

# Effects of variation among plant species on the interaction between a herbivore and its parasitoid

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**Abstract.** 1. Previous studies have demonstrated that phenotypic traits of plants have the potential to affect interactions between herbivores and their natural enemies. Consequently, the impact of natural enemies on herbivore vital rates and population dynamics may vary among plant species. This study was designed to investigate the potential for density-dependent parasitism of an aphid herbivore feeding on six different host plant species.

2. Population densities of the aphid *Aphis nerii* B de F (Homoptera: Aphididae) and its parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) were recorded within a single growing season on six different species of milkweed in the genus *Asclepias* L. (Asclepiadaceae). *Asclepias* species are known to vary in their quality as food for herbivores. Although data on plant quality were not available in this study, population data were analysed to determine the effects of different *Asclepias* species on rates of parasitism and aphid population growth.

3. Parasitism rates of *A. nerii* varied among *Asclepias* species but were temporally density dependent over at least some range of aphid density on all plant species. Aphid population growth rates also varied among *Asclepias* species, and declined with an increase in the maximum parasitism rates among plant species; however, in no case was density-dependent parasitism sufficient to prevent exponential population growth of aphids within the growing season. The results serve to emphasise that, if natural enemies are to regulate herbivore populations, density-dependent mortality is a necessary, but not sufficient, condition for regulation.

**Key words.** *Aphis nerii*, *Asclepias*, density dependence, *Lysiphlebus testaceipes*, milkweed, parasitism, plant–insect interactions, population dynamics, tritrophic interactions.

## Introduction

All populations, if left unchecked, have the potential to grow exponentially (Malthus, 1798). Density-dependent processes may limit exponential growth by acting to reduce population growth rates as densities rise (Varley *et al.*, 1973). Both competition for limited resources and mortality imposed by natural enemies have the potential to act in a density-dependent fashion. For insects that feed on plants,

variation in plant quality can have a profound effect on both levels of competition and mortality from natural enemies (Price *et al.*, 1980; Denno *et al.*, 1995; Abrahamson & Weis, 1997; Lill *et al.*, 2002). As a consequence, it might be expected that the expression of density dependence, and herbivore population dynamics, should vary among host plant species (Hunter *et al.*, 2000; Hunter, 2001).

The role of density-dependent parasitism in aphid population dynamics has been examined in a number of studies. Results have been variable, leading to no general consensus. Parasitism of aphids has been shown to be density dependent (Walker *et al.*, 1984; Murphy & Volkl, 1996; Colfer & Rosenheim, 2001), inversely density dependent (Walker *et al.*, 1984; Zhang & Chen, 1993), and density independent

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(Zhang & Chen, 1993; Ferguson & Stiling, 1996; Murphy & Volkl, 1996), varying with the species and system under study. Differences in these results may be due to a number of factors including competition from other aphid predators, intraguild predation, and variation in plant quality.

This study was designed to examine variation in the power of density-dependent parasitism acting on an insect herbivore feeding on different host plant species. The research was designed to address two specific questions: (1) does the form and strength of density-dependent parasitism vary among plant species, and (2) can within-season growth of an aphid population be limited by parasitism? The study was conducted by counting populations of the aphid, *Aphis nerii* B de F (Homoptera: Aphididae), and parasitism by *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae), on six species of plants in the genus *Asclepias* L. (Asclepiadaceae) growing in a common garden.

### System of study

Plants in the genus *Asclepias* vary in their quality for insect herbivores based, in part, on concentrations of cardenolides in their tissues (Malcolm *et al.*, 1989). Cardenolides are a group of cardiac-active steroids that act by blocking the  $\text{Na}^+/\text{K}^+/\text{ATPase}$  system which transports ions across cell membranes (Horisberger, 1994). Concentrations of cardenolides are known to vary both within and among species (Malcolm *et al.*, 1989), among plant parts, and through time (Nelson *et al.*, 1981).

