The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*

LI A. LIN[1] and ANTHONY R. IVES[2] [1]Madison West High School, Madison, Wisconsin and [2]Department of Zoology, University of Wisconsin–Madison, U.S.A.

Abstract. 1. Direct observations of *Aphidius colemani* foraging for *Aphis glycines* demonstrated that *A. colemani* attacks large aphid size classes selectively, in contrast to other Aphidiinae (Hymenoptera: Braconidae) species that generally prefer small or medium-sized nymphs of different host species.

2. To determine the effect of this size preference on the potential ability of *A. colemani* to control *A. glycines* outbreaks, the stage-dependent survival and fecundity of *A. glycines* were measured to parameterise a stage-structured demographic model for the density-independent population growth rate of the aphid.

3. Compared with hypothetical parasitoids that show either no size preference or preference for medium-sized host nymphs, the preference of *A. colemani* for large hosts caused a greater reduction in the population growth rate of *A. glycines*. This occurs in the model because, by attacking reproductive adults, *A. colemani* kills those aphids that have the greatest immediate effect on the population growth rate.

4. The strong effect of size preference by *A. colemani* is diminished somewhat by the continued reproduction of *A. glycines* adults, which can reproduce for up to 3 days following parasitism. Nonetheless, reproduction by parasitised aphids is not enough to compensate for the stronger, negative effect of the preference of *A. colemani* for large aphids, which removes individuals with the greatest reproductive value from the *A. glycines* population.

Key words. Host–parasitoid dynamics, Leslie matrix model, stage-selective predation.

Introduction

Many parasitoid species exhibit oviposition preferences for certain sizes, ages, or stages of individuals from the same host species (Mackauer, 1973; Hopper & King, 1984; Liu *et al.*, 1984; Wang & Liu, 2002). Host size/stage preference affects the fitness of parasitoid females by influencing the development rate and survival of their offspring (Lewis & Redlinger, 1969; Nechols & Kikuchi, 1985; Sequeira & Mackauer, 1993) and the size of their adult progeny (Kouame & Mackauer, 1991; Nicol & Mackauer, 1999;

Correspondence: A. R. Ives, Department of Zoology, University of Wisconsin–Madison, Madison, WI 53706, U.S.A. E-mail: arives@wisc.edu

Chau & Mackauer, 2001a). Host size/stage preference may also affect host–parasitoid population dynamics; for example, Murdoch *et al.* (1987) showed that when parasitoids attack only a narrow window of the developmental stages of a host, host–parasitoid population dynamics may be stabilised. Furthermore, host size/stage preference may change the outcome of competition among parasitoid species for a shared host species if the parasitoid species attack different host sizes or stages (Briggs *et al.*, 1993; Murdoch *et al.*, 1996). Despite the large literature demonstrating host size/stage preference by parasitoids, and the effects that size/stage preference can have on both parasitoid fitness and host–parasitoid population dynamics, little attention has been given to how host size/stage preferences affect the density-independent host population growth rate (but see Mondor & Roitberg, 2000).

Aphid parasitoids of the subfamily Aphidiinae (Hymenoptera: Braconidae) typically show oviposition preference for small or intermediate host instars (Liu *et al.*, 1984; Sequeira & Mackauer, 1987, 1992a; Weisser, 1994; Mackauer *et al.*, 1996; Ives *et al.*, 1999; Chau & Mackauer, 2000). Aphidiine species are solitary koinobionts that develop within still-growing aphid hosts, killing the aphids and forming mummies in which the parasitoid larva pupates only after the aphid host has reached its fourth or fifth (adult) instar. Several studies have investigated the fitness consequences to females that prefer small or intermediate host instars. Although offspring size increases with the host instar attacked, this increase is not linear because the hosts continue to grow following parasitism (Sequeira & Mackauer, 1992b). Furthermore, the potential size advantage of offspring derived from larger hosts may be mitigated by the increased development time of larger offspring (Kouame & Mackauer, 1991; Sequeira & Mackauer, 1992a,b; Chau & Mackauer, 2000). The potential advantages of ovipositing in larger hosts may be offset by the more effective defence mounted by larger hosts, such as dropping off plants or kicking during attack (Gerling *et al.*, 1990; Weisser *et al.*, 1994; Weisser, 1995). Finally, the preference for specific instars shown by a parasitoid species may change with different host species. For example, Chau and Mackauer (2001b) showed that the preference of *Monoctonus paulensis* (Braconidae, Aphidiinae) for hosts from different species depends on host instar; for example, females have a preference for third-instar *Acyrthosiphon pisum* over second-instar *Macrosiphum creelii* but no preference between second-instar *A. pisum* and first-instar *M. creelii*, possibly due to the better defences exercised by second-instar *M. creelii*.

In the work reported here, the size preference of the parasitoid *Aphidius colemani* (Viereck) (Hymenoptera: Braconidae, Aphidiinae) for soybean aphid hosts, *Aphis glycines* Matsumura (Homoptera: Aphididae), was investigated. *Aphidius colemani* was introduced into North America from Argentina in the early 1990s for biological control of the Russian wheat aphid *Diuraphis noxia* (Mordvilko), although its host range includes *A. glycines*. Despite multiple sites of introduction, *A. colemani* has become established only patchily in the U.S.A. (Elliott *et al.*, 1995; Burd *et al.*, 2001). *Aphis glycines* is an east and south-east Asian pest of soybeans that was discovered in North America in July 2000 (Gallepp, 2001). It is now found throughout the upper midwestern States in the U.S.A. and in Ontario, Canada, where it has reached very high densities in soybean fields and led to significant crop loss. Parasitism is negligible (D. B. Hogg, pers. comm.), and *A. colemani* is therefore a candidate species for a biological control programme against *A. glycines*.

