



Patch and prey utilization behaviors by *Aphelinus albipodus* and *Diaeretiella rapae* (Hymenoptera: Aphelinidae and Aphidiidae) on Russian wheat aphid (Homoptera: Aphididae)

Philip J. Lester^{*,1} and Thomas O. Holtzer

Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA

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Abstract

The patch and host utilization behaviors of the parasitoids *Diaeretiella rapae* (Kurdjumov) and *Aphelinus albipodus* (Hayat and Fatima) in relation to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), were examined on wheat plants. Individual female parasitoids were observed for 1 h after arriving on a wheat plant with varying *D. noxia* densities. The total amount of time spent on the leaf and the number of occasions a parasitoid left the leaf were dependent on aphid densities for *D. rapae*. In contrast, *A. albipodus* remained on a plant for almost the entire hour irrespective of aphid densities. After 1 h on the wheat plants, single *D. rapae* females produced up to 31 progeny from 40 aphids, while single *A. albipodus* produced a maximum of six progeny. These results can be explained by the differences between the parasitoids in prey handling times, searching, and host feeding behaviors, and parasitoid physiology. The mean oviposition time for *A. albipodus* was 119 s compared to 1 or 2 s for *D. rapae*. The time between attacks was also much greater for *A. albipodus* at all prey densities, partially a result of this parasitoid feeding on aphids. Our results agree with the observation that *A. albipodus* has many fewer eggs ready for oviposition compared to *D. rapae*. Therefore, it is not surprising that *A. albipodus* remained for extended periods on wheat plants with many aphids, allowing development of additional eggs and parasitization of more aphids. The patch and prey utilization rates by *A. albipodus* seem likely to limit its rate of spatial spread during a growing season relative to *D. rapae*. © 2002 Elsevier Science (USA). All rights reserved.

Keywords: Russian wheat aphid; Aphid parasitoid; Patch utilization; Movement; Abundance; Wheat

1. Introduction

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko), is a pest of small-grain crops in North America. Two parasitoids that have been introduced for the control of this aphid are *Aphelinus albipodus* (Hayat and Fatima) (Hymenoptera: Aphelinidae) and *Diaeretiella rapae* (Kurdjumov) (Hymenoptera: Aphidiidae) (Elliott et al., 1995; Mohamed et al., 2000). The abundance of these two parasitoids differs seasonally in the Rocky Mountain region. *D. rapae* populations can be observed throughout a growing season, while *A. albipodus* is

typically observed from July until October (Lester and Holtzer, unpublished data; Pike et al., 1997).

Hassell and Southwood (1978) describe three hierarchical levels for a forager: the habitat, patch, and host. For parasitoids of cereal aphids, the habitat can be defined as a wheat field and the host as an aphid. The intermediate level between the field and aphid is a wheat plant. An individual plant has been defined for aphid parasitoids as the patch or the elementary unit of foraging (Ayal, 1987). The foraging behavior of a parasitoid at the patch and host levels may impact the distribution and abundance of the parasitoid at the habitat level.

The relative abundances of *A. albipodus* and *D. rapae* may be related to behavioral and/or physiological aspects of their biology. Behavioral factors may include the ability of the parasitoids to find and attack prey or the length of time they remain on a patch. Physiological

* Corresponding author. Fax: +64-4-463-5331.

E-mail address: phil.lester@vuw.ac.nz (P.J. Lester).

¹ Present address: School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand.

factors that may limit the relative abundance of *A. albipodus* may include the ovipositional success rate per aphid sting or the time period necessary for egg maturation and oviposition. In this study, we examined the foraging behavior of both *A. albipodus* and *D. rapae*. The objective was to compare the foraging behaviors of both parasitoid species at the host and patch levels, in the laboratory. Because foraging behavior is likely to be dependent on aphid densities, parasitoids were examined over a range of aphid densities.

2. Materials and methods

Diuraphis noxia were reared on wheat plants, *Triticum aestivum* L. cv. 'TAM 107,' at 25 °C, 30–40% RH, and a photoperiod of 16:8 (L:D) h. The parasitoids were obtained from a colony reared by the Colorado Department of Agriculture, Palisade, CO. They were reared on *D. noxia* infested *T. aestivum* at 20 °C, 30–40% RH and a 16:8 (L:D) h photoperiod. Both species had been maintained in this colony since 1995. The *D. rapae* colony was initiated from a collection in China by USDA-APHIS personnel in 1994. The *A. albipodus* colony was collected from wheat fields in Western Colorado in 1996. Parasitoid mummies were placed in size "00" gelatin capsules using a fine paintbrush. Individual male and female pairs of newly emerged (<24 h) parasitoids were mated and given a drop of honey-water for food. The parasitoids were used in the experiments 1–4 h after mating and feeding.

