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The costs and consequences of parasitoid attack for the predatory hoverfly, *Episyrphus balteatus*

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ABSTRACT

Question: What are the life-history costs for a predatory insect of surviving parasitoid attack, and can parasitoid attack alter predator–prey interactions?

Hypotheses: Survivorship is influenced by host age. Hosts that suffer parasitoid attack grow more slowly and consume fewer prey. Those that survive attack are smaller as adults and show reduced survivorship.

Organisms: The aphidophagous hoverfly *Episyrphus balteatus*, its endoparasitoid wasp *Diplazon laetatorius* and its prey, the pea aphid, *Acyrthosiphon pisum*.

Site of experiments: All experiments were conducted in controlled temperature rooms and chambers in the laboratory.

Methods: *Episyrphus balteatus* larvae of each instar were exposed to attack by *Diplazon laetatorius*, then dissected to measure the encapsulation response (a measure of immunity). Second instar larvae were either attacked or not attacked by *D. laetatorius*. Their development rates and numbers of prey consumed were noted. The size and survivorship of surviving (immune) and control hoverflies were compared following eclosion.

Conclusions: Successful immune response increased with larval age (first instar 0%, second instar 40%, third instar 100% survival). Second instar larvae that successfully resisted parasitoid attack were larger as pupae (but not as adults) and showed reduced adult survivorship. Female adult survivors were more likely than male survivors to have died within 16 days of eclosion, but there was no difference between unattacked male and female control hoverflies. Attacked larvae, irrespective of immune status, consumed fewer aphids than unattacked individuals. *Episyrphus balteatus* suffers significant costs of resisting parasitoid attack, and parasitoid attack can reduce the top-down effects of an insect predator, irrespective of whether the host mounts an immune response or not.

Keywords: cost of resistance, *Diplazon laetatorius, Episyrphus balteatus*, immunity, pea aphid, tritrophic

INTRODUCTION

The field of ecological immunology is predicated on the assumption that trade-offs and costs constrain the evolution of resistance. Costs of resistance are often divided into two

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forms: the costs of maintaining an immune capability and the costs of deploying them against a natural enemy (Fellowes and Godfray, 2000, Schmid-Hempel, 2003). Few studies have unambiguously shown the maintenance costs of resistance. The most successful have used *Drosophila melanogaster* and its parasitoids as a model system (Kraaijeveld and Godfray, 1997; Fellowes *et al.*, 1998a). These studies have shown that increased encapsulation ability is associated with a reduction in larval feeding rates, which results in decreased competitive ability (Fellowes *et al.*, 1999a; Kraaijeveld *et al.*, 2001).

Deployment costs are more frequently observed (Fellowes and Godfray, 2000; Rolff and Siva-Jothy, 2003). Here, workers expose a host with either a natural (e.g. oviposition by a parasitoid wasp) or an artificial (e.g. a monofilament fibre) challenge. There are several advantages of using an artificial challenge, including the ability to ensure that the costs associated with an immune challenge can unambiguously be assigned to the presence of the foreign body. In contrast, natural enemies such as parasitoid wasps do not just insert an inert egg; they also inject a cocktail of venoms into the host during oviposition. The effects of venom are diverse but in general it appears to help subdue the immune system and prevent the destruction of the egg (reviewed in Quicke, 1997). However, while this adds a layer of complexity to our measurement of costs of mounting an immune response, they do reflect the real challenge that the host has to overcome in surviving attack. Several studies have shown that *Drosophila melanogaster* that survive parasitoid attack have reduced fecundity, adult size (Carton and David, 1983; Fellowes *et al.*, 1999b; Hoang, 2002) and puparium thickness (Fellowes *et al.*, 1998b).