*Aphis nerii*, or the oleander aphid, is an aposematic phloem-feeding specialist of oleander (*Nerium oleander* L. (Apocynaceae)) and species of *Asclepias*. These insects have bright yellow coloration with black legs, antennae, cauda, and cornicles. Aphids reproduce parthenogenetically and are not particularly mobile; individuals appear to stay on suitable host individuals, although winged forms are produced in response to crowding or declines in host quality (Groeters, 1989). *Aphis nerii* occur as highly aggregated colonies on host plants and have been shown to sequester cardenolides from their host plants (Rothschild *et al.*, 1970; Malcolm, 1990). Malcolm (1990) found that aphids sequestered almost all of the types of cardenolide present in the host plant *Asclepias curassavica* L. and so the cardenolide concentrations in the aphids covary with the host. There are apparently no large-scale fitness trade-offs from feeding on different hosts for *A. nerii*, suggesting that they possess a sequestration mechanism that renders them fitness insensitive to cardenolide variation among hosts (Groeters, 1993). This is consistent with the findings of Malcolm (1992) that, in the absence of predators, aphid populations grow at the same exponential rate on high and low cardenolide plants.

*Lysiphlebus testaceipes* is the major parasitoid of *A. nerii* and has a wide distribution in Nearctic America, into Neotropical America, and the Mediterranean (Stary, 1976).

*Lysiphlebus testaceipes* was imported into North America and the Mediterranean as a biological control agent and so likely has its origins in South America (Stary, 1970). It lays a single egg in the body of an aphid and, upon hatching, the larva feeds internally on the living aphid, causing it to appear swollen. After the death of the aphid, the aphid's cuticle turns brown to form a typical aphid mummy. The wasp pupates inside the aphid mummy and then emerges by cutting a circular hole in the top of the mummy (Stary, 1988). Hall and Ehler (1980) found that parasitism by *L. testaceipes* of *A. nerii* populations feeding on *Nerium oleander* was inversely density dependent.

Although the effect of cardenolides on aphid parasitoids has not been examined, cardenolides have been shown to affect the fitness of several enemies of *A. nerii*: coccinellids (Pasteels, 1978), lacewings (Malcolm, 1992), and spiders (Malcolm, 1989). Pasteels (1978) found that cardenolides disrupted wing development in coccinellids and Malcolm (1989) demonstrated that spiders fed *A. nerii* built severely disrupted webs and attacked fewer non-toxic, control aphids. Survival of lacewing larvae is much lower when feeding on *A. nerii* with high cardenolide content (Malcolm, 1992). It has been demonstrated that variable cardenolide content can also influence the mortality of *A. nerii* by influencing predation: aphid populations were smaller and more influenced by predation on a low cardenolide milkweed than on a high cardenolide milkweed (Malcolm, 1992).