Individual wheat plants were grown in 27 × 95 mm glass vials (VWRbrand TraceClean, Aurora, CO). When wheat plants were ≈70 mm high, 1, 5, 10, 15, 20, 30, or 40 late instar aphids were placed on a plant. The aphids were left for 24 h for feeding and release of chemical cues, which parasitoids may use for foraging. A single mated pair of parasitoids was then carefully placed in another glass vial, which was attached to the vial with the aphid-infested wheat plant. The time from introduction into the tube until the parasitoid found the leaf was recorded. The frequency, time, and timing of a number of parameters related to the patch and host were recorded during 1 h.

The parameters related to the patch were:

1. the time until the parasitoid walked or flew onto the aphid infested plant;
2. the total time the parasitoid remained on the plant;
3. the time until the first occasion the parasitoid left the leaf; and
4. the total number of occasions the parasitoid left the leaf during the 1-h period.

The total number of occasions the parasitoid left the plant was relevant because in some cases the parasitoids would leave and return to the plant on multiple occasions during the 1-h observation period.

The parameters related to the host were:

1. the number of attacks per aphid;
2. the number of stings per aphid;
3. the number of stings per parasitoid attack;
4. the time between aphid attacks;
5. the number of aphids attacked; and
6. the total number of emerged parasitoids four weeks after the experiment.

An "attack" was defined as a wasp approaching and stinging an aphid (perhaps multiple times) before moving away from the aphid by at least 1 cm. All attacks included at least one sting. A "sting" was defined as the parasitoid's ovipositor touching and entering the aphid. Such stings may be a result of the parasitoid assessing the aphid host, and an egg may not be oviposited with each sting. However, without dissection of the aphid or manipulation of the parasitoid immediately after each sting, it was not possible to determine whether or not an egg had been oviposited during each sting. Consequently, the aforementioned criteria were used for a "sting." After the 1-h observation, the parasitoids were removed and a small cage was placed over the wheat plant. The aphids and the wheat plants were returned to the rearing conditions. Any parasitoid mummies observed during the following weeks were transferred into size "00" gelatin capsules using a fine paintbrush. The total number of emerged wasps was assessed four weeks later. Mummies from which a parasitoid had not emerged were kept for another two weeks to determine if parasitoids would eventually emerge. Five replicates were used for each aphid density and parasitoid species treatment.

The response of the parasitoid to different prey densities was modelled with either a linear regression equation, or the first order exponential decay equation:

$$y = y_0 + A_1 e^{-(x-x_0)/t_1}, \quad (1)$$

where y is the response being modelled, y_0 is the y -axis offset, A_1 is the amplitude, and t_1 is the decay constant. The functional response of the parasitoids was defined as the number of attacks on the aphid population per hour. Type II functional responses were modelled using the equation of Royama (1971) and Rogers (1972):

$$N_a = N\{1 - \exp[-aT/(1 + aT_hN)]\}, \quad (2)$$

where N is the number of prey available, N_a is the number attacked and T is the experimental time. The parameters a (the rate of successful attack) and T_h (the time required to handle a prey item) were calculated by least-squares non-linear regression, using the quasi-Newton estimate method. The numerical response was modelled using the equations of Nwile and Nachman (1997), who used the model of Beddington et al. (1976), but included the constant b . When $b = 1$, proportionality between predation and oviposition is implied, $b > 1$ implies increasing conversion efficiency and $b < 1$

implies decreasing efficiency. Oviposition rate (E) was thus modelled as

$$E = e_1 N_a^b - e_0 \quad (E \geq 0), \quad (3)$$

where e_1 is a constant expressing the predator's efficiency in converting prey into predator eggs (per day), N_a is the number of prey attacked per predator per day, and e_0 is the metabolic cost per time unit measured in terms of reduced fecundity (predator eggs per day). The parameters e_1 , b , and e_0 were estimated using least-squares non-linear estimation, as for the functional response analysis.

Regression analyses used raw data, rather than the average of replicates in each density treatment. t Tests were performed on error estimates obtained from each regression analysis (Zar, 1984). These tests examined the hypothesis that the parameter estimates were not different between parasitoid species, or that the slope or intercept of the regression lines was not significantly different from zero.

