IMPROVED FITNESS OF APHID PARASITOIDS RECEIVING RESOURCE SUBSIDIES

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Abstract. The availability of nonhost resource subsidies affects the ability of parasitoids to overcome egg and time limitation and maximize lifetime reproductive success. We combined field and laboratory experiments to examine the effects of floral resource subsidies on the reproductive fitness of aphid parasitoids. Under controlled laboratory conditions, sugar resources significantly increased longevity and potential fecundity (egg load) in the endoparasitoids *Aphidius rhopalosiphi* and *Diaeretiella rapae* (Hymenoptera: Aphidiidae). Laboratory microcosm experiments showed that increased potential fecundity translated into significantly higher realized fecundity (i.e., rates of aphid parasitism) by *A. rhopalosiphi* receiving resource subsidies. Mechanisms of enhanced realized fecundity also operated under natural field conditions. Replicated field experiments on cultivated wheat, with host density controlled by experimental placement of aphids, showed that, in general, proximity to floral resource patches significantly increased rates of parasitism. Parasitism rates declined exponentially with increasing distance from floral patches, reaching zero beyond 14 m. Increased potential fecundity reduces the chances of parasitoids becoming egg-limited, whereas increased longevity reduces the chances of parasitoids becoming time-limited during host oviposition. Although the plasticity of egg load and longevity observed under varying conditions of resource availability is probably more relevant to parasitoid evolution, the individual fitness benefits from ephemeral resource patches are certainly important in the ecological enhancement of biological control agents.

Key words: aphid; Aphidiidae; Aphidius rhopalosiphi; *egg limitation; egg load; fecundity; fitness; flower-feeding; lifetime reproductive success; parasitoid; resource subsidies; time limitation.*

INTRODUCTION

Parasitoid fitness is affected by a wide range of environmental variables, including abiotic factors such as temperature (Singh et al. 2000*a*), photoperiod (Sagarra et al. 2000), and season (Ellers et al. 2001), as well as biotic factors including feeding (Singh et al. 2000*b*, Wäckers 2001) and mating (Starý 1970). Several of these factors can be manipulated to enhance parasitoid fitness by the addition of resource subsidies (e.g., Pickett and Bugg 1998, Landis et al. 2000).

There are two mechanisms by which resource subsidies (sensu Gurr et al. *in press*) can enhance top-down control by parasitoids. First, elements of the resource may enhance one or more measures of parasitoid fitness, such as longevity or fecundity (e.g., Andow and Risch 1985, Jervis et al. 1993, Landis et al. 2000). In this case, per capita attack rates increase (indirectly increasing reproductive output), but parasitoid density is not affected directly. Second, parasitoids may be attracted to, and aggregate around, resource patches

(e.g., Liang and Huang 1994), resulting in increased effectiveness by virtue of their greater density, rather than increased per capita efficacy.

The effects of resource subsidies on longevity and egg production can be crucial to parasitoid ecology, as these life-history parameters greatly limit lifetime reproductive success (Rosenheim 1996, 1999, Heimpel et al. 1998, Sevenster et al. 1998, Rosenheim et al. 2000). Theoretical models have attempted to predict whether lifetime reproductive success is dependent on available time for host searching and oviposition, or available physiological resources for egg maturation (Heimpel et al. 1996, 1998, Rosenheim 1996, 1999, Sevenster et al. 1998, Rosenheim et al. 2000). Furthermore, every oviposition event carries a certain opportunity cost, such that time or eggs used on a given host become unavailable to search for, or oviposit on, a potentially ''higher quality'' host (Rosenheim 1996), if host quality rather than number of progeny is being maximized. Early models (e.g., Rosenheim 1996) focused on pro-ovigenic species, in which the total resources available for egg production are fixed at eclosion. Assuming an optimal egg size, Rosenheim (1996) predicted that the proportion of parasitoids becoming egg-limited will be the proportion that live to reach age R/sk days, where R is the amount of resources available for reproduction, s is egg size (so that total

PLATE. 1. (Left) *Aphidius uzbekistanicus* attacking *Sitobian avenae*. (Center) *Aphidius ervi* attacking *Aulacorthum solani*. (Right) *Aphidius* attacking *Aphis gossypii*. Photographs by U. Wyss, Institute of Phytopathology, Kiel University, Germany.

potential fecundity is R/s), and k is the host encounter rate per day. However, in synovigenic species, R can be adjusted according to the physiological state of the female. Resources can be mobilized from other functions to mature eggs (Rivero and Casas 1999a), or conversely, mature eggs can be resorbed (Rosenheim et al. 2000) as required. A recent model of egg limitation in synovigenic species shows that the most important constraint on fitness is the *rate* of egg maturation (Rosenheim et al. 2000).