## Materials and methods

### Field samples

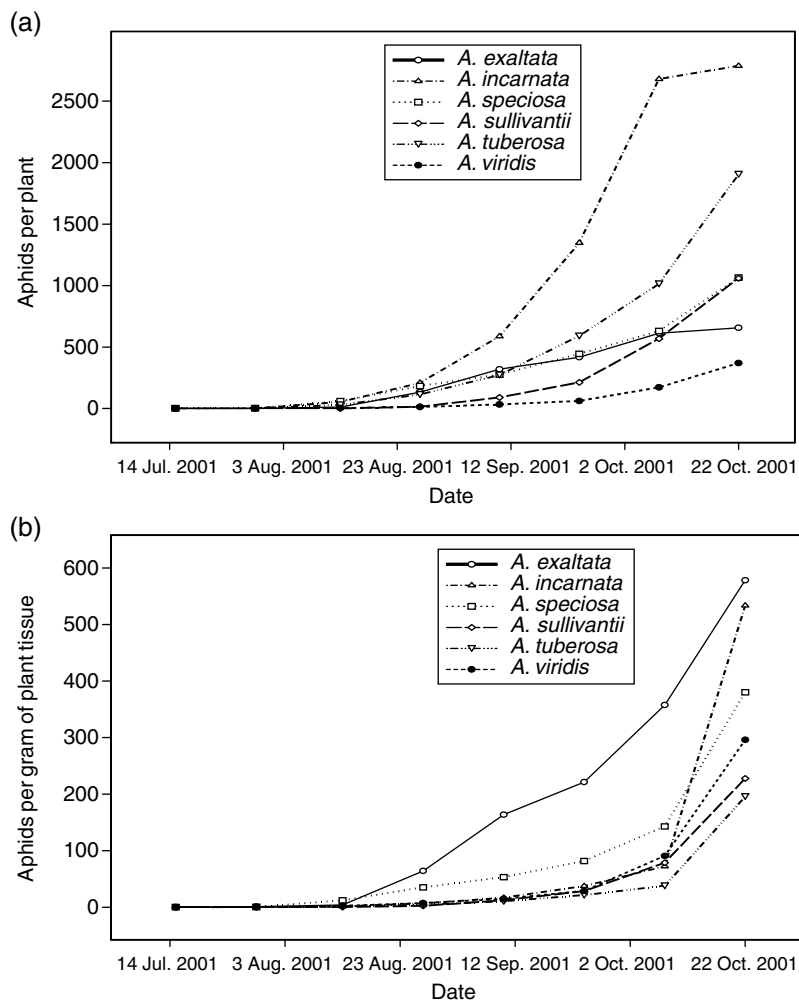
From July through to October 2001, *A. nerii* populations were counted on six species of *Asclepias* in a common garden located beside the University of Georgia's Botany Greenhouses, Athens, Georgia. Plants are grouped by species in blocks of 25 plants each, with 1 m between plants and between blocks. There are four blocks (100 plants) each of *A. exaltata* L., *A. speciosa* L., *A. tuberosa* L., and *A. viridis* L.; and two blocks (50 plants) each of *A. incarnata* L. and *A. sullivantii* L. The plants were watered for 2 h, twice a week, as weather dictated. To control fire ants, Orthene was applied to ant mounds as they appeared. Grass between plants was mowed every 2–3 weeks.

Plant biomass estimates, number of aphids, and number of aphid mummies were recorded from each plant in the garden every 2 weeks from 14 July to 22 October. At the beginning of November, plants senesced and aphid populations dropped to zero on all plants. Biomass estimates of the plants were made by measuring stem height and counting the number of leaves, and then scaling these numbers to dried weights of collected plant material. Aphid densities were then calculated as the number of aphids on an individual plant on a given date divided by the biomass estimate of that plant on that date.

## Data analysis

**Growth rate of aphid populations.** Preliminary observations suggested that aphid populations grew exponentially on all *Asclepias* species (Fig. 1) until the plants senesced at the end of the growing season. Therefore, to approximate the per capita rate of increase ( $r$ ) of aphids on each plant species, a linear model was found for each individual plant using the natural log of aphid density against time period (Berryman, 1999). The slope of this line is  $r$  for aphid growth on that plant. Differences in  $r$  among plant species were determined by ANOVA (SAS, 1999), using individual plants within each species as replicates. Although there were either 50 or 100 individual plants for each *Asclepias* species in the field, only plants that hosted aphids for at least four consecutive sampling dates were used in the analysis, causing variation among species in sample size (Table 1).

**Temporal density-dependent parasitism.** Population data were examined for evidence of both temporal and spatial density-dependent parasitism. Temporal density dependence describes how, as a prey population increases over time, its mortality changes for a single point in space. Spatial density dependence describes how, as average prey density varies among patches, prey mortality changes for a single point in time (Stewart-Oaten & Murdoch, 1990). Per cent parasitism was found by dividing the number of mummies by the total number of parasitised and unparasitised aphids on each plant at each time period. To examine temporal density dependence, average values of per cent parasitism on each sampling date were regressed against the density of aphids independently for each plant species. The resulting points were graphed as per cent parasitism against aphid density. To estimate the shape of parasitism response curves, the resulting data points for each species were fit to several potential equations, namely those of the