3. Results

3.1. Patch related parameters

The two parasitoid species displayed different responses to increasing aphid densities on wheat plants. The relationship between aphid density and patch arrival-time by *A. albipodus* was best fitted by a negative exponential decay function (Fig. 1A). The longest time recorded for a parasitoid to walk or fly onto the leaf was 84.93 min for *A. albipodus* in the single aphid treatment. This result is in contrast to the 40 aphids per plant treatment when *A. albipodus* arrived on the plants within 8 min after being placed with the plant. *D. rapae* did not significantly alter its time to arrive on the leaf with increasing aphid density, and generally arrived on the plant in less than 20 min (Fig. 1A, Table 1).

Once on the plant, *A. albipodus* stayed for a significantly longer period than did *D. rapae* (Fig. 1B). However, neither parasitoid species significantly altered the total time spent on a plant with aphid density. For *D. rapae*, the lack of a significant response to increasing aphid density in the total amount of time spent on a leaf was probably affected by the number of times it left and returned to the plant in each aphid density treatment. The amount of time until the first occasion *D. rapae* left the wheat plant significantly decreased with decreasing aphid densities. At a density of 30 aphids per plant, *D. rapae* would stay on the plant for an average of 26.82 ± 5.82 min (\pm SE) before leaving the plant. At a density of one aphid per plant, *D. rapae* generally left the plant within 5 min after each arrival, but returned to the plant an average of 11.6 times per hour (Figs. 1C and D). *D. rapae*'s rate of leaving and returning signif-

icantly decreased with increasing aphid density (Fig. 1, Table 1). In a natural environment of a field consisting of many wheat plants, once a parasitoid has flown from a plant it may not be able to return to that plant. Consequently, the lack of a significant response in the total time spent on a plant with increasing aphid densities by *D. rapae* may be an experimental artifact.

Aphehlinus albipodus seldom left and returned to the patch during the 1-h period. The leaving and returning responses of *A. albipodus* to increasing aphid densities did not differ from a slope of 0 and was significantly lower than *D. rapae* (Fig. 1C, Table 1). Commonly, on the few occasions when *A. albipodus* left the plant, it left by walking onto the soil from the leaf base. In contrast, *D. rapae* would generally leave the plant by flying. Any *A. albipodus* that had walked from the plant generally turned around and walked back onto the plant. Most *A. albipodus* had to be forcibly removed from the plant at the end of the 1-h observation period, whereas *D. rapae* had frequently left the plant by this time.

3.2. Host factors

Aphehlinus albipodus had fewer attacks on each aphid per hour than did *D. rapae* (Fig 2A, Table 2). Both species of parasitoids attacked aphids more often at the lowest aphid density, but the attack rate per aphid was observed to reach a lower limit at higher aphid densities. At the higher aphid densities, *D. rapae* had an attack rate per aphid \approx 2-fold higher than *A. albipodus* (Fig. 2A). Similarly, both parasitoid species increased their rate of stinging per aphid at the lowest density of one aphid per leaf (Fig. 2B). At all aphid densities, the numbers of stings per aphid by *D. rapae* were significantly higher and approximately twice that of *A. albipodus* (Fig. 2A). The number of stings per parasitoid attack on each aphid was similar between species, and did not change significantly with increasing aphid densities (Fig. 2C, Table 2). Thus, because the numbers of stings per parasitoid attack were similar in both species, the doubling in the total number of stings per aphid was primarily a result of *D. rapae* having a higher number of attacks per aphid than *A. albipodus*.

There were a variety of factors associated with the slower attack rate of *A. albipodus*. The exponential decay function predicted that the mean time between attacks at high aphid densities would be 6 min for *A. albipodus*, which was significantly higher than the mean of 1 min for *D. rapae* (from the 1-h long mean for the total duration of the experiment) (Fig. 2D, Table 2). This result may be related to the longer amount of time *A. albipodus* took for each oviposition sting. The mean oviposition time for *A. albipodus* was 119 ± 13 s (\pm SE) ($n = 28$, range = 13–324 s), versus only 1 or 2 s for *D. rapae*. Despite being fed honey-water prior to each experiment, *A. albipodus* spent time feeding on the aphids