Parasitoids are ubiquitous natural enemies of insects. Given that the consequences of successful parasitoid attack are almost always fatal, the adaptive significance of being able to avoid or repel attack is evident. Some insects, such as many of the Diptera, can mount an innate immune response to attack by endoparasitic wasps by utilizing the encapsulation pathway (Salt, 1970; Godfray, 1994). Melanotic encapsulation starts with the recognition of the parasitoid egg as non-self. Haemocyte production increases (Shrestha and Gateff, 1982) and a class of specialized haemocytes, the lamellocytes, flatten and adhere to the surface of the parasitoid egg. A second class of specialized haemocytes, the crystal cells, break down to release phenoloxidase. This catalyses a series of reactions resulting in the melanization of the surface of the multi-layered capsule (Strand and Pech, 1995). The parasitoid is then usually killed by asphyxiation (Salt, 1970), physical prevention of hatching (Schneider, 1959) or through the release of cytotoxic compounds (Nappi *et al.*, 1995; Nappi and Vaas, 1998; see Fellowes and Godfray, 2000, for a review).

However, studies of the deployment costs of resistance to parasitoid attack have concentrated on a very limited number of species. To date, no study has examined how surviving an immune challenge from a parasitoid wasp may be costly to insect predators, and whether the consequences of surviving attack alter predator–prey interactions. The marmalade hoverfly, *Episyrphus balteatus* De Geer (Diptera: Syrphidae), plays an important role in many temperate European agro-ecosystems. The adults are pollinators, while the larvae are voracious predators of a variety of aphid species (Rotheray, 1989). The larvae are attacked by several hymenopterous parasitoids, the most common of which is *Diplazon laetatorius* Fabricius (Hymenoptera: Ichneumonidae) (Fitton and Rotheray, 1982). *Episyrphus balteatus* larvae can successfully defend themselves against *D. laetatorius* attack via encapsulation (Schneider, 1959). Levels of attack in the field can be high, with parasitism rates reaching over 40% in southern England (S. Hazell and M. Fellowes, unpublished observations), suggesting that *D. laetatorius* may have important consequences for aphid–predator interactions by limiting *E. balteatus* population growth.

Furthermore, by altering patterns of resource allocation, parasitoid attack may have a subtle influence on the predatory behaviour of the host. For example, by allocating resources to defence, hosts may have fewer resources remaining to allocate to foraging, reducing their attack rates. There is evidence that parasitoid attack can alter the consumption rates of herbivorous insects (e.g. Slansky, 1978; Powell, 1989; Shi *et al.*, 2002; Elzinga *et al.*, 2003). The direction of this effect varies, with hosts that are attacked by solitary koinobiont endoparasitoids showing a reduction in consumption rate, whereas hosts attacked by gregarious parasitoids tend to increase consumption, suggesting that the developing parasitoid larvae influence the behaviour of their host (Elzinga *et al.*, 2003). To date, we have no information if a similar pattern is seen with predatory, as opposed to herbivorous, hosts. Predatory and phytophagous insects face different challenges (the victims of predators have the opportunity to escape), but if a similar pattern is present, then we would predict that attack by a solitary endoparasitoid should result in a reduction in prey consumption. In addition, the host immune response acts before parasitoid egg hatch. Therefore, if parasitoid larvae influence host foraging behaviour, then hosts that have survived attack may not show the same pattern of feeding behaviour as those that have succumbed to attack. This has not been tested.

Surviving parasitoid attack is likely to be associated with costs that may be expressed in terms of changes in life-history and behavioural traits. In this study, we examined the effects of larval age on *E. balteatus* encapsulation ability following attack by *D. laetatorius*. We also measured the life-history consequences of successfully resisting parasitoid attack, and whether resisting parasitoid attack alters the predatory behaviour of *E. balteatus*.

METHODS

Study system

Episyrphus balteatus is the most common aphidophagous hoverfly in the UK (Hart and Bale, 1997; Sutherland *et al.*, 2001). Several studies have demonstrated the importance of hoverflies in controlling aphid numbers (Chambers and Adams, 1986; Chambers *et al.*, 1986); some authors argue that hoverflies have an equal, if not greater, impact on aphid numbers than their other natural enemies (Smith, 1976; Entwistle and Dixon, 1989). Two hundred *E. balteatus* were collected at the Upper Wood Farm, University of Reading, Berkshire, UK. The adult hoverflies were maintained in a large population cage (0.8 × 0.8 × 1.0 m) and provided with a supply of pollen (Sigma-Aldrich, bee pollen, Type 3) and a honey–water solution. The cages were placed in a heated greenhouse where the temperature ranged from 16 to 25°C over the course of the experiment. Females were provided with bean plants infested with aphids for oviposition. Larvae were collected from the plants and reared in Petri dishes in a 22.5 ± 0.5°C incubator and were provided with an excess of pea (*Acyrthosiphon pisum*) and vetch (*Megoura viciae*) aphid prey. Before emergence, pupae were placed in the population cage.