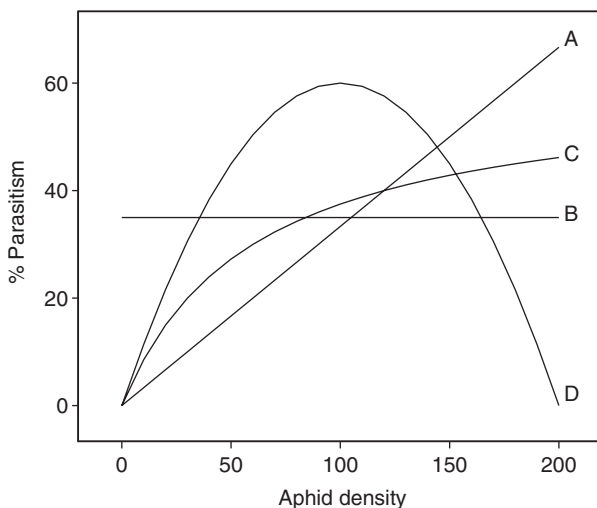
**Fig. 1.** (a) Numbers per plant and (b) densities per gram of plant tissue of *Aphis nerii* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Data are the means of 100 plants (*A. exaltata*, *A. speciosa*, *A. tuberosa*, and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*).

**Table 1.** Mean per capita rate of increase ( $r$ ) of *Aphis nerii* on six species of *Asclepias* in a common garden in Athens, Georgia. Means with the same letter are not significantly different.

| Species               | Mean $r$ | Standard error | $n$ | Tukey grouping |
|-----------------------|----------|----------------|-----|----------------|
| <i>A. exaltata</i>    | 1.107    | 0.031          | 34  | A              |
| <i>A. sullivantii</i> | 0.983    | 0.031          | 32  | B              |
| <i>A. speciosa</i>    | 0.903    | 0.021          | 73  | B C            |
| <i>A. incarnata</i>   | 0.894    | 0.026          | 46  | B C            |
| <i>A. viridis</i>     | 0.884    | 0.040          | 20  | B C            |
| <i>A. tuberosa</i>    | 0.840    | 0.026          | 48  | C              |

forms represented in Fig. 2. Data were fit to equations (Table 2) using the Proc NonLin procedure in SAS (1999). These equations can be described as a linear function (Fig. 2, line A), two alternative forms of a saturation curve (Fig. 2, line C), and a parabolic curve (Fig. 2, line D). The null hypothesis of density independence is represented by line B. Biologically, a linear function represents a density-dependent response to prey populations. Saturation curves represent initial density dependence falling to density independence at higher aphid densities. A parabolic curve represents initial density dependence to some threshold, followed by inverse density dependence beyond that threshold, presumably resulting from limitations on the numerical or behavioural responses of parasitoids (Holling, 1959).

*Spatial density-dependent parasitism.* To assess the evidence for spatial density dependence, average values of per cent parasitism for each individual plant (across all sampling dates) were regressed against aphid density, independently for each plant species. These data were graphed as per cent parasitism against aphid density and



**Fig. 2.** Possible forms of the relationship between densities of *Aphis nerii* and per cent parasitism by *Lysiphlebus testaceipes*. Letters represent the following relationships: A, linear density dependence; B, density independence (Holling type I); C, density dependence at low aphid densities and density independence at high aphid densities; and D, density dependence at low aphid densities and inverse density dependence at high aphid densities (Holling type III).

examined for significant relationships between aphid density and per cent parasitism.

*Effects of parasitism on per capita rates of aphid population growth.* Using parasitism rates from the analysis of temporal density dependence, regressions between mean growth rate of *A. nerii* populations and the maximum observed per cent parasitism experienced on different plant species were examined. Linear and non-linear regressions using the Proc NonLin procedure in SAS (1999) were compared.

