasitoid attacks, thus violating the implicit assumption of absence of variation in risk of predation as a function of aphid food deprivation, we performed a choice test experiment assessing the preference of parasitoids towards food-deprived and nonfood-deprived aphids. We placed one aphid deprived of food for 48 h and another with no food deprivation simultaneously on a petri dish and recorded the times to first antennation and to first oviposition of a mated *A. ervi* female introduced into the petri dish. We performed 14 replicates, and compared the frequency of preferences with the chi-square test.

RESULTS

Effect of Food Deprivation on Aphid Survival

Aphid survival decreased as food deprivation time increased, with 50% survival occurring after approximately 48 h of food deprivation. Thus, 48 h represents a period of food deprivation relevant in terms of stressing the aphid, while presumably preserving its capacity for displaying antipredator behaviours.

Effect of Food Deprivation on Antipredator Behaviour

The overall behaviour of aphids differed significantly between treatments (Wilks' lambda=0.67, $F_{10,98}$=2.14, P=0.027). All variables except the number of kicks differed significantly between treatments (Table 1). As food deprivation increased, walking away and nonfeeding times decreased (Fig. 1a, b), while feeding time increased (Fig. 1c). The number of kicks towards the parasitoid did not increase with food deprivation (Fig. 1d), and most aphids displaying kicking behaviour did not leave the leaf (data not shown). The number of aphids dropping off the leaf differed significantly only between nonfood-deprived and 48 h of food deprivation treatments (Fig. 1e). The proportion of aphids that successfully avoided oviposition by the parasitoid (relative to those that suffered ovipostion) was significantly higher only in the nonfood-deprived treatment (Fig. 2).

Effect of Food Deprivation on Parasitoid Attack

When we offered an individual parasitoid the choice between a nonfood-deprived aphid and an aphid deprived of food for 48 h, there were no preferences for any treatment (out of 14 parasitoids, seven showed first contact with a nonfood-deprived aphid and seven with a food-deprived aphid; Yates-corrected chi-square test: χ^2_1=0.14, P=0.70). Similarly, the times to first antennation and to first oviposition did not differ between treatments (time to first antennation: nonfood-deprived: 6.93 ± 0.99 min; 48 h of food deprivation: 5.98 ± 1.19 min; Wilcoxon matched-pairs signed-ranks test: T=59, N=16, P=0.64; time to first oviposition: nonfood-deprived: 3.99 ± 1.32 min; 48 h of food deprivation: 4.88 ± 1.56 min; T=24, N=11, P=0.72).