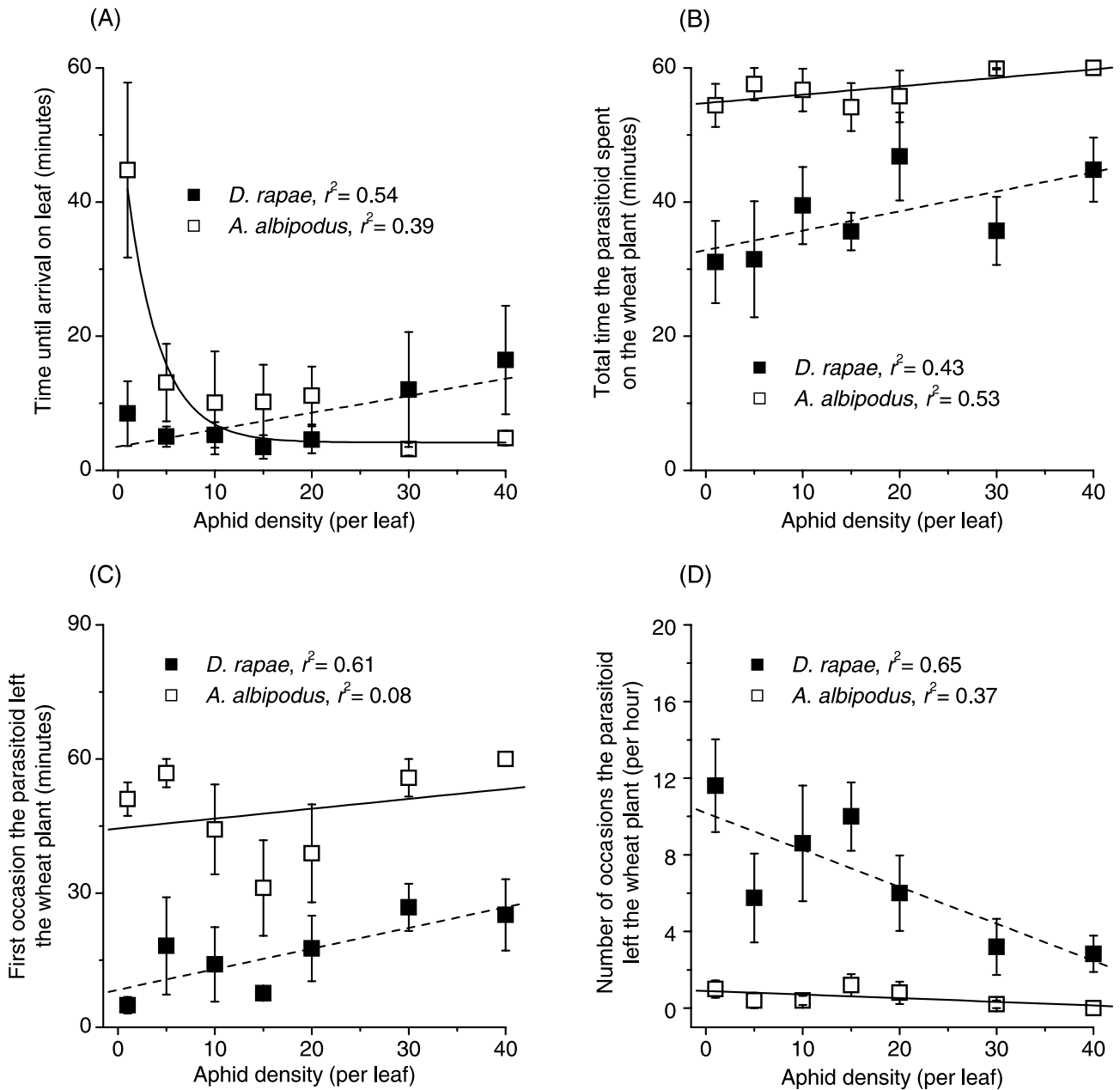


Fig. 1. The change in the parasitoids arriving and leaving the wheat plant in relation to changing densities of *D. noxia* on an individual wheat plant. Data are means \pm SE.

after the first or second initial aphid it stung and on other occasions during the experiment. *D. rapae* was not observed to feed on the aphids. Further, *A. albipodus* commonly appeared to rest and preen itself after each attack, while this behavior was less frequently observed for *D. rapae*.