## Results

### Aphid population growth rate

Aphid population growth was approximately exponential on all *Asclepias* species and showed no signs of decline prior to senescence of host plants in the fall of 2001 (Fig. 1b). Plant species identity was a significant predictor of aphid per capita growth rate ( $r$ ) ( $F=10.65$ , d.f. = 5,247,  $P<0.0001$ ; Table 1). Aphid population growth rate on *A. exaltata* was significantly higher than on all other species, and aphid growth on *A. sullivantii* was significantly higher than that on *A. tuberosa* (Table 1).

### Temporal density-dependent parasitism

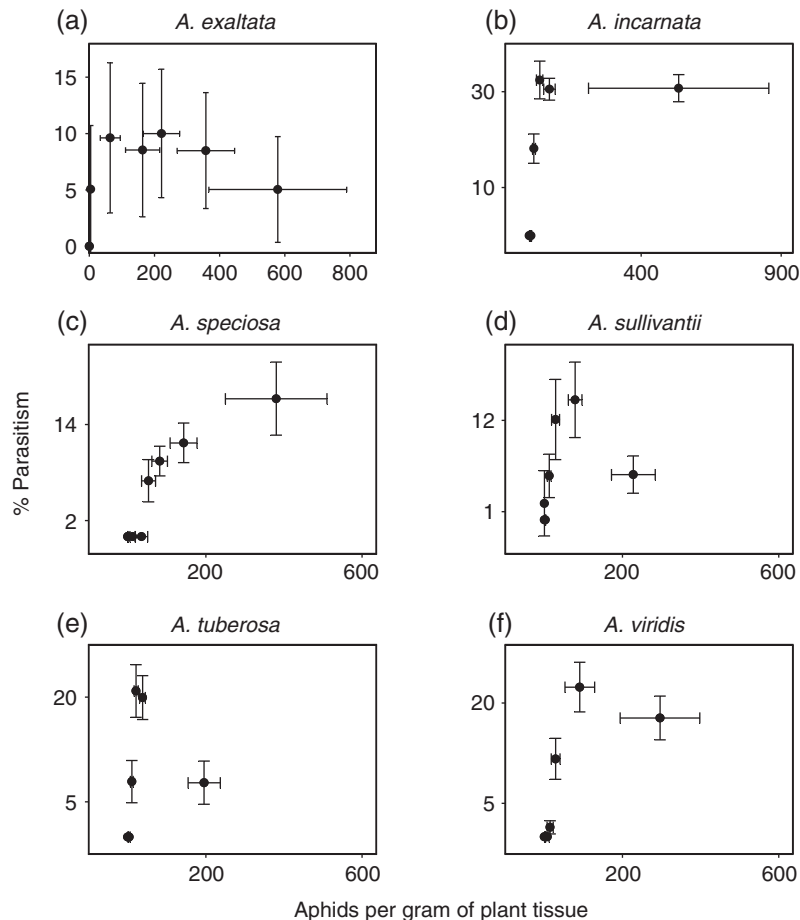
There was evidence of temporal density-dependent parasitism over at least some range of aphid densities on all plant species (Fig. 3). In other words, there was an initial increase in per cent parasitism with aphid density on all host plants; however, the exact form of density dependence among plant species remains equivocal. Figure 3 suggests that parasitism on *A. incarnata* and *A. speciosa* might best be described by saturation curves (parasitism reaching a plateau, Fig. 2, line C). On the four other host species, per cent parasitism appears to decline at high aphid densities, suggesting a switch from density-dependent to inverse density-dependent parasitism (Fig. 3). Regression analyses (Table 2) suggest that both saturation curves (density dependence falling to density independence) and parabolic curves (density dependence falling to inverse density dependence) provide good descriptions of the data, although  $r^2$  values are generally higher for the parabolic curves. In either

**Table 2.**  $R^2$  and  $P$ -values for the regression equations describing temporal density-dependent parasitism of *A. nerii* by *L. testaceipes* on six species of *Asclepias* in a common garden in Athens, Georgia. Refer to Fig. 2 for a visual representation of these equations. Equations are of the following forms: linear ( $y = a * x$ ), saturation I [ $y = (a * x)/(a + x)$ ], saturation II ( $y = a + b * x^q$ , where  $q < 1$ ), and parabolic ( $y = a * x^2 + b * x$ ).