DISCUSSION

The present study shows that as the energetic stress of the aphid *A. pisum* increased, the predominant antipredator response against *A. ervi* changed from walking away and dropping to kicking. Thus, the hypothesis that antipredator behaviour of an aphid changes as a function of internal stress was supported. In general, despite the large number of studies concerning antipredatory behaviour, choice among several escape options has been poorly studied (Lima 1998). Even though state variables have
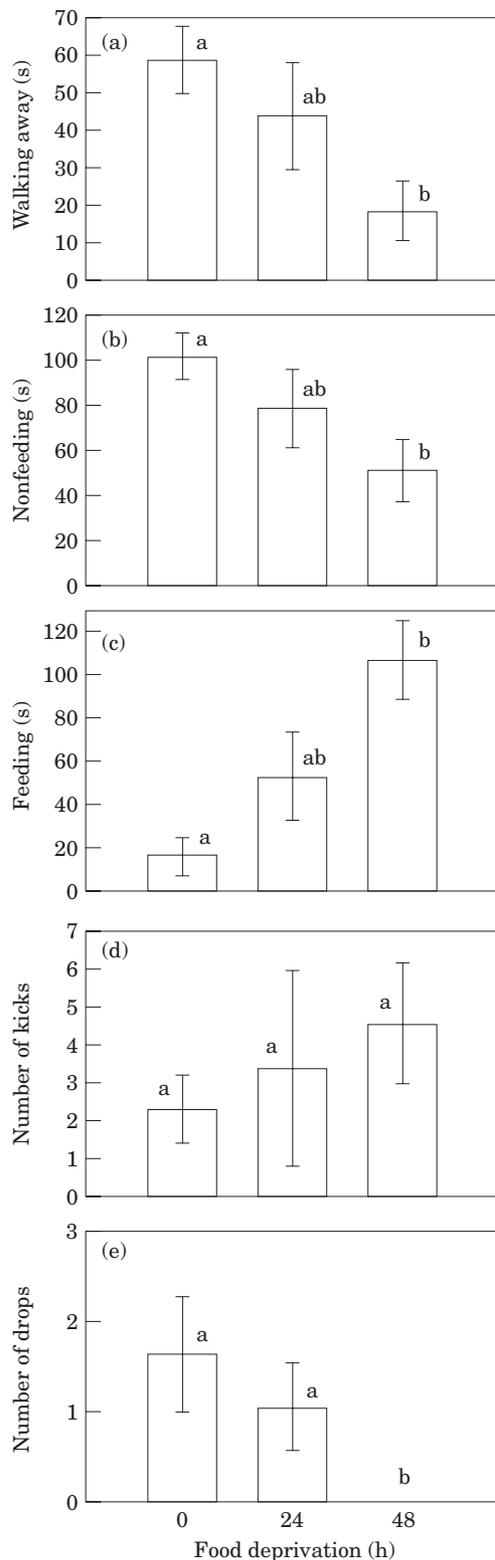
Figure 1. Behaviour of *Acyrthosiphon pisum* when attacked by the parasitoid *Aphidius ervi*. Aphids were subjected to three levels of food deprivation: 0, 24 and 48 h. (a) Cumulative time performing walking away behaviour, (b) cumulative nonfeeding time, (c) cumulative feeding time, (d) number of kicks and (e) number of drops. Means (±SEs) marked with different letters were significantly different (*P*<0.05). Dropping and walking away were the two antipredatory behaviours that changed as a function of aphid internal state.
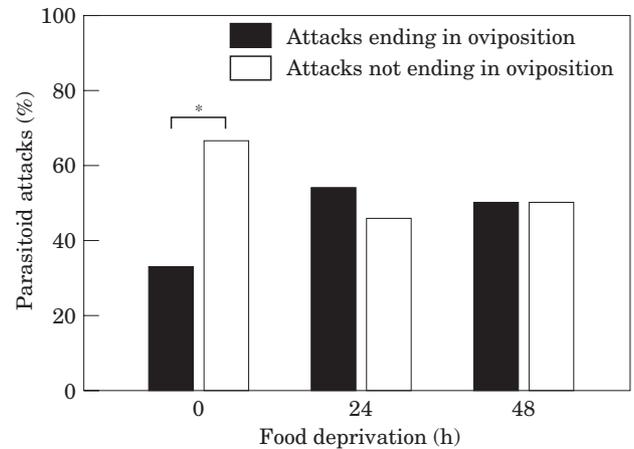

Figure 2. Proportion of attacks by the parasitoid *Aphidius ervi* on the aphid *Acyrthosiphon pisum* ending with oviposition and not ending with oviposition relative to the total number of attacks, as a function of food deprivation time. *Significant difference (*P*<0.05) between both proportions (*Z* test for proportion). Unconstrained aphids avoided oviposition by parasitoids to a higher extent than constrained ones.

been largely incorporated into foraging models (Mangel & Clark 1986), choice among several available options of antipredator behaviours have not been addressed (Houston et al. 1993). The choice of antipredator behaviours by aphids described herein can be viewed within the broader framework of the study of costs and benefits of inducible defences. This framework incorporates inducible defences (e.g. morphological, physiological and behavioural defences) used by vertebrates, invertebrates, and plants in terrestrial, marine and freshwater habitats (Tollrian & Harvell 1999). Thus, the antipredatory choices made by *A. pisum* may be the evolutionary result of processes balancing costs and benefits of the facultative use of a given defensive strategy (Agrawal & Karban 1999).

The experiment assessing the effect of aphid food deprivation on parasitoid preference confirmed the implicit assumption that, regardless of aphid state, the risk of predation did not vary with food deprivation. Thus, since it was equally likely for parasitoids to find and oviposit on food-deprived and nonfood-deprived aphids, antipredator behaviours in treatments were exclusively due to changes in the aphid energetic budget rather than to responses to differential risk of predation. Food deprivation treatments, although causing depressed abdomens and less humid epidermis in aphids, may not have been severe enough to produce changes in host size or shape, which are known to be important for host choice by braconid parasitoids (Kouamé & Mackauer 1991; Battaglia et al. 1995; Mackauer et al. 1996). Nevertheless, food deprivation treatments produced internal changes in the aphids, not perceived by the parasitoid, that affected aphid antipredator behaviours.