The combined result of these behaviors was that *A. albipodus* attacked fewer aphids per hour compared to *D. rapae* (Fig. 2E). The maximum number of aphids attacked by *A. albipodus* was always fewer than 12, while *D. rapae* would commonly sting >95% of the aphids in an experiment irrespective of the aphid density

(i.e., up to 38 aphids). The only situation where *A. albipodus* was observed to be more efficient in attacking aphids was when aphids were in leaf rolls at the base of the wheat plant. While both parasitoid species attempted to attack these aphids, *A. albipodus* appeared to be more successful. This parasitoid was sufficiently small to enable it to walk down the leaf tube. If the space inside the tube was insufficient to allow *A. albipodus* to turn around to sting an aphid while still in the tube, it would walk out of the leaf roll, turn, and back in to sting an aphid. *D. rapae* would attempt to attack aphids by trying to thrust its ovipositor through a gap in a leaf,

Table 1
Estimates of slopes and intercepts for parameters, which were modelled using a linear response to prey density \pm SE^a

	Slope			Intercept		
	<i>D. rapae</i>	<i>A. albipodus</i>	t_{slope}	<i>D. rapae</i>	<i>A. albipodus</i>	$t_{\text{intercept}}$
<i>Patch parameters</i>						
Time until arrival on the leaf	0.25 \pm 0.20 ns	–	–	3.52 \pm 4.25 ns	–	–
Total time on the plant	0.29 \pm 0.13*	0.13 \pm 0.13 ns	0.16 ns	32.81 \pm 2.83***	54.76 \pm 2.84***	21.95***
First occasion leaving the leaf	0.58 \pm 0.18**	0.23 \pm 0.18 ns	0.35 ns	7.34 \pm 3.87 ns	47.82 \pm 3.87***	40.48***
Number of occasions a parasitoid left the leaf	-0.19 \pm 0.04***	-0.02 \pm 0.04 ns	0.17**	10.27 \pm 0.94***	0.90 \pm 0.94 ns	9.37***
<i>Host parameters</i>						
Number of stings per parasitoid attack per aphid	-0.02 \pm 0.35 ns	-0.02 \pm 0.02 ns	0.00 ns	2.23 \pm 0.25***	2.01 \pm 0.24***	0.22 ns

Data in this column also indicate the difference in parameter means between species. ns, Not significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Statistics within species columns indicate if the slope, or the intercept, was significantly different from 0. “–” Indicates the data were best fit using an exponential decay function, the parameters of which are presented in Table 2.

^a t tests examined the hypothesis that the slope (t_{slope}) or intercept ($t_{\text{intercept}}$) were not different between parasitoid species.

which appeared to be a less effective method than that of *A. albipodus*.

No parasitoids developed or emerged from aphids attacked by *A. albipodus* in the one aphid per plant treatment. The aphids in this treatment appeared to be killed by *A. albipodus* feeding, because after feeding they appeared deflated and subsequently died on the wheat plant. The flattened carcasses of these aphids could still be observed on the wheat plants three weeks after parasitoid feeding. Similarly, individual flattened and dead aphids were observed in other treatments and appeared to have died as a result of *A. albipodus* feeding.

In all treatments, the maximum number of parasitoids emerging from mummies was 6 for *A. albipodus* and 33 for *D. rapae* (Fig. 2F). The mean ratio of “parasitoids emerged:” “number of aphids attacked” was 0.36 ± 0.04 for *A. albipodus* and 0.72 ± 0.04 (\pm SE) for *D. rapae* ($n = 25$, analysis of results from aphid densities $1 < x < 40$). Parameters in the functional response and numerical response analyses were not analyzed statistically because *D. rapae* did not reach an asymptote in either analysis, which impacts the derivation of equation parameters (Fig. 2, Table 3).

4. Discussion

The manner in which a parasitoid species utilize aphid patches is of fundamental relevance to their population dynamics. We cannot understand how parasitoids regulate aphid populations without knowledge such as the length of time parasitoids spend on each plant, their tendency to leave aphid infested plants, or the ratio of aphids that are stung to that which yield adult parasitoids. This study has illuminated a number of differences between two parasitoid species in their foraging behavior for *D. noxia*.

Diaeretiella rapae did not change its arrival time on a leaf with increasing aphid densities, even though the

amount of chemical attractants produced by the aphids must have substantially increased with increased aphid densities. Vaughn et al. (1996) found that *D. rapae* did not respond to volatile compounds from aphid infested grasses and suggested that this parasitoid seemed unlikely to be able to learn to do so. It appears only to respond to volatile chemicals from cruciferous crops (Vaughn et al., 1996), and on these crops has been observed to decrease the time it takes to arrive at a patch as aphid densities increase (Shukla et al., 1992). Aphelinid parasitoids, in contrast, may respond to host cues even as inexperienced females. This result appears to occur because these parasitoids are able to respond to chemicals from the aphid mummies in which they have matured (Wickremasinghe and van Emden, 1992). Our results concur with this chemical legacy hypothesis; we observed *A. albipodus* arriving on leaves more quickly at higher aphid densities, even when these parasitoids were inexperienced. Extrapolating the data on plant leaving at low aphid densities, *A. albipodus* would search only 16 plants every 12 h, compared to 86 plants by *D. rapae*. However, in the absence of additional information it is difficult to assess which parasitoid species would be able to discover prey populations faster.