Diplazon laetatorius is a koinobiont endoparasitoid of aphidophagous hoverflies and has a worldwide distribution (Fitton and Rotheray, 1982). Oviposition occurs into both host eggs (>48 h old) and larvae, although reportedly not in third instar larvae (Rotheray, 1981). Most populations are thelytokous, although several males have been reported in North America (Kamal, 1924). *Diplazon laetatorius* were reared from *E. balteatus* larvae collected at Upper Wood Farm, University of Reading, Berkshire, UK. *Diplazon laetatorius* were given access to plants on which there were *E. balteatus* eggs and larvae of various ages. The larvae were then reared as normal. The surviving larvae were kept separate from the main culture to avoid inadvertent selection for increased resistance. On emergence the *D. laetatorius* were kept in a perspex cage (30 × 30 × 30 cm) and given honey–water solution and occasionally *E. balteatus* eggs (< 48 h post oviposition) for host feeding.

Age and resistance

Approximately 200 even-aged *E. balteatus* eggs were allowed to hatch and develop on bean plants infested with *A. pisum* at 22.5°C (16 h/8 h light/dark cycle). Forty randomly selected larvae were removed and parasitized after 72 h, twenty after 120 h and a further twenty after 168 h, corresponding to the first, second and third instars. Following removal from the plant, all larvae were kept individually in 50 mm Petri dishes and given an excess of aphids. Following attack, the larvae were reared in a 22.5 ± 0.5°C incubator. The larvae were dissected approximately 200 h after the start of the experiment to establish whether parasitism was either successful or unsuccessful due to capsule formation.

Parasitoid attack, mortality and predatory behaviour

Approximately 200 even-aged *E. balteatus* eggs were allowed to hatch and develop on bean plants infested with *A. pisum* at 22.5°C (16 h/8 h light/dark cycle). After 96 h, ninety first instar larvae were selected at random and placed individually into 50 mm diameter Petri dishes. Sixty of the larvae were parasitized by adding an individual adult *D. laetatorius* to each dish, while the remaining thirty remained as unattacked controls. Wasps that had attacked a larva were not reused. The larva and wasp were then observed until oviposition occurred, after which the wasp was removed. Fifteen third instar pea aphids were added to all of the dishes. The larvae were then given twenty third instar aphids on day 2, thirty and thirty-five fourth instar aphids on days 3 and 4 respectively, and forty and forty-five fifth instar aphids on days 5 and 6 respectively. The numbers of aphids provided was increased over time to ensure that the hoverfly larvae were provided with an excess of prey. Each day the number of aphids eaten and the status of the hoverfly larvae (alive or dead) were recorded, the dishes were cleaned and any aphids remaining from the previous day were removed.

Results from the experiment investigating the effects of age on resistance suggested that all first instar larvae would succumb to attack. To examine the consequences of resisting attack, the experiment was repeated with second instar larvae. The assay was conducted as before, with the exception of the numbers of aphids provided as prey to the larvae. Thirty fourth instar pea aphids were added to all of the dishes on day 1, thirty-five fourth instar aphids on day 2, thirty-five fifth instar aphids on days 3 and 4, and ten fifth instar aphids on days 5, 6 and 7 as required, again to ensure that the larvae were provided with an excess of prey.

On the day of pupation, all pupae were weighed (mg) using a CAHN 29 automatic electrobalance®. The length and width (at the widest point when viewed from above) of the pupae were measured using a dissecting microscope (mm).