Several authors have examined the effects of floral resources on local parasitoid densities in agricultural systems (e.g., Root 1973, Hooks et al. 1998). Floral resources may directly increase natural enemy densities by reducing emigration, whereas colors and scents of flowers may attract other predators and parasitoids from areas lacking these resources (Haslett 1989). Increased reproduction (due to increased longevity or egg load) or immigration, combined with reduced emigration, may therefore lead to increased local abundance of parasitoids in areas containing floral resource subsidies (but see Root 1973, Hooks et al. 1998). However, the extent to which parasitoid fitness is enhanced by floral resources and the spatial scale over which effects on immigration and emigration operate, remain to be determined (Landis et al. 2000). In natural environments, other factors such as numerical responses to patches of high host density (e.g., Jarosik and Lapchin 2001), crop edge effects (Dyer and Landis 1997), or windbreak effects (Corbett and Rosenheim 1996) may overwhelm the effects of floral resources on parasitoid aggregation. Additionally, nonfloral resource subsidies such as aphid honeydew may also be important for parasitoid fitness (e.g., Singh et al. 2000b), particularly in agricultural systems where high aphid densities occur.

The present study examines the extent to which floral resources enhance the longevity and fecundity of two species of aphid parasitoid in the laboratory. (Plate 1 shows typical parasitoid attacks on aphids.) The degree to which these changes in fitness parameters translate into higher realized rates of aphid parasitism are examined in laboratory microcosms and a field experiment. Microcosm and field experiments are conducted

with constant aphid densities, so that effects of host density and honeydew do not mask the effects of floral resource subsidies.

METHODS

The aphid parasitoid system

Experiments were conducted on *Aphidius rhopalosiphi* De Stefani-Perez and *Diaeretiella rapae* McIntosh (Hymenoptera: Aphidiidae) to determine the effects of floral resource subsidies on longevity and egg load. In laboratory trials, experimental treatments were established in a 15°C ± 2°C controlled temperature room, with a reversed 12-hr day/night cycle, at the University of Canterbury, Christchurch, New Zealand. In all experiments, mummified (parasitised) aphids were placed individually in 75-mL plastic Labserv containers with a damp piece of tissue paper. Each container had a circular hole (6 mm diameter) in the lid with a 500-μm mesh covering. Individual parasitoids were randomly allocated to one of several treatments including pollen and nectar. A gel mixture containing 0.25 g agar, 5 g honey, 5 g sucrose, and 25 mL of distilled water was used as a substitute for nectar so that parasitoids would not become trapped and drown. Pollen was cut from the stamens of one buckwheat *Fagopyrum esculentum* Moench (Polygonaceae) c.v. Kitawase plant. Each parasitoid in the pollen treatment received a quantity of pollen equivalent to that provided by five buckwheat flowers.

Statistical analyses for laboratory and field experiments were conducted using MINITAB version 13.1 (Ryan and Joiner 1994) and Statistica versions 5.5 and 6.0 (StatSoft 2003).

Longevity

Parasitoid emergence and death were recorded at 12-hour intervals to assess the effects of resource subsidies on longevity.

Aphidius rhopalosiphi.—Experiments on *A. rhopalosiphi* were carried out from 29 November 2001 to 10 January 2002. Mummies used in this experiment were collected from the Biological Husbandry Unit (BHU), an experimental organic farm at Lincoln University,

Canterbury, New Zealand, and were randomly assigned to different treatments. Initially, the species of parasitoids within the mummies were unknown. Of the parasitoids that emerged from 100 mummies that were collected, only 45 female *A. rhopalosiphi* were used in the analyses. This was necessary because the absence of a published key for male Aphidiidae made reliable identification impossible. Parasitoid and hyperparasitoid species other than *A. rhopalosiphi* were too rare to allow statistical analysis, so data for these species were discarded. Fifteen individual *A. rhopalosiphi* females were provided with sugar gel, 15 were provided with buckwheat pollen, and 15 individuals in the control treatment were given no resource provisioning (only damp tissue paper, as in all other treatments).

Diaeretiella rapae.—Mummified aphids containing *D. rapae* were obtained from Bioforce Ltd. (Auckland, New Zealand). Because individuals of this species were obtained from a culture (and sample sizes were limited), males and females were assumed to be of the same species, so no distinction was made between sexes for the purposes of analysis. This experiment was conducted from 16 April to 5 May 2001.