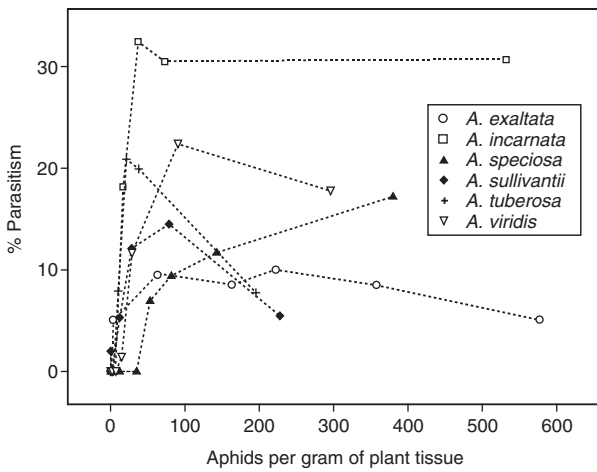
| Species               | Linear<br>(Fig. 2, A)          | Saturation I<br>(Fig. 2, C)    | Saturation II<br>(Fig. 2, C)   | Parabolic<br>(Fig. 2, D)       |
|-----------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| <i>A. exaltata</i>    | $R^2 = 0.1244$<br>$P = 0.3915$ | $R^2 = 0.8175$<br>$P = 0.0008$ | $R^2 = 0.9075$<br>$P = 0.0638$ | $R^2 = 0.8406$<br>$P = 0.0040$ |
| <i>A. incarnata</i>   | $R^2 = 0.2910$<br>$P = 0.1676$ | $R^2 = 0.6665$<br>$P = 0.0073$ | $R^2 = 0.9033$<br>$P = 0.0299$ | $R^2 = 0.9158$<br>$P = 0.0006$ |
| <i>A. speciosa</i>    | $R^2 = 0.8063$<br>$P = 0.0025$ | $R^2 = 0.5456$<br>$P = 0.0230$ | $R^2 = 0.9456$<br>$P = 0.0122$ | $R^2 = 0.9649$<br>$P < 0.0001$ |
| <i>A. sullivantii</i> | $R^2 = 0.1176$<br>$P = 0.4056$ | $R^2 = 0.6778$<br>$P = 0.0064$ | $R^2 = 0.7613$<br>$P = 0.2560$ | $R^2 = 0.9284$<br>$P = 0.0004$ |
| <i>A. tuberosa</i>    | $R^2 = 0.0458$<br>$P = 0.6108$ | $R^2 = 0.5711$<br>$P = 0.0185$ | $R^2 = 0.6789$<br>$P = 0.3766$ | $R^2 = 0.9351$<br>$P = 0.0003$ |
| <i>A. viridis</i>     | $R^2 = 0.5097$<br>$P = 0.0467$ | $R^2 = 0.4800$<br>$P = 0.0386$ | $R^2 = 0.8501$<br>$P = 0.0677$ | $R^2 = 0.9738$<br>$P < 0.0001$ |

case, parasitism of *A. nerii* by *L. testaceipes* is clearly limited at high aphid densities, which may explain why aphid population growth remains exponential (Fig. 1b) through to the

end of the season. In addition, there is obvious variation among host plant species in the form and strength of density-dependent parasitism (Fig. 4).



**Fig. 3.** Temporal density-dependent parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Each data point represents a single sample date and is the mean of 100 plants (*A. exaltata*, *A. speciosa*, *A. tuberosa*, and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*) (horizontal and vertical bars indicate 95% CI).



**Fig. 4.** A comparison of parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Each data point represents a single sample date and is the mean of 100 plants (*A. exaltata*, *A. speciosa*, *A. tuberosa*, and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*).