Preliminary observations revealed that *A. colemani* prefers late nymphal and adult instars of *A. glycines*. Because this contrasts with the pattern typically found for aphidiine parasitoids, the host-size preferences shown by *A. colemani* for *A. glycines* were first investigated. To quantify the importance that size preference might have for the ability of *A. colemani* to control *A. glycines* outbreaks, experiments were performed to construct a life table for *A. glycines* containing stage-specific development times, adult survival, and fecundity. A stage-specific model was then developed to combine the data on size preferences of *A. colemani* and the life-table data for *A. glycines*. This allowed the exploration of the quantitative effect of host-size preferences of *A. colemani* on the density-independent population growth rate of *A. glycines*.

Methods

Study organisms

Aphis glycines undergoes multiple parthenogenic generations during the summer on soybean *Glycine max* (L.) Merr. Nymphs go through four instars before reaching adulthood (instar 5), and are predominantly apterous (wingless) during the summer months. Instars are not readily distinguishable morphologically, so size (body length from head to siphon) was used as a surrogate for stage. Adults and nymphs are relatively sedentary, leading to colonies of hundreds or thousands of aphids on soybean leaves. A winged generation is produced in September that leaves soybeans and migrates to the overwintering host, buckthorn *Rhamnus* spp. (Takahashi *et al.*, 1993). A sexual generation is produced on buckthorn and, after mating, eggs are laid on the buckthorn for overwintering. The second generation of the spring migrates from buckthorn to soybean fields. The soybean aphid is a significant pest in China and south-east Asia (Wang *et al.*, 1962; van den Berg *et al.*, 1997). In addition to causing direct harm to soybeans, *A. glycines* is a vector of several soybean viruses, including the soybean mosaic virus (Halbert *et al.*, 1986).

Aphidius colemani attacks numerous common pests, including *Aphis gossypii*, *Myzus persicae*, and *Diuraphis noxia*, and has been imported from South America to Europe and North America as a biological control agent. It is a solitary parasitoid, with only a single larva surviving within a host. Observations suggest that it shows no inhibition against self-superparasitism, at least over short time periods (<1 h); lack of inhibition against superparasitism over short time periods appears to be the rule for aphidiine parasitoids (Mackauer, 1983; Cloutier, 1984; Chow & Mackauer, 1991; McBrien & Mackauer, 1991; Michaud & Mackauer, 1995; Ives *et al.*, 1999; Mackauer & Chau, 2001). As is typical of the genus *Aphidius* (Völkl & Mackauer, 2000), *A. colemani* parasitises very quickly, so there is little handling time. Host location once parasitoids have landed on a plant probably involves visual cues, with chemical cues only used in very close proximity or following contact with antennae and/or ovipositor (Mackauer *et al.*, 1996; Battaglia *et al.*, 2000).

Experiments

Several experiments were performed in order to produce a model to quantify how host-size preference by *A. colemani*

affects the potential population growth rate of *A. glycines*. The size preference shown by *A. colemani* foraging for *A. glycines* on soybean leaves was measured then experiments on development times and fecundity were used to construct a life table for *A. glycines*. Because adult *A. glycines* will continue to reproduce following parasitism, a further experiment was performed to measure the fecundity of same-aged parasitised and unparasitised adults.

Host-size preference by Aphidius colemani. Host-size preference by *A. colemani* for *A. glycines* was measured by placing a soybean leaf with 100–200 aphids upside down in a Petri dish. The soybean leaves containing aphids were selected from plants grown in a greenhouse that were inoculated with a few aphids. Therefore, the size distribution of aphids and the condition of the leaf (e.g. abundance of honeydew, damage caused by aphid feeding) mimicked the conditions found in the field. The number and size of all aphids on the underside of the leaf (which contained almost all of the aphids) were measured using an ocular micrometer in a dissecting microscope. A single female parasitoid was added to the Petri dish and watched under a microscope, and the size of all aphids attacked by the female was measured. Attacks can be observed clearly, although the observed attacks did not necessarily lead to successful parasitism, which cannot be determined visually. The parasitoid was removed from the Petri dish after either it attacked 20 aphids or was inactive for at least 3 min. This procedure was repeated five times with five separate females using the same leaf. A total of 10 trials with different leaves was used, so the size preference of a total of 50 parasitoids was recorded.

Because instars could not be distinguished morphologically, for the presentation of the results and the stage-structured model, aphids were placed into size categories: I (<0.625 mm), II (0.625–0.781 mm), III (0.781–0.9375 mm), IV (0.9375–1.094 mm), and V (>1.094 mm). Analysis of the data from the experiment on development times (below) showed that these size categories correspond roughly to the five instars (analyses not presented).

Development time of Aphis glycines. The development time of *A. glycines* was measured for 22 aphids kept individually on soybean leaves in 10 cm diameter × 7 cm high plastic containers. The base of each leaf was placed in a vial containing water, and aphids were moved to fresh leaves at least every 4 days. All containers were kept in a plant growth chamber with a LD 16:8 h cycle; the day and night temperatures were 25 and 20 °C respectively. At the start of the experiment, adult aphids were placed on each leaf until they reproduced. The adult aphid and all the offspring except one were then removed. The size of the remaining offspring was measured under a dissecting microscope daily, and the leaves were searched for exuvia. Aphids were monitored until they reproduced.