Given that antipredator behaviours were affected by the aphid physiological state, it is interesting to consider the energetic demands of each behavioural alternative. To our knowledge, the direct energetic cost of dropping

behaviour has not been assessed, but since it implies a short jump, which under natural conditions leads to falling from the plant, it is likely to involve a comparatively low cost. However, dropping to the ground also reduces feeding opportunities, and implies relocation to different host plants or plant tissues, which may require considerable time and energy, and expose the aphid to ground predators (Losey & Denno 1998b). Hence, dropping is predicted to occur only when energy stores offset the costs of relocating to a new host plant, as in the case of well-fed aphids from a high-quality plant (Stadler et al. 1994). Indeed, in aphids subjected to 48 h of starvation, this behaviour was not observed (Fig. 1e).

Walking away from the predator is expected to be less costly than dropping. Thus, although an aphid cannot feed on the plant while walking, it can easily stop walking and reinitiate feeding more readily (Klingauf 1987). Walking away decreased with increasing food deprivation period but, unlike dropping, we still observed walking away after 48 h of starvation (Fig. 1a). Lastly, kicking is expected to be the least costly antipredator behaviour, since using hind tarsi to avoid ovipositor contact may be performed while the aphid continues feeding, and thus does not involve lost feeding opportunities. We observed no significant differences between treatments in the number of kicks (Fig. 1d).

The fact that time devoted to feeding increased as food deprivation increased suggests a behavioural response orientated to re-establishing the energetic budget by increasing food intake. This may be related to the fact that at the adult stage, as in the case of the aphids used in the present work, energy allocation to gonadal growth increases exponentially due to sclerotization of embryos, which are not available for resorption, thus increasing energy demands and reducing reallocation possibilities (Stadler 1995; Stadler & Mackauer 1996).

Given that food-deprived and nonfood-deprived aphids are comparable to aphids feeding on poor- and high-quality plants, respectively, the results of the present study are in general agreement with the findings of Stadler et al. (1994) in showing evidence that dropping occurs when aphids have acquired sufficient energy to offset lost feeding opportunities. Nevertheless, in the work of Stadler et al. (1994), changes in aphid antipredator behaviours occurred in relation to aphid stage (i.e. gonadal investments) and plant quality (high versus low), whereas in the present work, aphid developmental stage was constant and thus antipredator behaviours occurred in response to direct changes in the aphid nutritional state (i.e nonfood- and food-deprived treatments). In contrast, Dill et al. (1990) found less dropping and walking away behaviours on high-quality host conditions, but these differences may be due to the uncharacterized physiological state of the aphids studied.

Antipredator behaviours seems to have allowed unconstrained aphids to avoid parasitization to a higher extent than constrained ones (33 versus 50%) (Fig. 2). Although constrained aphids (48 h of food deprivation treatment) showed less antipredator behaviours and longer feeding times, the success of parasitoid attacks (i.e. attacks ending in oviposition) reached only 50%, implying that aphids adopting antipredator behaviours avoided parasitization by 50%. Under natural conditions, these proportions are affected by the habit of aphids to form colonies. This has been shown to reduce predation risk (Cappuccino 1988; Turchin & Kareiva 1989) and to increase the variance of the probability of encountering individual aphids by parasitoids (Ives et al. 1999). Hence, the mortality values found here may be even lower under natural conditions. Similarly, aphid aggregated distributions also reduce parasitoid efficiency via, for example, the release of alarm pheromone, which causes dropping of nearby aphids (Roitberg & Myers 1978; Ives et al. 1999). Nevertheless, aphid aggregation may eventually increase attraction of parasitoids (Michaud & Belliure 2000), and dropping aphids may be further attacked if they return to the plant or if the parasitoid pursues aphids on the ground (Ives et al. 1999). However, given that an aphid colony is usually conformed by genetically identical organisms, the benefit of dropping behaviour should be assessed not only in terms of individual fitness but also in terms of inclusive fitness (Mcallister et al.1990); for instance, if an aphid is effectively parasitized, dropping will increase parasitoid mortality and thus reduce the probability of further parasitod attacks on the aphid colony.