After arriving on aphid-infested plants, *D. rapae* appeared more efficient in its use of each patch. It would generally find and sting the majority of aphids much faster than *A. albipodus*, then exit the leaf in an aphid density-dependent fashion much sooner than *A. albipodus*. The length of time each parasitoid species remained on a plant was probably affected by the parasitoids host feeding, oviposition behavior, and physiology.

Aphelinus albipodus is synovigenic; it is dependant on the availability of food to survive and produce eggs (Bernal et al., 1997). In our study, *A. albipodus* stung and consumed hemolymph in each of the aphid density treatments examined despite being fed prior to the experiment. At least one aphid appeared to have been killed by this feeding in each treatment. Though this

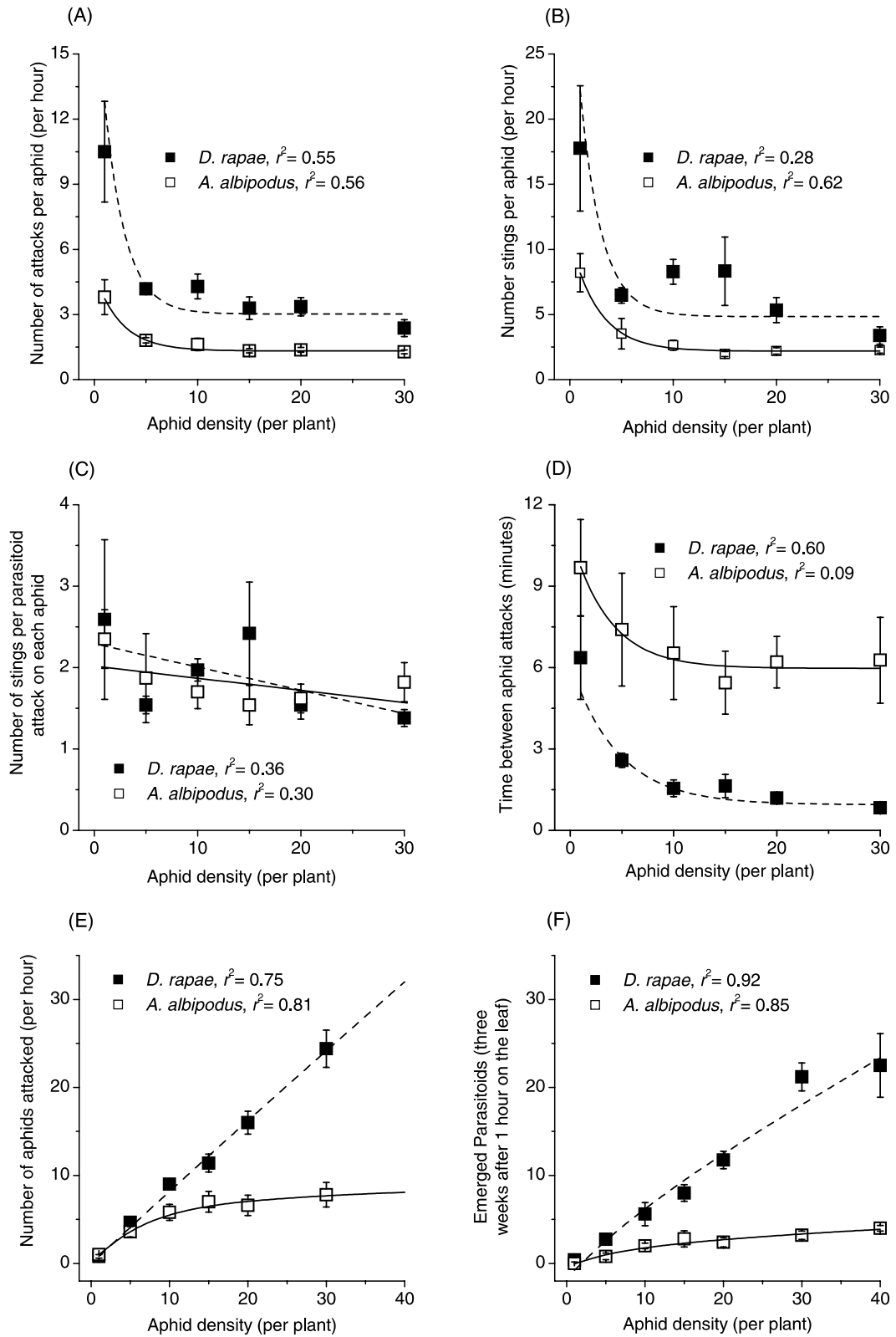


Fig. 2. Parasitoids' attack behavior on aphids, in relation to changing densities of *D. noxia* on an individual wheat plant. Data are means \pm SE.

feeding may keep the parasitoid alive and help produce eggs, the host consequently will not directly contribute to the next generation of parasitoids. When aphid

populations are low, the growth rate of *A. albipodus* populations may be reduced because of the adult parasitoids' feeding on the aphids instead of the aphids

Table 2

Estimates of slopes and intercepts for parameters, which were modelled using a negative exponential decay response to prey density \pm SE

	y_0			A_1			t_1		
	<i>D. rapae</i>	<i>A. albipodus</i>	t_{y_0}	<i>D. rapae</i>	<i>A. albipodus</i>	t_{A_1}	<i>D. rapae</i>	<i>A. albipodus</i>	t_{t_1}
<i>Patch parameters</i>									
Time until arrival on the leaf	–	4.16 \pm 1.85	–	–	47.90 \pm 21.93	–	–	6.46 \pm 1.61	–
<i>Host parameters</i>									
Number of stings per aphid per hour	0.00 \pm 0.00	1.50 \pm 0.42	1.50*	35.50 \pm 9.62	8.49 \pm 1.73	27.01*	5.27 \pm 1.51	4.07 \pm 1.16	1.20 ns
Number of attacks per aphid	1.27 \pm 0.48	1.00 \pm 0.18	0.27 ns	9.29 \pm 3.4	3.37 \pm 0.86	5.92*	7.93 \pm 1.99	4.61 \pm 1.96	3.32 ns
Time between aphid attacks	0.53 \pm 0.14	1.70 \pm 0.47	1.17*	6.98 \pm 1.78	6.89 \pm 3.15	0.10 ns	4.58 \pm 1.56	41.35 \pm 10.50	0.93 ns