Consequences of mounting a successful immune challenge

The adult control (unattacked) and surviving (attacked) *E. balteatus* emerging from the second trial were placed in separate standard population cages and reared as described above. Times of emergence were recorded. The numbers of flies dying from each group were recorded each day. For logistical reasons, the sexes of flies that had died were recorded for each group on days 10 and 17 only (when the experiment was terminated). After death, the length of the hoverfly thorax was measured using a dissecting microscope.

Statistical analysis

All analyses were performed using S-Plus 6.1 (Insightful Corp., 2002). The effects of larval age on encapsulation ability, the effects of parasitism status on larval mortality, pupal mortality and sex ratio, and of sex on longevity were compared using χ^2 tests. The time to pupation and time to eclosion data were compared using Kruskal-Wallis analysis of variance (ANOVA). Larval consumption rate was analysed using a one-way ANOVA with outcome [i.e. attacked pupae which survived to become adult *E. balteatus*, attacked pupae which became *D. laetatorius* (wasps), pupae which died before eclosion (dead) and control treatment] as the explanatory factors. The biometric data were analysed using analysis of covariance (ANCOVA) with the number of aphids eaten as the covariate, pupal length, width and weight as the dependent variables and group (control or surviving) as the explanatory factor. A Mann-Whitney *U*-test was performed to test for differences in the longevity of control versus surviving hoverflies. Sex effects on survivorship were compared using a χ^2 test.

RESULTS

Age and resistance

There was a significant effect of age on encapsulation ability ($\chi^2 = 16.1$, d.f. = 2, $P < 0.0004$). None of the first instar larvae, 40% of the second instar larvae and all of the third instar larvae survived attack.

Pre-adult mortality and predatory behaviour

Parasitism by *D. laetatorius* did not have a significant effect on larval mortality when larvae were parasitized at either the first ($\chi^2 = 1.29$, d.f. = 1, N.S.) or second instar ($\chi^2 = 0.61$, d.f. = 1, N.S.). Larval mortality was greater for first instar larvae (44%) than for second instar larvae (16%). Larvae that succumbed to attack significantly increased their time taken to reach pupation for both first [Kruskal-Wallis H (3, $n = 47$) = 9.42; $P < 0.03$] and second [Kruskal-Wallis H (3, $n = 75$) = 26.38; $P < 0.0001$] instar larvae. Larvae that successfully mounted an immune challenge did not show a change in time taken to reach pupation [second instar larvae only; Kruskal-Wallis H (1, $n = 57$) = 0.72; N.S.].

Attacked pupae were significantly more likely to die (i.e. not become either hoverflies or parasitoids) compared with unattacked pupae (first instar: $\chi^2 = 9.34$, d.f. = 1, $P < 0.002$; second instar: $\chi^2 = 19.3$, d.f. = 1, $P < 0.0001$). Mortality of parasitized pupae was greater in trial one (62.5%) using first instar larvae than in trial two using second instar larvae (29%).

Larvae that resisted attack did not take significantly longer to eclose than the unattacked control larvae [second instar only: Kruskal-Wallis H (1, $n = 57$) = 3.83; N.S.].

The effect of parasitism on larval consumption rate

There were significant differences between groups in both trials in terms of the total numbers of aphids consumed (first instar: $F_{2,38} = 24.88$, $P = 0.0001$; second instar: $F_{3,71} = 5.9$, $P = 0.002$; Fig. 1). For the larvae attacked in their second instar, the control larvae consumed significantly more aphids than larvae that had successfully encapsulated a parasitoid egg (Tukey's HSD, $P = 0.005$).

Biometric data

Variation in pupal mass was partly explained by the number of aphids consumed ($F_{1,54} = 18.53$, $r^2 = 0.26$, $P < 0.0001$; Fig. 2). There was also a significant effect of number of aphids consumed on pupal size, but this explained little of the variance in the model (pupal width: $F_{1,54} = 4.49$, $r^2 = 0.08$, $P = 0.04$; Fig. 3). When the number of aphids consumed was controlled for in the analysis, capsule-bearing pupae were larger (pupal mass: $F_{1,54} = 6.93$, $P = 0.01$; pupal width: $F_{1,54} = 3.72$, $P = 0.06$; Fig. 3) than control pupae.