Twenty parasitoids were individually exposed to sugar gel and 20 were provided with only damp tissue paper (controls). No pollen treatment was used in this experiment.

Egg load

We conducted a series of laboratory experiments to determine the effects of resource subsidies on parasitoid egg load. Female *A. rhopalosiphi* used in these experiments were collected from the BHU and maintained in culture at Lincoln University. The experiments were carried out between 6 February and 25 March 2002. Female *D. rapae* were obtained from Bioforce Ltd. and experiments on this species were conducted between 8 July and 23 August 2001. Twenty-five newly emerged female parasitoids were individually assigned to each of three treatments to examine the effects of floral resources on egg load. The treatments comprised sugar gel, buckwheat pollen, and a control (damp tissue paper). Five randomly selected females from each treatment were euthanized and dissected at each of five time intervals (6, 12, 24, 48, and 72 hours post-emergence) to assess egg load. Ovaries were removed by grasping the ovipositor with fine forceps and gently pulling until the ovipositor and ovaries became detached from the abdomen. Ovaries were placed on a microscope slide and stained with a 0.01% solution of methylene blue. Pressing gently on the cover slip caused the ovaries to burst, releasing the eggs, which could then be counted under a dissecting microscope. Only fully matured eggs were recorded, because the degree of egg maturation may vary with resource availability, whereas the number of oogonia (immature eggs) is fixed at eclosion.

Microcosm experiments

Laboratory experiments were conducted to determine whether changes in life-history parameters resulting from resource subsidies translated into an increase in rates of parasitism. Aphids (*Metopolophium dirhodum* Walker, Hemiptera: Aphididae) used in these experiments were obtained from Crop and Food Research, Lincoln, New Zealand, and female *A. rhopalosiphi* were reared from parasitised aphids collected from the BHU. Both species were subsequently maintained in culture at Lincoln University.

Experiments were carried out in four Perspex chambers within one 15°C (±1°C), 16/8 h day/night cycle controlled environment room at Lincoln University, 24 February–14 April 2002. Four treatments were conducted simultaneously in different chambers and were repeated eight times. Each experimental chamber contained one female *A. rhopalosiphi*, water, and a pot (20 cm in height, 15 cm in diameter) of wheat *Triticum aestivum* (L.) (Gramineae) (c.v. Wasp) seedlings that contained ~300 aphids (*M. dirhodum*). This provided a surfeit of potential hosts, so that maximum levels of parasitism could be recorded. The first experimental treatment was a control, with no additional resources provided. Sugar gel was provided to females in the second treatment, and the third comprised buckwheat plants (c.v. Kitawase) with all flowers removed. The final treatment included an entire buckwheat plant to test whether the resources of this species can be utilized by *A. rhopalosiphi*, and whether the combination of several plant attributes produces different effects from each of the resources (pollen, nectar, and plant architecture) in isolation.

Each experimental replicate ended with the death of the female parasitoid. In approximately one-third of the replicates, particularly buckwheat treatments that contained more foliage, parasitoids could not always be located. When a dead parasitoid could not be found, an individual was assumed to be dead if it had not been observed for three days. The difficulty in locating many individuals made it impossible to measure longevity effectively; therefore, it is not certain whether increased lifetime fecundity was the result of increased longevity, egg load, or both. If mummified aphids appeared on the wheat seedlings prior to parasitoid death, the pot was replaced with another, containing ~300 aphids. This was necessary to prevent new parasitoids emerging during the experiment.

After a period of seven days following removal of a pot or termination of an experiment, aphids were examined for signs of mummification, and the number of aphids parasitized per treatment was recorded.