Fecundity of Aphis glycines. Fecundity was measured for 24 adult apterous aphids each on separate soybean plants. Each plant was in a 12 × 12 × 12 cm pot, and a Mylar plastic tube with screen windows and a screen top was placed over the plant. Plants were kept in a plant growth chamber with a LD 16:8 h cycle; the day and night temperatures were 25 and 20 °C respectively. Single fourth-instar aphids were placed onto individual soybean leaves in a plastic container (see above) and were checked daily for exuvia. When the fourth exuvium was found, indicating that the aphid had reached the adult instar, the single, apterous aphids were transferred to the plants. The number of offspring produced was counted daily and removed. After 2 weeks, the aphids were placed onto new plants to ensure that plant quality was not reduced over the course of the experiment. Aphids were monitored until they died.

Fecundity of parasitised Aphis glycines. The fecundities of 20 parasitised aphids were measured in a manner similar to that used to measure fecundity of unparasitised aphids. Fourth-instar aphids were placed on a soybean leaf in a Petri dish with five female *A. colemani*. They were watched, and after an aphid was attacked, it was removed and placed singly on a leaf in a plastic container. The leaf was checked for an exuvium to ensure that the aphid moulted within 24 h, then leaves were checked daily, and offspring were counted and removed. This was done until a mummy was formed. This experimental design measures the reduction in fecundity caused by parasitism to newly reproductive adults. Newly reproductive adults were selected rather than older adults, because high natural parasitism and/or predation under field conditions will make newly reproductive adults relatively more common than older adults, and therefore the experiment is likely to give a reasonable representation of the impact of parasitism on fecundity in the field. To assess the impact of parasitism on fecundity, the fecundities of parasitised aphids from this experiment were compared with the fecundities of the newly reproductive aphids in the preceding experiment without parasitism.

Results

Host-size preference by Aphidius colemani

Aphidius colemani showed strong preference for large-sized (later-instar) aphids. An example of one of the 10 replicate leaves selected at random is shown in Fig. 1. The number of aphids and the number of attacks made on aphids in each of the different size categories are shown in Fig. 1a. Because individual aphids were not identified, the data include multiple attacks on the same aphid, which can result in more attacks scored for a given size category than the number of aphids in the category. These data were used to calculate a measure of preference for different size categories. For each size category, the ratio of the number of aphids attacked to the number present was calculated. Each of these ratios was then divided by the sum of the ratios from all size categories, to give a measure of preference for that replicate leaf (Fig. 1b). This measure of preference combines the behaviour of all five parasitoids foraging on the leaf. Because the overall objective was to assess the impact of size preference on aphid population growth, the
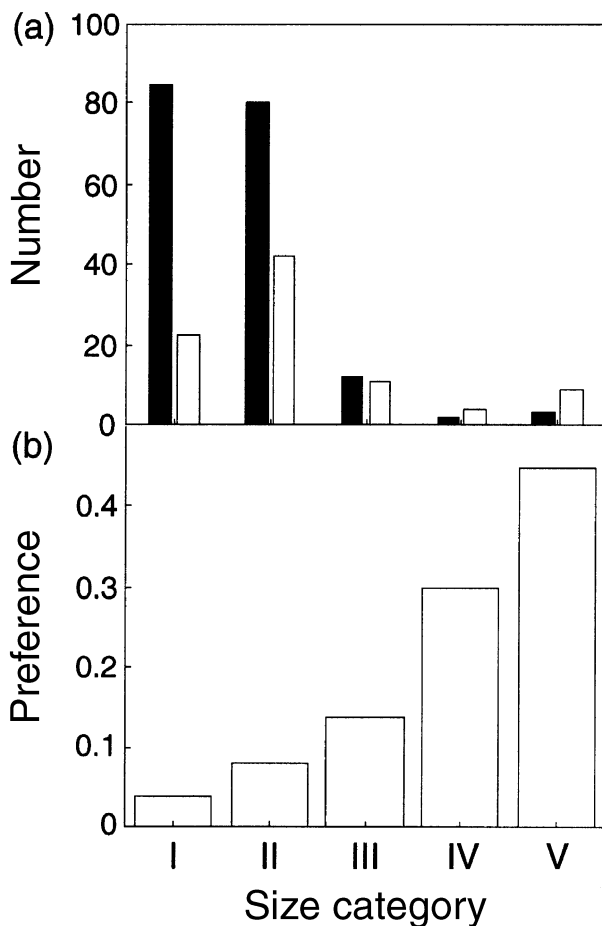
Fig. 1. Preference of *Aphidius colemani* for different size categories of *Aphis glycines* in one of the 10 replicate trials on a soybean leaf. The trial illustrated was selected at random using a random number generator; (a) gives the number of aphids in each of the size categories (black bars) and the cumulative number of attacks made by five *A. colemani* (white bars); (b) gives the preference for aphids in the size categories obtained from the data in (a). Preferences were calculated as the ratio of the number of aphids attacked in each category to the number present in each category, then standardised so that the sum of preference values equals 1. Size categories are: I (<0.625 mm), II (0.625–0.781 mm), III (0.781–0.9375 mm), IV (0.9375–1.094 mm), and V (>1.094 mm).

variable of interest was the cumulative effect of parasitoids on aphids, rather than the behaviour of individual parasitoids. Pooling observations from the parasitoids foraging on the same leaf mimicked the case of multiple parasitoids visiting a plant in the field and included any possible effect of superparasitism.