*Spatial density-dependent parasitism*

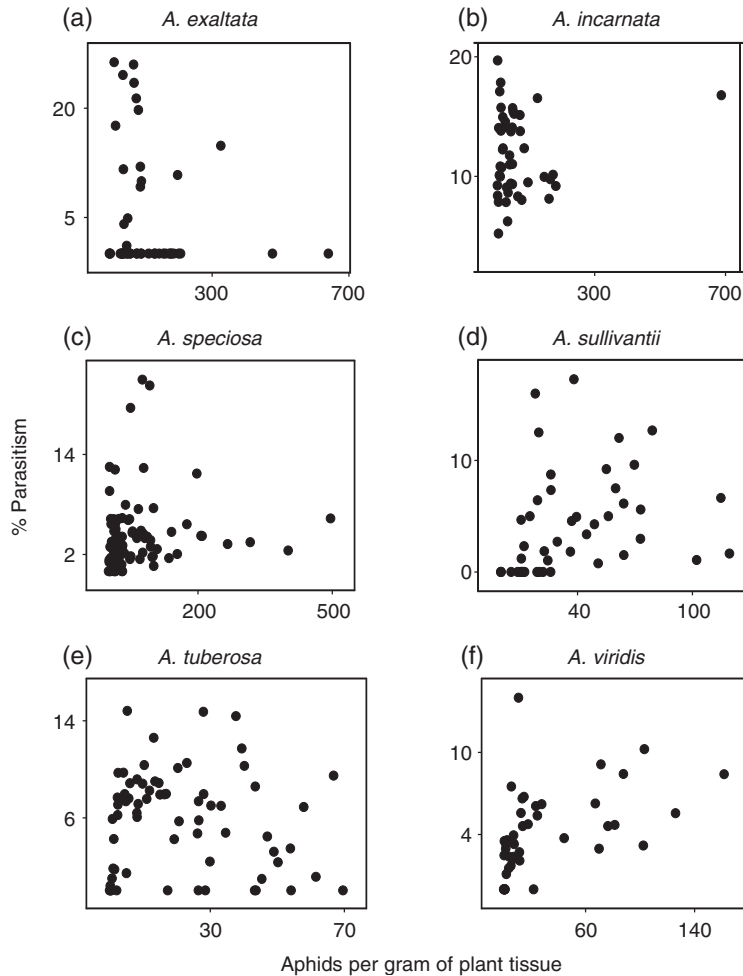
There was no evidence that aphid parasitism rates were spatially density dependent on any of the plant species (Fig. 5).

*Effects of parasitism on per capita rates of aphid population growth*

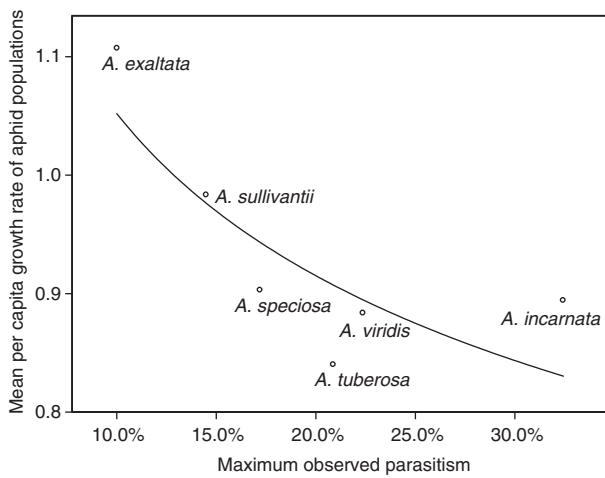
The mean population growth rate of *A. nerii* was negatively correlated with the maximum observed parasitism on each *Asclepias* species. Figure 6 shows the points for each species with the regression line which best describes this relationship ( $y = 245.1 - 244.5x^{0.000807}$ ,  $P = 0.0435$ ).

**Discussion**

As in many aphid–parasitoid systems (Walker *et al.*, 1984; Murphy & Volkl, 1996; Volkl & Stechmann, 1998),



**Fig. 5.** Spatial density-dependent parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Each data point represents an individual plant and is the mean of seven sampling dates. No statistically significant relationships exist.