Field experiment

Study site.—Field experiments were conducted at the organic Biological Husbandry Unit (BHU) at Lincoln University. Field 1 measured ~32 × 150 m and field
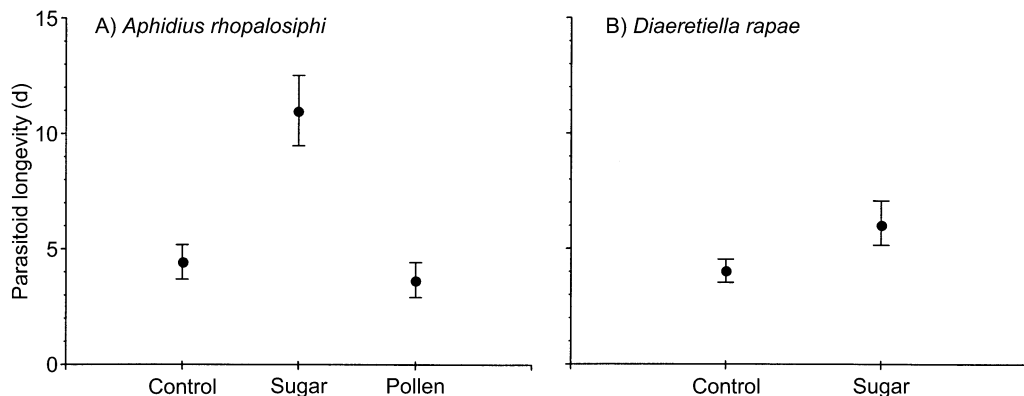
FIG. 1. Mean ($\pm$ 95% CL) longevity of (A) *Aphidius rhopalosiphi* and (B) *Diaeretiella rapae* in control (damp tissue only), sugar gel, and pollen (*A. rhopalosiphi* only) treatments. Mean and confidence limits for *D. rapae* are back-transformed from $\log_{10}$-transformed variates.

2 was $\sim$57 $\times$ 130 m. Both fields were drilled with wheat *T. aestivum* (c.v. Otane) on 1 October 2001. Two 5 $\times$ 5-m patches of buckwheat *F. esculentum* (c.v. Kitawase) were hand sown within each field, with patches located 20 m from either end of each field. The four buckwheat patches were partially sown ($\sim$50% cover) on 4–5 October 2001, and the remaining 50% of each patch was sown on 26–30 November 2001. This produced two cohorts of buckwheat plants, approximately one month apart, so that the second cohort was still flowering after the first had ceased. A 1 m $\times$ 1 m patch of wheat was left in the center of each buckwheat patch to allow measurement of parasitism rates within the patch.

Four transects radiating from each side of each buckwheat patch were measured and marked with bamboo stakes at 2-m intervals, such that one transect ran between the two floral patches in each field and a further three transects ran from each patch to the edges of the field. Field experiments were conducted along these transects.

When distances from buckwheat patches were measured, a 1-m² patch of wheat within the buckwheat was considered to be the 0-m point, and the edge of the buckwheat patch was recorded as 2 m from the zero point.

Field experiment.—We conducted a manipulative field experiment to determine the effects of floral resource subsidies on rates of parasitism at a fixed aphid density. Experiments began after natural aphid populations had declined to <0.5 aphids/100 plants. Two trials were conducted in field 1 (beginning on 4 and 9 January 2002, respectively) and one was conducted in field 2 (beginning on 7 January 2002).

Experimental aphids were placed in the field using small cages that were clipped onto a leaf, providing shelter and excluding natural enemies while aphids adjusted to the new environment. Clip cages were constructed from 14 mm diameter plastic tubing (see Noble 1958).

Five fourth-instar apteriform aphids (*M. dirhodum*) were clip-caged onto the abaxial surface of the highest (flag) leaf of wheat plants located at 4-m intervals along each transect within the wheat fields. Leaves with clip cages were marked with a 4 $\times$ 20-mm section of white parcel tape folded around the leaf. Two days after the aphids were positioned, the clip cages were removed to expose aphids to parasitism. Any first-instar aphids produced during this two-day period were removed so that five aphids were exposed to parasitism in each replicate. After two days of exposure, any aphids that were still present were removed and reared at 15°C for 8 days and the proportion of aphids mummified was recorded.

The proportions of experimental aphid colonies parasitized were analyzed with respect to distance from the nearest field margin (edge effects), distance from the leeward end of the field (wind drift effects), and distance from the buckwheat patch (floral resource effects) using logistic regression. Distance categories were established in field experiments as fixed, 4-m intervals from floral patches, but each position was also measured with respect to distance from the nearest field margin and distance from the leeward end of the field.