The size preferences from all 10 trial leaves were combined to give an average measure of size preference by *A. colemani* (Fig. 2). The preference for the smallest size category is 0.053, while that for the largest size category is 0.34. This implies that, on average, the largest aphids are 6.4 (=0.34/0.053) times more likely to be attacked than are the smallest aphids.
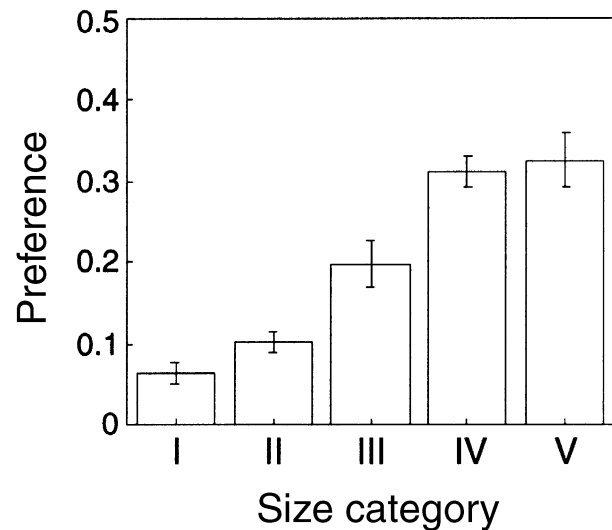

Fig. 2. Preference of *Aphidius colemani* for different size categories of *Aphis glycines*. Preferences were calculated as the ratio of the number of aphids attacked in each category to the number present in each category, then standardised so that the sum of preference values equals 1. These preferences were then averaged among trials. Bars give the standard errors from the 10 trials.

Development time of Aphis glycines. Aphid size, as measured by body length, increased roughly linearly with time until adulthood (Fig. 3). Of the 22 aphids, 17 (77%) reached adulthood 7 days after birth while the remaining five aphids reached adulthood after 8 days.

Fecundity of Aphis glycines. The fecundity of *A. glycines* increased following first reproduction, peaking 6 days after reaching adulthood at an average of four offspring per day. As aphids aged further, fecundity declined
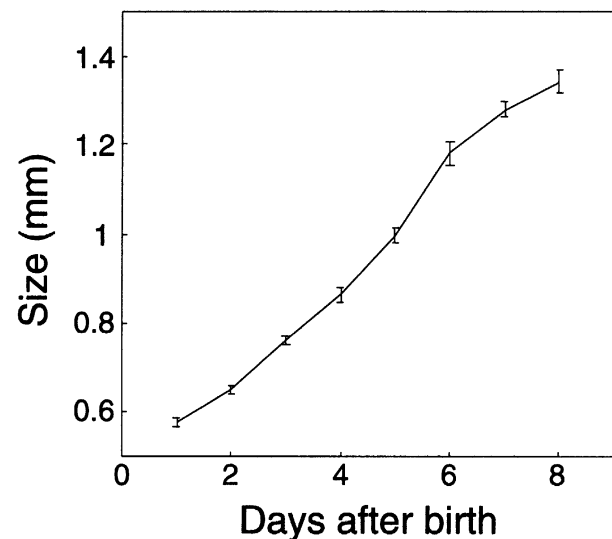

Fig. 3. Growth of 20 *Aphis glycines* from birth to adulthood. Size (±1 SE) is the body length of aphids.

(Fig. 4). The average daily fecundity was 2.56. All aphids survived to 8 days after reaching adulthood, after which mortality increased, with all aphids dying by day 24 (Fig. 4). The average daily survival was 0.858, calculated as the proportion of the surviving population that dies in the next 24-h period averaged over the 24 days of the experiment.

Fecundity of parasitised Aphis glycines. The fecundity of aphids parasitised immediately before moulting to adulthood was compared with the fecundity of unparasitised aphids (Fig. 5). On the first day of reproduction, the fecundity of parasitised aphids was only slightly lower than that of unparasitised aphids, but the fecundity of parasitised aphids declined on the following day, and no aphid reproduced after 3 days following parasitism. Mummies were formed from one aphid on day 7, 17 aphids on day 8, and two aphids on day 9 following parasitism.

Size-structured model of *Aphis glycines* population growth

Data from the experiments on *A. glycines* development and fecundity were used to construct a stage-structured Leslie matrix model of aphid population growth. Stages were based on the five size categories that correspond roughly to instars, and small changes (± 0.1 mm) in the boundaries between categories had little quantitative effect on the output of the model (analyses not presented). The effect of size preference was incorporated by imposing mortality on different size categories in proportion to the size preference shown experimentally for *A. colemani*. To account for continued reproduction of parasitised adult aphids, additional stages were added to the model for adults parasitised 1, 2, and 3 days previously.