**Fig. 6.** Regressions between the per capita rate of increase of *Aphis nerii* and maximum observed parasitism by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Data points represent individual *Asclepias* species and are the means of per capita rates of increase calculated from between 20 and 73 individual plants per species (see text for details).

parasitoids did not play a significant role in regulating population growth of *A. nerii* on *Asclepias* species. Aphid densities continued exponential growth up to the end of the growing season (Fig. 1b). Aphid parasitoids often exploit a small number of available hosts, and parasitism rates tend to range between 1% and 10% (Mackauer & Volkl, 1993). Although parasitism rates reached over 30% on some host plants in this study (Fig. 3), these rates were still not sufficient to regulate aphid population growth within the season.

In contrast to Hall and Ehler (1980), who found parasitism rates of *A. nerii* on *Nerium oleander* to be inversely density dependent, the results of this study found a density-dependent response by *L. testaceipes* to *A. nerii* population levels over at least some range of aphid densities on all *Asclepias* species. Therefore, while *L. testaceipes* could potentially regulate aphid densities, its density-dependent response was not sufficient to regulate aphid populations. A similar result has been observed in other studies examining the relationship between aphids and their parasitoids. Murphy and Volkl (1996) found density-dependent parasitism of aphid populations; however, the parasitoid populations remained low and never increased sufficiently to regulate the growth of aphid populations. Several potential factors leading to reduced parasitoid efficiency in regulating aphid populations have been suggested: hyperparasitism (Walker *et al.*, 1984), predation of parasitised aphids (Ferguson & Stiling, 1996), and parasitoid foraging behaviour (Mackauer & Volkl, 1993).

Variation among plant species appears to have an influence on the interaction between *A. nerii* and *L. testaceipes* since species identity was a significant predictor of aphid growth rate (Table 1) and parasitism (Fig. 4). These differences among plant species may result from both indirect

and direct influences of the host plant on *L. testaceipes* populations.

There does not seem to be much support for *Asclepias* plants indirectly influencing parasitoid populations by influencing aphid abundance or distribution. While previous studies have found that growth rates of *A. nerii* are higher on high cardenolide plants than on low cardenolide plants, it is thought to be the result of higher predation and parasitism rates on the low cardenolide plants (Malcolm, 1992). It has also been suggested that there is no fitness cost to *A. nerii* from variation in cardenolide content of host plants (Groeters, 1993) and that *A. nerii* growth rates are not affected by variation in cardenolide content (Malcolm, 1992); however, *L. testaceipes* populations may still be indirectly influenced by host plant mediated changes in prey quality.

*Asclepias* plants may influence parasitoids through aphid honeydew. Malcolm (1990) found that the honeydew secreted by *A. nerii* consists of 46% cardenolides. These cardenolides may be recognisable as cues to parasitoids and lead to differential oviposition rates on different plant species. Evidence from the literature seems to suggest that host plant mediated changes in prey quality and direct effects on *L. testaceipes* populations through variation in plant quality may be more important than indirect effects mediated through changes in growth rates of *A. nerii*. Future work will investigate the role of plant chemistry in this interaction and test these predictions.

This study has focused on within-year population dynamics of *A. nerii* populations. While important regulatory processes operate on short-term time scales, such as those examined in this study, there may also be population regulation acting over yearly time scales (Sequeira & Dixon, 1997). Overall abundance in one year may be influenced by abundance in the previous year. Aphid populations observed in this study showed no evidence of population regulation; however, if these populations were observed on a yearly time scale, evidence of population regulation may be seen.

This study adds to the growing body of knowledge that variation in plant quality can affect the population ecology of parasitoids and the impact of parasitoids on herbivore populations (Price *et al.*, 1980; Abrahamson & Weis, 1997; Hunter, 2003). Moreover, the data serve to emphasise the point that, if parasitoids are to regulate the populations of insect herbivores, density-dependent parasitism is a necessary, but not sufficient, condition for population regulation.

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