RESULTS

Longevity

Aphidius rhopalosiphi.—Survival times of *A. rhopalosiphi* females ranged from 1.5–7.0 days in the control to 2.0–6.5 days in the pollen treatment, and to 6.0–15.5 days in the sugar treatment. Data for the three treatments were all normally distributed (Ryan-Joiner test, $r > 0.97$, $P > 0.1$ in all cases). Longevity differed significantly between treatments (one-way ANOVA, $F_{2,42} = 54.23$, $P < 0.001$), as parasitoids exposed to the sugar treatment survived between three and four times longer than those in the control or pollen treatments (Fig. 1A). However, longevity of females in the pollen treatment did not differ significantly from that
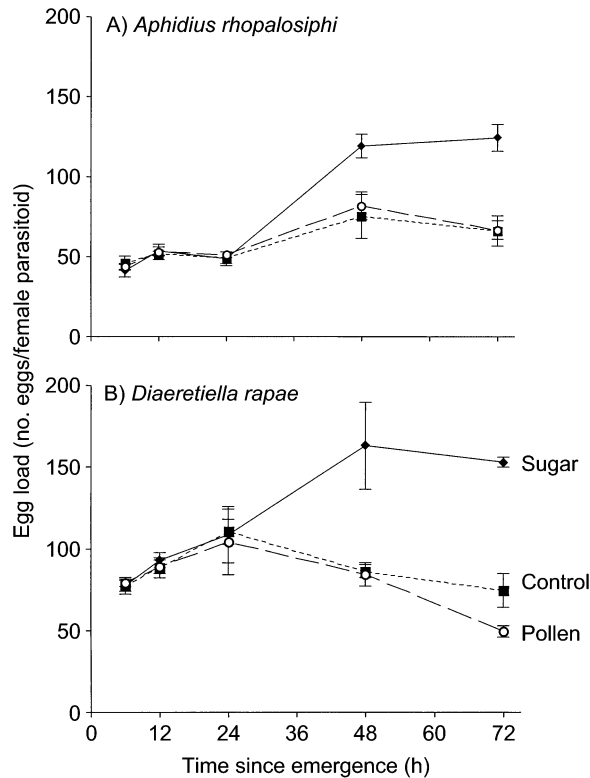
FIG. 2. Egg load (no. eggs/female parasitoid, mean ±1 SE) of (A) *Aphidius rhopalosiphi* and (B) *Diaeretiella rapae* at 6, 12, 24, 48, and 72 hours post-emergence, in control (damp tissue only), sugar gel, and pollen treatments.

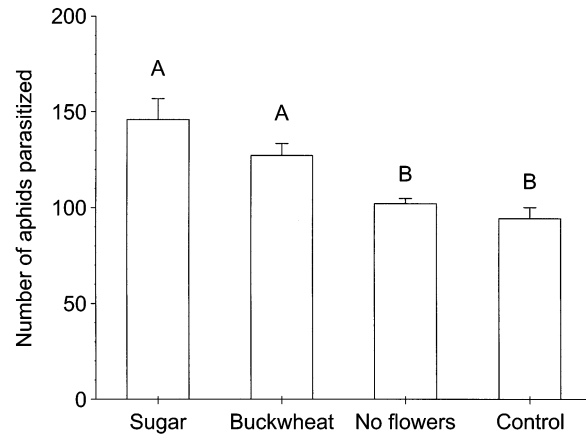

FIG. 3. Mean (+1 SE) number of *Metopolophium dirhodum* aphids parasitized by *Aphidius rhopalosiphi* in treatments comprising a control (water only), sugar gel, buckwheat plant with flowers removed (no flowers), or whole buckwheat plant (buckwheat). Columns sharing the same letter (A or B) do not differ at $P = 0.05$ (Tukey's pairwise comparisons).

of females in control treatments (Tukey's pairwise comparisons, Fig. 1A).

Diaeretiella rapae.—Longevity of *D. rapae* ranged from 2.0 to 6.5 days in control individuals and from 2.5 to 14.0 days in those provided with sugar. The data were log_{10}-transformed to achieve normality (Ryan-Joiner test on log_{10}-transformed variates, $r > 0.97$, $P > 0.1$ in both cases). Longevity was significantly greater in individuals provided with sugar than in control individuals (t test, $t = -4.0$, $P < 0.001$, df = 38; Fig. 1B).

Egg load

Aphidius rhopalosiphi.—Egg load ranged from 23 to 145 eggs/female parasitoid across all treatments and time intervals. A two-way ANOVA revealed that mean egg load varied significantly with treatment ($F_{2,60} = 14.3$, $P < 0.001$) and time ($F_{4,60} = 36.49$, $P < 0.001$), but not all treatments had the same effect on egg load through time (treatment × time interaction effect, $F_{8,60} = 6.59$, $P < 0.001$) (Fig. 2A). Provision of sugar significantly increased egg load over control and pollen treatments after 48 h (one-way ANOVA, $F_{2,12} = 5.25$, $P = 0.023$) and after 72 h ($F_{2,12} = 17.24$, $P < 0.001$), but not at earlier time intervals (6, 12, and 24 h, all $P > 0.05$) (Fig. 2A).