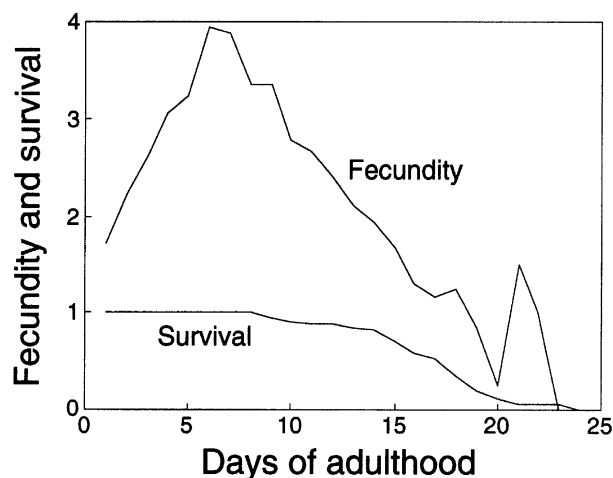The stage-structured model consists of a matrix whose elements give the stage-specific demographic transitions of
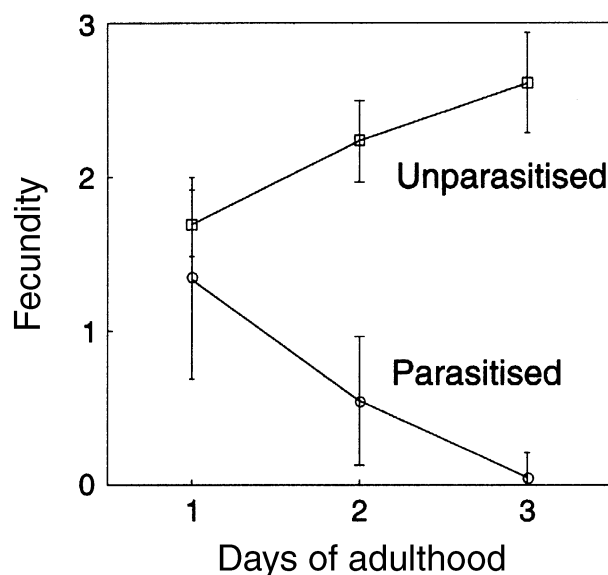

Fig. 5. Daily fecundity of 20 parasitised and 24 unparasitised *Aphis glycines* measured from the day of moulting to adulthood. Bars give ± 1 SE.

the population. This matrix, parameterised from the laboratory experiments, is given in Table 1. Stages S_1–S_5 are the size categories I–V, with S_5 giving the newly moulted adults that have yet to reproduce. Stage A is unparasitised reproductive adults. Stages P_1–P_3 are reproductive adults that were parasitised 1, 2, and 3 days previously. Parameters p_1–p_5 give the stage-specific survival from parasitism on the different stages, and have the form $p_i = \exp(-a_i y)$, where a_i is the preference of parasitoids for aphids in size category i (e.g. Fig. 2) and y is the abundance of parasitoids. The variable y was used as an overall scaling term for the impact of parasitism. The i–jth element of the matrix for the non-reproductive stages (S_1–S_5) gives the probability that an individual moves from stage j to stage i between days t and $t + 1$. For example, the elements in the first column of the matrix were derived from the development experiment; of the aphids in size category I, the proportions that were in categories I, II, and III at the following sample were 0.27, 0.68, and 0.05 respectively. To incorporate parasitism, these values are multiplied by p_1, which assumes that parasitism occurs before aphids graduate to larger size categories. For unparasitised adult survival, the average daily survival was used as calculated from the fecundity experiment. Therefore, adult survival is that obtained under controlled laboratory conditions and does not include other sources of mortality likely to occur in nature. Aphid fecundity appears in the right-hand side of the upper row of the matrix, as reproduction introduces new aphids into the smallest size category. The daily fecundity of unparasitised aphids, A, was obtained from the fecundity experiment, and the fecundity of parasitised aphids, P_1–P_3, was assumed to equal the average fecundity of unparasitised aphids decreased by the proportional reduction in fecundity of

Fig. 4. Daily fecundity and survival of 24 *Aphis glycines* measured from the day of moulting to adulthood to the day of death.

Table 1. Stage-structured model of *Aphis glycines* population growth, including host-size preference. The element in row i and column j gives the transition probability for an individual in stage j at time t to be in stage i at time $t+1$. Blanks represent zeros.

	S_1	S_2	S_3	S_4	S_5	A	P_1	P_2	P_3
S_1	$0.27\,p_1$					2.56	2.30	0.63	0.049
S_2	$0.68\,p_1$	$0.40\,p_2$							
S_3	$0.05\,p_1$	$0.54\,p_2$	$0.26\,p_3$						
S_4		$0.06\,p_2$	$0.70\,p_3$	$0.25\,p_4$					
S_5			$0.04\,p_3$	$0.75\,p_4$	$0.48\,p_5$				
A					$0.52\,p_5$	$0.86\,p_5$			
P_1					$1-p_5$	$0.86\,(1-p_5)$			
P_2							0.86		
P_3								0.86	

newly moulted adults caused by parasitism (Fig. 3). This assumption supposes that the proportional reduction in fecundity caused by parasitism to newly reproductive adults is the same as the proportional reduction caused by parasitism to older females. Survival of parasitised adults caused by factors other than parasitism was assumed to equal the average survival of unparasitised adults.

In the absence of parasitism ($p_i = 1$ for all i), analysis of the stage-structured model (Caswell, 1989) gives an intrinsic rate of increase of $r = 0.2579$ and a population doubling time of 2.6872 days. This stage-structured model does not incorporate the age-specific survival and fecundity of adults (Fig. 3). In order to determine the possible inaccuracy caused by ignoring age-specific adult survival and fecundity, a stage-structured model was constructed that included 24 stages for adults corresponding to ages 1–24 following moulting to adulthood, with each stage having the survival and fecundity given in Fig. 3. This expanded model gave an estimate of $r = 0.2569$ and a population doubling time of 2.6984 days, which is sufficiently similar to the values obtained from the more simple model to justify using the model including only a single stage for unparasitised reproductive adults (Table 1).