Resistance and adult traits

Being attacked did not alter the sex ratio of surviving adults ($\chi^2 = 1.94$, d.f. = 1, N.S.), which was approximately 1 : 1 on emergence. Males had a significantly longer thorax than females ($F_{1,42} = 8.33$, $P = 0.006$), but capsule-bearing adults were not significantly smaller than the controls ($F_{1,42} = 0.31$, N.S.). Adult size was not correlated with longevity ($F_{1,42} = 0.32$, N.S.). No significant interactions were observed between thorax length, sex and length of adult survivorship. Capsule-bearing adults showed reduced longevity (Mann-Whitney U-test: $Z = 2.71$, $P = 0.007$; Fig. 4). Although there was no effect of sex on the survivorship of control adults ($\chi^2 = 0.83$, d.f. = 1, N.S.), capsule-bearing females died significantly earlier than capsule-bearing males ($\chi^2 = 4.45$, d.f. = 1, $P = 0.035$).

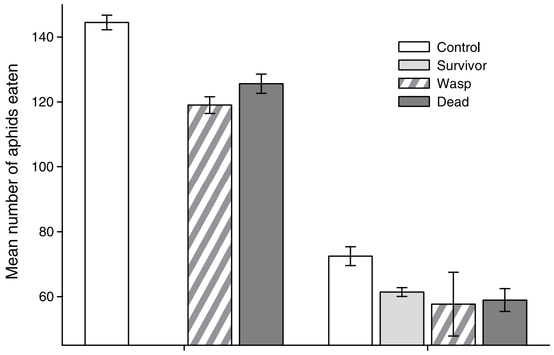

Fig. 1. Mean (± standard error) number of aphids consumed post treatment by control (unattacked), survivor (attacked but surviving), wasp (successfully parasitized) and dead (neither wasp nor hoverfly) first and second instar *Episyrphus balteatus* larvae.

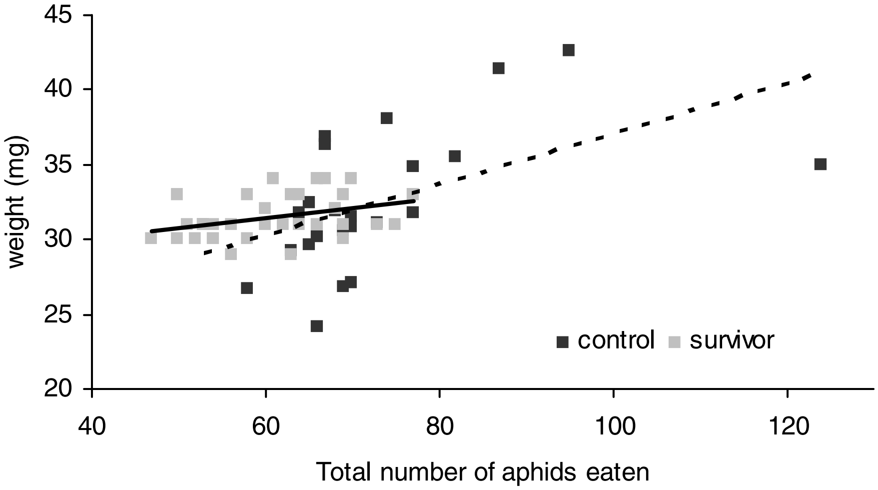

Fig. 2. Relationship between *Episyrphus balteatus* pupal weight (mg) and the total number of aphids consumed for control (unattacked) and surviving (attacked) hoverflies.