Diaeretiella rapae.—Egg load ranged from 38 to 207 eggs/female across all treatments and time intervals. As with *A. rhopalosiphi*, the mean egg load of *D. rapae* was significantly affected by treatment ($F_{2,60} = 15.86$, $P < 0.001$) and time ($F_{4,60} = 4.52$, $P = 0.003$), and the variation in egg load with time was not the same for every treatment (treatment × time interaction effect, $F_{8,60} = 5.48$, $P < 0.001$) (Fig. 2B). Sugar significantly increased egg load over control and pollen treatments after 48 h (one-way ANOVA, $F_{2,12} = 7.71$, $P = 0.007$) and after 72 h ($F_{2,12} = 58.46$, $P < 0.001$). As with *A. rhopalosiphi*, there was no significant effect of treatment on egg load at the earlier time intervals (6, 12, and 24 h, all $P > 0.05$) (Fig. 2B).

Microcosm experiments

The number of aphids parasitized by *A. rhopalosiphi* (of ~300 provided) ranged from 72 in the control treatment to 192 aphids in the sugar treatment. There was significant variation in the number of hosts parasitized among treatments (one-way ANOVA, $F_{3,28} = 15.64$, $P < 0.001$); aphids in the sugar and whole buckwheat treatments experienced significantly greater rates of parasitism than did those in the control and no-flower buckwheat treatments (Fig. 3).

Field experiment

The proportion of aphids parasitized was not significantly affected by distance to the nearest field margin or distance to the leeward end of the field (logistic regression, $P > 0.05$ in all three trials), but distance from the floral patch significantly affected rates of parasitism in all three field trials (logistic regression, $P < 0.05$ in all three trials). When data from the three trials were combined, the effect of proximity to floral resources was highly significant (logistic regression, Z
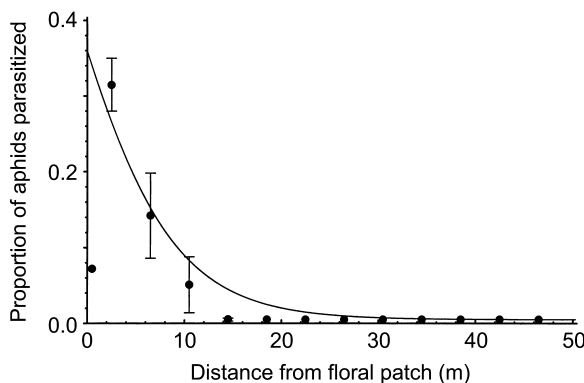
Fig. 4. Mean (±95% CL) proportion of experimentally placed *Metopolophium dirhodum* aphids parasitized by *Aphidius rhopalosiphi* at increasing distances from the nearest floral resource patch. The equation of the logistic regression on binomial proportions is: $y = \exp(-0.688 - 0.178x)/(1 + \exp(-0.688 - 0.178x))$. For the purposes of graphical presentation only, mean (±95% CL) proportions were calculated from arcsine square-root transformed variates and then back-transformed for display. The logistic regression function is not a fitted line through the back-transformed means.

$= 5.56$, $P < 0.001$) (Fig. 4). Rates of parasitism showed a negative exponential decline with increasing distance from the floral resource patches, such that the proportion of aphids parasitized would be predicted to reach less than 0.01 by 22 m, and by 40 m from the floral patch, mean rates of parasitism would be predicted to be one-thousandth of those recorded at 2 m. In this experiment, no parasitism was recorded beyond 14 m from the floral patches. Surprisingly, rates of parasitism were considerably lower within the buckwheat patch itself (i.e., at 0 m) than within the wheat field immediately adjacent to the floral patch, where they were at their highest (Fig. 4).

DISCUSSION

Carbohydrate-rich resource subsidies enhance rates of aphid parasitism by *Aphidius rhopalosiphi*, and the mechanisms resulting in improved fitness also operate in another genus within the Aphidiidae. Longevity and potential fecundity of *A. rhopalosiphi* and *Diaeretiella rapae* were significantly enhanced by sugar-based resource subsidies under experimental conditions. Moreover, realized fecundity of *A. rhopalosiphi* (measured by rates of parasitism in the laboratory) increased significantly when sugar was provided. Flowering buckwheat also caused an increase in rates of parasitism, indicating that the floral nectar of this species is accessible to *A. rhopalosiphi*. Importantly, rates of parasitism in microcosm experiments were in accordance with those expected from longevity and egg load experiments, and both were congruent with experiments that tested the impact of buckwheat plants on *A. rhopalosiphi* parasitism under field conditions.