t tests examined the hypothesis that the y -axis offset (t_{y_0}), amplitude (t_{A_1}) and the decay constant (t_{t_1}) were not different between parasitoid species. Data in this column indicate the difference in parameter means between species. ns, Not significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. “–” Indicates the data were best fit using a linear response function, the parameters of which are presented in Table 1.

being utilized as a host for new parasitoid generations. Host feeding likely increased the amount of time on a plant for *A. albipodus*, compared to *D. rapae*, which does not feed on hosts.

Both parasitoids appeared to exhibit super-parasitism, as indicated by the exponential decay exhibited in response of the number of stings per aphid to changing aphid densities. In the absence of super-parasitism such responses would likely be linear, with a slope of zero. Super-parasitism has been observed elsewhere in aphelinid and aphidiid parasitoids (Walter, 1993; Michaud, 1996). However, without dissection of the hosts it is difficult to determine the extent of super-parasitism in *A. albipodus* or *D. rapae*. For *A. albipodus*, this response may also have been associated with host feeding behavior. Further, both parasitoids may not have oviposited on each ovipositor probe.

A further cause for *A. albipodus*'s long duration time on each plant relative to *D. rapae* was its long period for each oviposition. We observed that each oviposition sting by *A. albipodus* required approximately 2 min. Long oviposition times by aphelinids have been noted elsewhere (Cate et al., 1973; De Faris and Hopper,

1999). The long duration of oviposition stabs may be related to the large egg size of many aphelinids, which pass slowly through the ovipositor (Le Ralec et al., 1996). In addition, large egg size appears to limit the ovarian egg load of parasitoids such as *A. albipodus*. Bernal et al. (1997) found that the egg load of newly emerged (<6 h old) *A. albipodus* is ca. 6.5 \pm 2.5 eggs per female. In comparison, *D. rapae* are thought to become egg limited at aphid densities greater than 80 (Bernal et al., 1994; Shukla et al., 1992). The results from our numerical response assay are in agreement with these findings.