Variation in nutritional state among aphids may result under natural conditions by feeding on plants or plant tissues differing in quality (e.g. variation in phloem sap content and/or chemical defences between and within plants) (Memmott et al. 1995; Stadler & Mackauer 1996). Thus, given the results presented herein, at the within-plant level, higher and lower occurrences of antipredatory behaviours would be expected on rich and poor tissues, respectively. Similarly, variation in quality between plants may be positively correlated with the frequency of antipredatory behaviour. It may be speculated that the frequently observed nonrandom spatial patterns of parasitism in the *A.ervi*–pea aphid system, as well in other systems (Pacala & Hassell 1991; Olson et al. 2000), may be partly explained by the deployment of behavioural responses such as those described herein.

References

Abrahams, M. & Dill, L. M. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**, 999–1007.

Agrawal, A. A. & Karban, R. 1999. Why induced defenses may be favored over constitutive strategies in plants. In: *The Ecology and Evolution of Inducible Defenses* (Ed. by R. Tollrian & C. D. Harvell), pp. 45–61. Princeton, New Jersey: Princeton University Press.

Andrade, M. C. B. & Roitberg, B. D. 1995. Rapid response to intraclonal selection in the pea aphid (*Acyrthosiphon pisum*). *Evolutionary Ecology*, **9**, 397–410.

Anholt, B. R. & Werner, E. E. 1998. Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evolutionary Ecology*, **12**, 729–738.

Aoki, S., Kurosu, U., Shibao, H., Yamane, S. & Fukatsu, T. 1998. Defense by a few first-instar nymphs in the closed gall of *Dinipponaphis autumna* (Homoptera, Aphididae, Hormaphidinae). *Journal of Ethology*, **16**, 91–96.

Battaglia, D., Pennacchio, F., Romano, A. & Tranfaglia, A. 1995. The role of physical cues in the regulation of host recognition and acceptance behavior of *Aphidius ervi* Haliday (Hymenoptera: Braconidae). *Journal of Insect Behavior,* **8**, 739–750.

Blackman, R. L. & Eastop, V. F. 1984. *Aphids on the World's Crops: an Identification and Information Guide.* New York: J. Wiley.

Bowers, W. S., Nault, L. R., Webb, R. E. & Dutky, S. R. 1972. Aphid alarm pheromone: isolation, identification, synthesis. *Science*, **177**, 1121–1122.

Bowers, W. S., Nishino, C., Montgomery, M. E., Nault, L. R. & Nielson, M. W. 1977. Sesquiterpene progenitor, germacrene A: an alarm pheromone in aphids. *Science*, **196**, 680–681.

Cappuccino, N. 1988. Spatial patterns of goldenrod aphids and the response of enemies to patch density. *Oecologia*, **76**, 607–610.

Cartar, R. V. 1991. A test of risk-sensitive foraging in wild bumble bees. *Ecology*, **72**, 888–895.

Chau, A. & Mackauer, M. 1997. Dropping of pea aphids from feeding site: a consequence of parasitism by the wasp, *Monoctonus paulensis*. *Entomologia Experimentalis et Applicata*, **83**, 247–252.

Dill, L. M., Fraser, A. & Roitberg, B. D. 1990. The economics of escape behaviour in the pea aphid, *Acyrthosiphon pisum*. *Oecologia*, **83**, 473–478.

Dixon, A. F. G. 1958. Escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Transactions of the Royal Entomological Society of London*, **10**, 319–334.

Foster, W. A. & Rhoden, P. K. 1998. Soldiers effectively defend aphid colonies against predators in the field. *Animal Behaviour*, **55**, 761–765.

Gerling, D., Roitberg, B. D. & Mackauer, M. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: influence of oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae). *Journal of Insect Behavior*, **3**, 501–514.

Godfray, H. C. J. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton, New Jersey: Princeton University Press.

Grand, T. C. & Dill, L. M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral Ecology*, **8**, 437–447.

Hardie, J., Holyoak, M., Taylor, N. J. & Griffiths, D. C. 1992. The combination of electronic monitoring and video-assisted observations of plant penetration by aphids and behavioural effects of polygodial. *Entomologia Experimentalis et Applicata*, **62**, 233–239.

Hopkins, G. W. & Dixon, A. F. G. 1997. Enemy-free space and the feeding niche of an aphid. *Ecological Entomology*, **22**, 271–274.

Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 375–397.

Ives, A. R., Schooler, S. S., Jagar, V. J., Knuteson, S. E., Grbic, M. & Settle, W. H. 1999. Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. *American Naturalist*, **154**, 652–673.