Elevated female longevity and elevated egg load following the provision of resource subsidies support the-

oretical arguments for the importance of omnivory in promoting top-down community regulation by parasitoids (e.g., Polis and Strong 1996). Resource subsidies increase the resource capital that a parasitoid has available for allocation to one or more life-history parameters (Rivero and Casas 1999*a*). Both *A. rhopalosiphi* and *D. rapae* were able to use these resources to both mature eggs and increase their longevity, thus increasing their potential lifetime fecundity. A similar effect of honeydew on egg load was observed in the aphidiid *Lipolexis scutellaris* Mackauer (Singh et al. 2000*b*). This contrasts with the suggestion that adult food is unimportant for egg maturation in aphidiids (Starý 1970), and confirms the synovigenic status of the Aphidiidae. Furthermore, the increase in egg load exhibited by females in the sugar treatments may be conservative if the maximum egg load recorded (145 eggs in *A. rhopalosiphi* and 207 eggs in *D. rapae*) represents a limit on the capacity for egg storage in these species. If oviposition were occurring, more eggs might be matured, increasing maximum fecundity. This scenario becomes more plausible if nutritional resources can be used for egg maturation over a long period, as demonstrated by Rivero and Casas (1999*b*), with a concomitant increase in longevity.

If resource subsidies result in increased egg load, time is likely to become a limiting factor in the maximum number of progeny produced. Time is considered to be limiting if a parasitoid dies without exhausting its supply of mature eggs (Heimpel et al. 1998, Sevenster et al. 1998, Rosenheim 1999), i.e., before age *R/sk*. The proportion of parasitoids becoming time-limited can be approximated to $1 - \exp(-\mu R/sk)$ (adapted from Rosenheim 1996), where μ is the constant daily mortality rate. Both *A. rhopalosiphi* and *D. rapae* showed significant increases in longevity when provided with sugar gel. However, this increase in longevity will only marginally reduce the likelihood of time limitation if the mortality rate, μ, is determined by, for example, high predation pressure rather than physiological factors.

At spatial and temporal scales relevant to ecological interactions, individual parasitoids will probably fall somewhere along a continuum between extremes of egg and time limitation (Rosenheim 1999). The interplay of multiple selective forces in the environment (e.g., predation risk or environmental adversity) may force individuals to incur opportunity costs from suboptimal search or oviposition decisions without actually becoming egg- or time-limited (Rosenheim 1999). As a result, the importance of egg vs. time limitation is probably greater in an evolutionary context than in an ecological one. In this sense it is the plasticity of longevity and egg load exhibited by *A. rhopalosiphi* and *D. rapae* that bears evolutionary significance, whereas the fitness benefit of an individual parasitoid receiving resource subsidies is probably not evolutionarily relevant. Having said this, it is short-term individual- and popula-

tion-level responses that are of primary importance in an applied, ecological context, such as the use of parasitoids in biological control.

When aphid density was experimentally controlled in a field environment, the proximity to floral resources significantly affected rates of aphid parasitism. Incongruously, however, rates of aphid parasitism were markedly lower within the buckwheat patches themselves than within the wheat field surrounding the floral patches (Fig. 4). At face value, this seems somewhat counterintuitive, as parasitoids within the floral patches should have the greatest access to resource subsidies, and should therefore be capable of exerting very high levels of parasitism on aphids within the patch. However, this was clearly not the case for these data. Instead, host-plant quality within the floral patch may be different from that in the remainder of the field, thereby affecting parasitism levels, Alternatively, the results are compatible with the concept of spatiotemporal partitioning between feeding and host-searching behaviors; female parasitoids may respond to different visual or chemical cues at different times depending on their physiological state. For example, female parasitoids (Hymenoptera: Braconidae and Ichneumonidae) prefer food odors to host plant odors when starved of sugar supplements (Wäckers 1994, Jacob and Evans 2001). If the same holds true for female *A. rhopalosiphi* within buckwheat patches, then the data indicate that they may have been feeding rather than searching for hosts. By chance alone, females are more likely to find proximally located host patches after feeding, because as search radius increases, the number of experimentally placed host patches per unit area decreases exponentially.

The benefits of floral feeding for the parasitoid will depend on the amount of time spent feeding. If subsidies are obtained from hosts, for example, by host feeding or from aphid honeydew resources, food and host searching may take place at the same time, governed by the same chemical cues (Shaltiel and Ayal 1998). However, if food patches are spatially or temporally separated from host patches, different factors may determine the trade-off in time spent feeding vs. searching for a host. Costs associated with increased mortality risk or time-limited suboptimal exploitation of host patches may limit the amount of time spent foraging for food (Sirot and Bernstein 1996). In order to maximize reproductive success, these costs must be outweighed by the fitness advantages of feeding on floral resources.