The model was used to compare four cases of parasitism that provide informative contrasts illustrating the consequences of parasitoid host-size preference. The first corresponds to the data obtained in the experiments, with host-size preferences a_i obtained from the observations on *A. colemani* foraging (Fig. 2): a_1–$a_5 = \{0.053, 0.096, 0.19, 0.32, 0.34\}$. The second is the case of no size preference, which is obtained by setting all values of a_i to 0.2. Because aphidiine parasitoids typically prefer small or intermediate instars, a third case was analysed in which size preferences correspond to the preferences that the congener *Aphidius ervi* shows for the five instars of pea aphids as reported by Ives *et al.* (1999): a_1–$a_5 = \{0.1224, 0.2755, 0.3980, 0.1837, 0.0204\}$. In the final case, parasitoids show the preferences measured for *A. colemani* but parasitised adults do not reproduce. The rationale for considering this fourth case is that the continued reproduction of parasitised *A. glycines* will decrease the impact of parasitism on the aphid population growth rate, and this case makes it possible to quantify the magnitude of this effect.

In performing these comparisons, each of the four cases was standardised so that the same proportion of the entire aphid population was parasitised. This was done numerically by finding that value of y which leads to the target overall parasitism rate. Therefore, the comparisons are between cases in which parasitoids attack the same proportion of aphids, but these attacks are distributed differentially among size categories. In reality, the overall success of parasitoids might depend on their size preferences. For example, a parasitoid species that prefers small hosts might achieve an overall higher parasitism rate, because female parasitoids require less time to avoid the defences mounted by larger hosts (Weisser, 1994). Nonetheless, many other factors will affect the parasitism rates of different species. Therefore, the analyses compare hypothetical parasitoids that have the same parasitism rates and differ only in how attacks are distributed among stages.

The intrinsic rate of increase of aphids as a function of the total daily parasitism rate by the four hypothetical parasitoids is shown in Fig. 6a. For size preferences shown by *A. colemani*, a daily parasitism rate of 25% leads to a value of $r = 0$, implying successful aphid control. The size preference shown by *A. colemani* leads to lower values of r than either no size preference or preference for second and third size stages exhibited by *A. ervi*; the overall levels of parasitism required for zero aphid population growth rates are 29 and 31% when there is no preference or *A. ervi* preference respectively. Finally, if parasitised adult aphids could not reproduce after attack by *A. colemani*, suppression of aphid population growth rates would be greater, and an overall parasitism rate of only 18% would be sufficient to achieve $r = 0$. Note that even though the adult aphids preferred by *A. colemani* still reproduce following attack, the preference of *A. colemani* for larger aphids nonetheless leads to greater suppression of aphid population growth rates than either no preference or the preference shown by *A. ervi*.

The analyses producing Fig. 6a assumed no source of mortality other than parasitism and senescence of adults (under laboratory conditions). To mimic other possible sources of mortality in the field (e.g. predation), consider the case in which daily survival of all stages is reduced by 0.8 (Fig. 6b). While this decreases the overall population
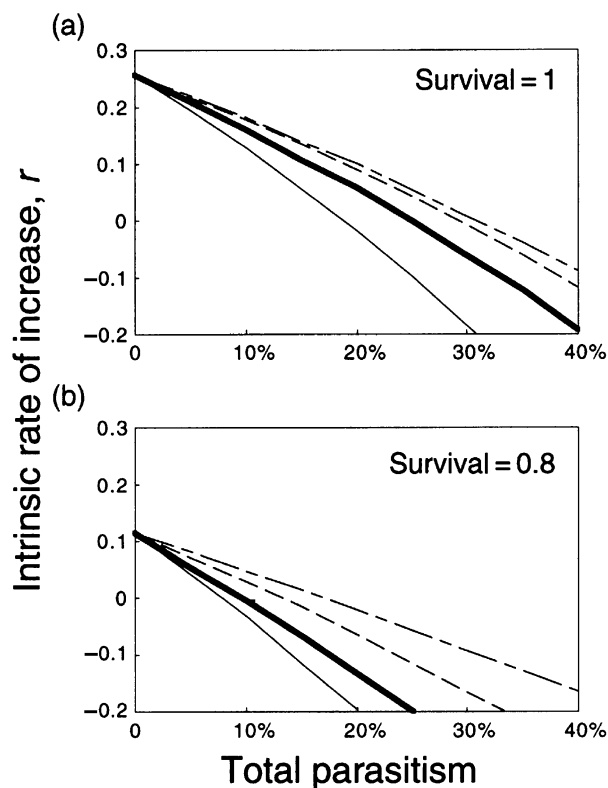
Fig. 6. Estimates of the aphid intrinsic rate of increase, *r*, as a function of the percentage parasitism (all stages combined) per day; (a) gives the case in which background daily survival is 1, (b) gives the case when background survival is 0.8. The four cases shown in each panel are: thick line = *Aphidius colemani* size preference with parasitised aphids reproducing, dashed line = no size preference with parasitised aphids reproducing, dot–dashed line = *Aphidius ervi* size preference with parasitised aphids reproducing, thin line = *A. colemani* size preference with parasitised aphids not reproducing.

growth rate of aphids, causing population suppression at lower overall parasitism levels, the general pattern for the effect of the different size-preference cases remains the same. In fact, additional sources of mortality augment the relative suppression of aphid population growth rates caused by preferring larger aphids. When survival from other sources equals 1 (Fig. 6a), the percentage parasitism required for zero aphid population growth when parasitoids show *A. colemani* size preference relative to *A. ervi* size preference is 0.8 (=25/31%), while this ratio is 0.5 (=9/18%) when survival from other sources is 0.8 (Fig. 6b).