Thus in many respects, the results we observed for the length of time *A. albipodus* spent on each host was not surprising. *A. albipodus* spent time feeding on aphids, had a longer oviposition time for each egg, and had a smaller number of eggs to oviposit in each aphid patch. With such a reduced number of eggs per parasitoid, it would be beneficial for *A. albipodus* to stay in an aphid-infested patch for a much longer period, until it is able to develop more eggs and oviposit them in a high proportion of the available aphids. Perhaps *A. albipodus* stays in or near aphid-infested patches until it is able to oviposit in most of the aphids present. Due to these physiological and behavioral differences, *D. rapae* would be able to move through an aphid population much more quickly.

The mean ratio of “parasitoids emerged:” “number of aphids attacked” was 0.36 for *A. albipodus* and 0.72 for *D. rapae*. Without dissecting the attacked aphids, it is impossible to determine if an egg was oviposited at the time of a sting by either parasitoid, so this statistic may be misleading. As discussed above, newly emerged *A. albipodus* have an egg-load of approximately 6.5 eggs per female (Bernal et al., 1997). In our experiment, we would have expected *A. albipodus* to have at least this many eggs, because it was fed honey-water and was 24–28 h old at the time of the experiments. *A. albipodus* successfully produced approximately four offsprings,

Table 3

Functional and numerical response parameters \pm SE

Parameters	<i>A. albipodus</i>	<i>D. rapae</i>	$t_{\text{parameter}}$
<i>Functional response</i>			
a	7.41 \pm 2.90	1.74 \pm 1.01	5.67
T_h	0.11 \pm 0.06	0.001 \pm 0.002	0.10
<i>Numerical response</i>			
e_1	1.65 \pm 0.54	0.62 \pm 0.49	1.03
b	0.33 \pm 0.23	1.01 \pm 0.54	0.68
e_0	1.72 \pm 0.97	0.56 \pm 0.41	1.16

A description of each parameter is shown in the text. The column $t_{\text{parameter}}$ shows the difference in the parameter between species, and results from t tests that examined the hypothesis that the parameters were not different between parasitoid species. ns, Not significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

although it stung many more aphids. Consequently, *A. albipodus* may have been either egg limited or had a low success rate in *D. noxia*. Parasitoids can assess their hosts using their ovipositor (Austin and Browning, 1981). Perhaps some *D. noxia* that *A. albipodus* probed with its ovipositor were rejected, though the long oviposition duration in most aphids makes this scenario seem unlikely. If *A. albipodus* was egg limited, are they able to develop eggs while remaining in a patch and recognize which aphids that have been stung but in which an egg has not been oviposited? Alternatively, perhaps *D. noxia* is not the best host for this parasitoid. Other aphid species are used as hosts by *A. albipodus* (Elliott et al., 1999). Parasitoid mortality within aphid hosts can occur in aphids for many reasons, including egg encapsulation (e.g., Brodeur and Vet, 1995). Whatever the reason for the reduced survival rate of *A. albipodus* in *D. noxia*, reduced survival likely reduces the population growth rate of *A. albipodus* during a growing season and perhaps contributes to its later appearance in wheat fields relative to *D. rapae* (Lester and Holtzer, unpublished data; Pike et al., 1997).

A further factor for the limited early season abundance of *A. albipodus* populations relative to *D. rapae* is climate. The developmental threshold for *D. rapae* has been estimated at 2.1 °C (Bernal and Gonzalez, 1993), compared to a threshold in excess of 10 °C for *A. albipodus* (Bernal et al., 1997). *Aphelinus albipodus* also has vastly different diapause requirements compared to *D. rapae* (Bernal et al., 2001).

From our results demonstrating *D. rapae*'s relatively efficient utilization of aphid-infested patches, it seems reasonable that *D. rapae* would be more abundant during the growing season. However, surveys indicate that *D. rapae* parasitism rates are nearly always less than 5% (Feng et al., 1992; Mohamed et al., 2000; Wraight et al., 1993). However, these same surveys also indicate a high hyperparasitism rate of *D. rapae*. Perhaps natural enemies limit *D. rapae* populations, while few natural enemies attack *A. albipodus*. Our results demonstrate some differences in parasitoid foraging that may account for the observed abundances of the parasitoids. However, field studies will be needed to determine the effects of other trophic levels on parasitoid abundance and spread, and to determine if the factors we have identified influence parasitoid abundance and distribution.

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