Costs associated with floral feeding

There are direct and indirect costs associated with floral feeding for parasitoids. Direct predation or hyperparasitism may be higher at close proximity to floral patches and may lead to higher mortality of parasitoid adults (reviewed in Rosenheim 1998) and larvae (Ferguson and Stiling 1996). Alternatively, the presence of predators or hyperparasitoids may modify primary parasitoid behavior such that individuals more readily leave patches containing higher order predators (Höller et al. 1993; but see Völkl et al. 1995). Predator-mediated departure from host patches may reduce the efficacy of aphid natural enemies (Höller et al. 1993, Rosenheim 1998), and a high risk of adult mortality (for any reason, including predation) may cause individuals to leave floral patches after intermediate levels of feeding rather than achieve complete satiation (Sirot and Bernstein 1996).

There are indirect costs associated with floral feeding when individuals choose to feed temporarily on flowers and forego the opportunity to search for hosts or mates (Sirot and Bernstein 1996, Jacob and Evans 2001). This may be of particular importance in situations where competition for hosts is great, or floral resources are widely separated from host patches, incurring greater costs in terms of traveling time and energy expenditure. A number of studies of host-feeding parasitoids have examined the opportunity costs associated with feeding rather than ovipositing on hosts (e.g., Heimpel and Rosenheim 1995, Rivero and Casas 1999*b*). It was found that high host availability, long life expectancy, and high egg loads favored investment in future reproduction (i.e., host feeding) over current reproduction (i.e., oviposition) (Heimpel and Rosenheim 1995). Although *Aphidius* does not host feed, the time costs associated with floral feeding still require a decision whether to maximize current reproduction (via host-searching and oviposition) over future reproductive potential (via floral feeding).

When will resource subsidies be useful?

It is not imperative that the fitness benefits of increased longevity and fecundity occur simultaneously. Rather, they may manifest themselves to varying degrees at different times, perhaps as a strategy of ecological or evolutionary bet-hedging. For example, increases in longevity will be most beneficial for time-limited populations of natural enemies that occur where host densities are low (Rosenheim 1996). Increased longevity provides parasitoids with more time for host-searching, allowing an increase in the total number of hosts located and, consequently, increased lifetime reproductive success. Additionally, if a parasitoid species has evolved a strategy of producing numerous small eggs, at little cost per egg, the probability of becoming time-limited increases, as more hosts are required for the additional eggs. According to Rosenheim's (1996) model, the death of a parasitoid before its egg supply is completely exhausted constitutes time limitation. A decrease in egg size (s) extends this time (R/sk days), which can be further increased if resource subsidies allow an increase in the physiological resources allocated to reproduction (R), as the present study demonstrates.

If longevity were generally determined by extrinsic factors such as predation, rather than intrinsic physiological constraints, then resource subsidies would have little impact on lifetime reproductive success. Additionally, if a population were predominantly egg-limited, individuals would, by definition, exhaust their maximum egg supply before death, so that extending this post-exhaustion period would provide no additional fitness benefits.

Situations in which parasitoids are predicted to gain maximum advantages from increased longevity (e.g., where predation rates are low, mate encounter rates are low, or hosts are rare) tend to occur at the beginning and end of the crop season. If population densities of *A. rhopalosiphi* and *M. dirhodum* are at their lowest at the beginning and end of the summer (J. Tylianakis, *unpublished data*), they presumably could not sustain high densities of fourth-trophic-level predators. These conditions would lead to time limitation of the *A. rhopalosiphi* population. Conversely, in midsummer, aphid population densities are often at their highest (Wratten and Powell 1990) and parasitoids are more likely to be egg-limited. Parasitoid densities are also high at this time, and could potentially sustain high population densities of predators and hyperparasitoids (leading to high mortality rates), so fitness benefits from enhanced longevity would be minimal. Conversely, if hosts are abundant, as they are in midseason, egg limitation is more likely to occur and resource-subsidy-based enhancement of fecundity is of paramount importance. However, leaving the host patch to acquire resources at this time may be unnecessary, because high aphid densities would produce large quantities of honeydew that can effect a similar fecundity enhancement to floral nectar (Singh et al. 2000b). Floral resources may therefore be most important at times when aphid densities are low and other nonfloral resources (e.g., aphid honeydew) are unavailable.

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