Discussion

In contrast to other aphidiine parasitoids that show a host-size preference for small or intermediate hosts (Liu *et al.*, 1984; Sequeira & Mackauer, 1987, 1992a; Weisser, 1994; Mackauer *et al.*, 1996; Ives *et al.*, 1999; Chau & Mackauer, 2000), *A. colemani* exhibited a preference for attacking large *A. glycines* hosts. Although the size preference of

A. colemani on other hosts has not been investigated, the size range of *A. glycines* is similar to that of two other common hosts, *A. gossypii* and *Myzus persicae*, which have apterae size ranges of 0.9–1.8 and 1.2–2.1 mm respectively (Blackman & Eastop, 2000); *A. glycines* apterae are reported to have an average size of 1.89 mm (Takahashi *et al.*, 1993), although the adults from the development experiment in the present study had a mean length of 1.31 ± 0.016 mm, which is nonetheless within the published size ranges of *A. gossypii* and *M. persicae*. This suggests that the preference of *A. colemani* for larger-sized *A. glycines* was not the result of *A. glycines* being an unusually small host species.

Analysis of the stage-structured model for *A. glycines* showed that this preference for larger hosts reduces the aphid population growth rate more than would occur if *A. colemani* showed either no size preference or the size preference exhibited by *A. ervi*. The explanation for this result is that, by attacking larger aphids, *A. colemani* removes individuals with the highest reproductive value in the population (Caswell, 1989; Gotelli, 1998). The higher reproductive value of larger aphids is the consequence of larger aphids being reproductive or nearly reproductive. Therefore, these individuals are contributing to the aphid population growth rate either currently or with a short time delay. Smaller aphids require more time before they become reproductive, and therefore have lower reproductive value. The difference in reproductive value between large and small aphids is more than enough to offset the continued reproduction of parasitised adult aphids. Even though reproduction of parasitised aphids reduces the suppression of the aphid population growth rate (Fig. 6), a preference for larger aphids nonetheless leads to greater suppression.

This mechanism affecting the impact of host-size preference on the host population growth rate is qualitatively distinct from processes investigated by previous models that include host-size preferences or invulnerable host stages. The analyses in the present manuscript address the density-independent intrinsic rate of increase of the host population, rather than either the stability of host–parasitoid dynamics or the equilibrium density of the host population. Murdoch *et al.* (1987) showed that an invulnerable stage class can stabilise otherwise unstable host–parasitoid dynamics, especially when the invulnerable stage class is adult rather than juvenile hosts. Thus, for host–parasitoid systems in which host suppression requires stably maintained parasitism pressure, biological control may be favoured by parasitoids that attack juvenile rather than adult hosts. For many aphid species, however, the concept of stability is difficult to apply in biological control, at least at the scale of individual fields. In many crops, aphid pests are characterised by boom-and-bust dynamics, in which suppression of aphid population outbreaks and damage is dictated largely by the ability of natural enemy pressure to keep up with exponentially growing aphid populations (e.g. Rauwald & Ives, 2001). In such situations, reducing the aphid intrinsic rate of increase may limit the transient explosion of the aphid population and maintain better within-field control.

Previous theoretical work has also examined the consequences of host-size selection on competition between parasitoids and the reduction in the equilibrial population density of the host (Godfray & Waage, 1991; Briggs, 1993; Murdoch *et al.*, 1996). In these models, attacking juvenile stages of a host often gives a parasitoid species a competitive advantage over species that attack adult stages, and attacking juvenile stages leads to lower equilibrium host population densities. This contrasts the effect demonstrated here that attacking adults will lead to lower intrinsic rates of increase. An explanation for this contrast is that the equilibrium host density is dictated not only by the reduction of hosts from parasitism but also by the reproductive success of the parasitoid. When there is background host mortality from other factors, parasitoids may increase their reproductive success by attacking hosts earlier in development before this background mortality reduces host numbers (Murdoch *et al.*, 1996). The resulting increase in parasitoid reproduction will in turn increase the density of parasitoids relative to hosts and consequently reduce the host equilibrium population density. In the analyses of the present article, only the effect of parasitism on the density-independent host intrinsic rate of increase was assessed, so parasitoid reproduction was not included. For aphid species that exhibit exponential growth in agricultural fields, an effect of host-size selective parasitism on the aphid intrinsic rate of increase may be more predictive of pest outbreaks than an effect calculated for an equilibrium population density.

The effect of host-size preferences by parasitoids on the host intrinsic rate of increase is apparently under-appreciated. The only discussion of this effect in the literature was given by Mondor and Roitberg (2000), who demonstrated using a model of aphid–parasitoid interactions, that variation in parasitoid preference among aphid instars may change the peak density achieved by aphids during a host–parasitoid cycle, but does not change the stability of the dynamics qualitatively. As discussed above, host-size preferences may change the stability of other types of host–parasitoid system, and may also affect the equilibrium density of the host in systems in which host–parasitoid dynamics are stable. Thus, there is clearly no simple recommendation for the possible benefits of preferences for juvenile versus adult hosts for parasitoids used in biological control. Furthermore, numerous other factors, such as climatic matching and overall searching efficiency, will affect the success of biological control agents. Nonetheless, host-size preferences by parasitoids have been studied extensively from a behavioural and evolutionary perspective, and this considerable existing information on size preferences may be useful as one of many other types of information to determine the potential efficacy of parasitoid species in biological control.