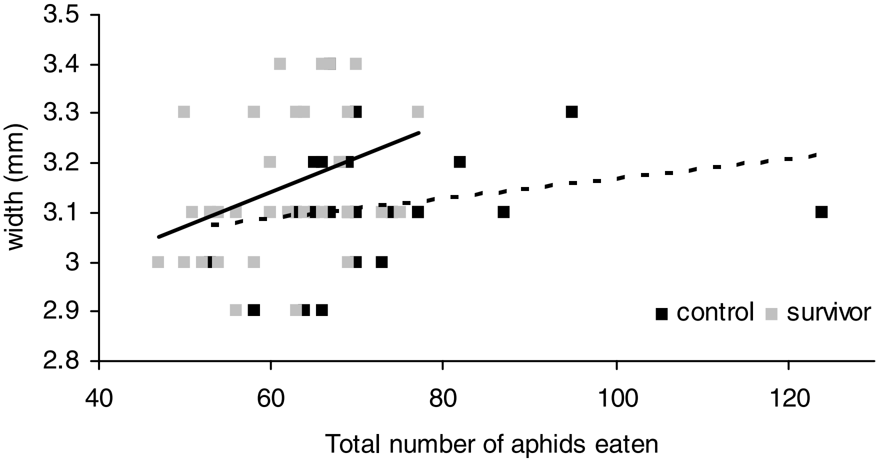

Fig. 3. Relationship between pupal width and the total number of aphids consumed by control (unattacked) and surviving (attacked) *Episyrphus balteatus*.

DISCUSSION

Whether natural selection should result in an increase in the ability to resist attack by a natural enemy depends on the likelihood of attack (the intensity of selection) and the constraints on the evolution of the trait (costs and trade-offs). Our understanding of the ecological immunology of host–parasitoid systems is restricted to one very well understood system based on *Drosophila melanogaster*, and a small number of less well studied systems. If we are to gain a general understanding of host–parasitoid interactions, it is imperative that we broaden our view to include a wider range of taxa, at all trophic levels. The hoverfly predator *Episyrphus balteatus*, its parasitoid *Diplazon laetatorius* and aphid prey provide an

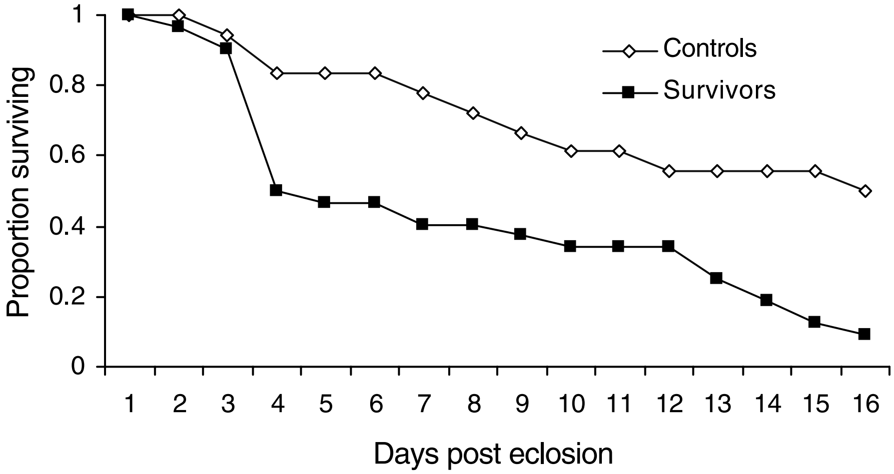

Fig. 4. The proportion of control (unattacked) and surviving (attacked) adult *Episyrphus balteatus* remaining alive over time (days) following eclosion.

excellent model tritrophic system to address such issues. Furthermore, they enable us to ask questions about previously unconsidered ecological consequences of immunity.

In this study, we found that the ability of *E. balteatus* to successfully resist attack by the parasitic wasp *D. laetatorius* is influenced by host age; increased resistance is seen as the *E. balteatus* larvae progress through their instars. Studies of *D. melanogaster* have also shown that encapsulation ability increases with age and that the increase in encapsulation ability correlates strongly with the numbers of circulating haemocytes in the larval haemocoel (Eslin and Prevost, 1996, 2000; Fellowes and Godfray, 2000; Kraaijeveld *et al.*, 2001). It is likely that the number of circulating haemocytes also increases with age in *E. balteatus*. Surprisingly, attack by *D. laetatorius* did not result in increased larval mortality in either first or second instar larvae. Attacked larvae spent longer as both larvae and pupae. However, these differences are likely to be a result of parasitoid development rather than an innate response to attack. When the development times for surviving and control flies only were compared, no differences were found, reflecting previous work with *D. melanogaster* (Fellowes *et al.*, 1998b).