Klingauf, F. A. 1987. Host plant finding and acceptance. In: *Aphids: Their Biology, Natural Enemies and Control* (Ed. by A. A. Minks & P. Harrewijn), pp. 209–220. Amsterdam: Elsevier.

Kouamé, K. L. & Mackauer, M. 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. *Oecologia*, **88**, 197–203.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.

Lima, S. L. & Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist*, **153**, 649–659.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Losey, J. E. & Denno, R. F. 1998a. The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecological Entomology*, **23**, 53–61.

Losey, J. E. & Denno, R. F. 1998b. Interspecific variation in the escape responses of aphids: effect on risk of predation from foliar-foraging and ground-foraging predators. *Oecologia*, **115**, 245–252.

Mcallister, M. K., Roitberg, B. D. & Weldon, K. L. 1990. Adaptive suicide in pea aphids: decisions are cost sensitive. *Animal Behaviour*, **40**, 167–175.

Mackauer, M., Michaud, J. P. & Völkl, W. 1996. Host choice by aphidiid parasitoids (Hymenoptera: Aphidiidae): host recognition, host quality, and host value. *Canadian Entomologist*, **128**, 959–980.

Mangel, M. & Clark, C. W. 1986. Towards a unified foraging theory. *Ecology*, **67**, 1127–1138.

Memmott, J., Day, R. K. & Godfray, H. C. J. 1995. Intraspecific variation in host plant quality: the aphid *Cinara cupressi* on the Mexican cypress, *Cupressus lusitanica*. *Ecological Entomology,* **20**, 153–158.

Michaud, J. P. & Belliure, B. 2000. Consequences of foundress aggregation in the brown citrus aphid *Toxoptera citricida*. *Ecological Entomology*, **25**, 307–314.

Nault, L. R., Montgomery, M. E. & Bowers, W. S. 1976. Ant–aphid association: role of aphid alarm pheromone. *Science*, **192**, 1349–1351.

Olson, A. C., Ives, A. R. & Gross, K. 2000. Spatially aggregated parasitism on pea aphids, *Acyrthosiphon pisum*, caused by random foraging behavior of the parasitoid *Aphidius ervi*. *Oikos*, **91**, 66–76.

Pacala, S. W. & Hassell, M. P. 1991. The persistence of host–parasitoid associations in patchy environments. II. Evaluation of field data. *American Naturalist*, **138**, 584–605.

Powell, G., Hardie, J. & Pickett, J. A. 1993. Effects of the antifeedant polygodial on plant penetration by aphids, assessed by video and electrical recording. *Entomologia Experimentalis et Applicata*, **68**, 193–200.

Roitberg, B. D. & Myers, J. H. 1978. Adaptation of alarm pheromone responses of the pea aphids *Acyrthosiphum pisum* (Harris). *Canadian Journal of Zoology*, **56**, 103–108.

Stadler, B. 1995. Adaptive allocation of resources and life-history trade-offs in aphids relative to plant quality. *Oecologia*, **102**, 246–254.

Stadler, B. & Mackauer, M. 1996. Influence of plant quality on interactions between the aphid parasitoid *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae) and its host, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphidiidae). *Canadian Entomologist*, **128**, 27–39.

Stadler, B., Weisser, W. & Houston, A. 1994. Defense reactions in aphids: the influence of the state and future reproductive success. *Journal of Animal Ecology*, **63**, 419–430.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Szentesi, A. & Wink, M. 1991. Fate of quinolizidine alkaloids through three trophic levels: *Laburnum anagyroides* (Leguminosae) and associated organisms. *Journal of Chemical Ecology*, **17**, 557–1574.

Tollrian, R. & Harvell, C. D. 1999. The evolution of inducible defenses: current ideas. In: *The Ecology and Evolution of Inducible Defenses* (Ed. by R. Tollrian & C. D. Harvell), pp. 306–321. Princeton, New Jersey: Princeton University Press.

Turchin, P. & Kareiva, P. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*, **70**, 1008–1016.

Weisser, W. W., Braendle, C. & Minoretti, N. 1999. Predator-induced morphological shift in the pea aphid. *Proceedings of the Royal Society of London, Series B*, **266**, 1175–1181.

Werner, E. E. & Anholt, B. R. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*, **142**, 242–272.