In the present experiment, we used parasitoids rather than an artificial immune insult to investigate the costs of survival. While this prevented us from unambiguously measuring the costs of immunity, it did reflect the reality of parasitoid attack. Not only do the larvae have to successfully encapsulate a parasitoid egg, they must also cope with the cocktail of venom and other counter-defences utilized by the parasitoid. We argue that while implants provide useful insights into the costs of immunity, they do not reflect ecological reality.

Control larvae consumed significantly more aphids than the attacked larvae, irrespective of whether the attacked larvae produced a wasp, a hoverfly, or neither (Fig. 1). With herbivorous insect hosts, the literature contains reports of both increased and decreased food intake depending on the system considered (Elzinga *et al.*, 2003). However, in these cases attacked and non-attacked larvae are compared, rather than those that survived attack through an immune response and their unattacked controls. For example, parasitization by the braconid *Cotesia plutellae* was found to increase the food intake of the diamondback moth, *Plutella xylostella* (Shi *et al.*, 2002). Conversely, tobacco budworm, *Heliothis virescens*, reduced their food intake following parasitization by the braconid *Microplitis demolitor* (Powell, 1989). The differences in consumption rate in our assay may reflect the simple small arenas that the larvae were reared in, where the contact rate between prey and predator was likely to be artificially high. Consequently, the reduction in feeding rate seen in these trials may be an underestimate of the situation found in the field, where *E. balteatus* larvae are foraging in complex three-dimensional environments with patchy prey distribution. Nevertheless, the direction of the effect (a reduction in consumption rate) is the same as that seen in herbivorous insects attacked by solitary, endoparasitic wasps (Elzinga *et al.*, 2003). We speculate that the lack of differences in consumption rate between the hoverfly larvae that resist attack and those that succumb suggests that this is not due to host manipulation by the developing host larvae, but rather that the reduction in predatory behaviour is a result of the physiological trauma associated with attack.

While larvae that fail to encapsulate the parasitoid egg show a reduced development rate, capsule-bearing larvae do not show a similar reduction. Larvae attacked at the second larval instar stage ate fewer aphids but were found to weigh more (Fig. 3) and be marginally larger (Fig. 4) as pupae when the number of aphids consumed was controlled. We speculate that this apparently contradictory result may have a simple cause: parasitism often results in a reduction of active foraging behaviour (Duodu and Davis, 1974). The small arena size and frequent contact with prey may allow parasitized larvae to enjoy a contact rate equal to that of the actively foraging control larvae without the energy expenditure, hence the marginally larger pupae. This difference in weight did not result in differences in adult size, although adult hoverflies that had successfully resisted attack exhibited reduced longevity. This reduced survivorship was more pronounced for female hoverflies. The effects of surviving attack seem to be less pronounced than those suffered by *D. melanogaster*. *Drosophila melanogaster* that survive attack are significantly smaller and have reduced fecundity, but longevity was not affected (Fellowes *et al.*, 1999b). *Episyrphus balteatus* fecundity was not measured in these experiments due to logistical constraints, but it is likely that the reduced longevity of surviving adults would have significantly reduced their realized fecundity as adult females do not usually start producing eggs until 8–10 days post eclosion (S. Hazell, unpublished observations). Sex-based differences in the consequences of resistance have been found in a range of taxa (e.g. Zuk, 1990; Møller *et al.*, 1998; Agnew *et al.*, 1999; Fellowes *et al.*, 1999b) and presumably represent differences in allocation of resources to reproduction. We speculate that the lack of differences in adult size, but concurrent reduction in longevity, reflects reduced allocation to fat resources rather than growth during the larval stage.

All organisms have natural enemies, and resisting attack is generally considered to be of adaptive benefit. Here, we show that surviving parasitoid attack is costly in terms of adult survivorship. In addition, parasitoid attack alters predator–prey interactions, with attacked *E. balteatus* larvae consuming fewer prey individuals. Together, these results suggest that the influence of parasitoids on tritrophic systems may be more complex than previously considered. Furthermore, we would suggest that if the field of ecological immunology is to advance, then studies such as these must move from the laboratory to the field.

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