Acknowledgements

References

Battaglia, D., Poppy, G., Powell, W., Romano, A., Tranfaglia, A. & Pennacchio, F. (2000) Physical and chemical cues influencing the oviposition behaviour of *Aphidius ervi*. *Entomologia experimentalis et applicata*, **94**, 219–227.

van den Berg, H., Ankasah, D., Muhammad, A., Rusli, R., Widayanto, H.A., Wirasto, H.B. *et al.* (1997) Evaluating the role of predation in population fluctuations of the soybean aphid *Aphis glycines* in farmers' fields in Indonesia. *Journal of Applied Ecology*, **34**, 971–984.

Blackman, R.L. & Eastop, V.F. (2000) *Aphids on the World's Crops: an Identification and Information Guide*. John Wiley & Sons, Chichester, U.K.

Briggs, C.J. (1993) Competition among parasitoid species on a stage-structured host and its effect on host suppression. *American Naturalist*, **141**, 372–397.

Briggs, C.J., Nisbet, R.M. & Murdoch, W.W. (1993) Coexistence of competing parasitoid species on a host with variable life cycles. *Theoretical Population Biology*, **44**, 341–373.

Burd, J.D., Shufran, K.A., Elliott, N.C., French, B.W. & Prokrym, D.A. (2001) Recovery of imported hymenopterous parasitoids released to control Russian wheat aphids (Homoptera: Aphididae) in Colorado. *Southwestern Entomologist*, **26**, 23–31.

Caswell, H. (1989) *Matrix Population Models*. Sinauer Associates, Inc., Sunderland, Massachusetts.

Chau, A. & Mackauer, M. (2000) Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): a preference for small pea aphids. *European Journal of Entomology*, **97**, 347–353.

Chau, A. & Mackauer, M. (2001a) Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): assessing costs and benefits. *Canadian Entomologist*, **133**, 549–564.

Chau, A. & Mackauer, M. (2001b) Preference of the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae) for different aphid species: female choice and offspring survival. *Biological Control*, **20**, 30–38.

Chow, A. & Mackauer, M. (1991) Patterns of host selection by 4 species of aphidiid (Hymenoptera) parasitoids – influence of host switching. *Ecological Entomology*, **16**, 403–410.

Cloutier, C. (1984) The effect of host density on egg distribution by the solitary parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). *Canadian Entomologist*, **116**, 805–811.

Elliott, N.C., Burd, J.D., Armstrong, J.S., Walker, C.B., Reed, D.K. & Peairs, F.B. (1995) Release and recovery of imported parasitoids of the Russian wheat aphid in eastern Colorado. *Southwestern Entomologist*, **20**, 125–129.

Gallepp, G. (2001) UW Soybean Plant Health: UW-Madison experts find soybean pest in Wisconsin. UW-Extension, 14 April 2001. http://www.plantpath.wisc.edu/soyhealth/newaphid.htm

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

Godfray, H.C.J. & Waage, J.K. (1991) Prediction modelling in biological control: the mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *Journal of Applied Ecology*, **28**, 434–453.

Gotelli, N.J. (1998) *A Primer of Ecology*. Sinauer Associates, Sunderland, Massachusetts.

Halbert, S.E., Zhang, G.X. & Pu, Z.Q. (1986) Comparison of sampling methods for alate aphids and observations of epidemiology of soybean mosaic-virus in Nanjing, China. *Annals of Applied Biology*, **109**, 473–483.

Hopper, K.R. & King, E.G. (1984) Preference of *Microplitis cropeipes* (Hymenoptera: Braconidae) for instars and species of *Heliothis* (Lepidoptera: Noctuidae). *Environmental Entomology*, **13**, 1145–1150.

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

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

Lewis, W.J. & Redlinger, L.J. (1969) Suitability of eggs of the almond moth *Cadra cautella* of various ages for parasitism by *Trichogramma evansecens*. *Annals of the Entomological Society of America*, **62**, 1482–1484.

Liu, S.S., Morton, R. & Hughes, R.D. (1984) Oviposition preferences of a hymenopterous parasite for certain instars of its aphid host. *Entomologia experimentalis et applicata*, **35**, 249–254.

Mackauer, M. (1973) Host selection and host suitability in *Aphidius smithi*. *Perspectives in Aphid Biology* (ed. by A. D. Lowe), pp. 20–29. Entomological Society of New Zealand, Christchurch.

Mackauer, M. (1983) Quantitative assessment of *Aphidius smithi* (Hymenoptera: Aphidiidae): fecundity, intrinsic rate of increase, and functional response. *Canadian Entomologist*, **115**, 399–416.

Mackauer, M. & Chau, A. (2001) Adaptive self superparasitism in a solitary parasitoid wasp: the influence of clutch size on offspring size. *Functional Ecology*, **15**, 335–343.

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

McBrien, H. & Mackauer, M. (1991) Decision to superparasitize based on larval survival: competition between aphid parasitoids: *Aphidius ervi* and *Aphidius smithi*. *Entomologia experimentalis et applicata*, **59**, 145–150.

Michaud, J.P. & Mackauer, M. (1995) Oviposition behavior of *Monoctonus paulensis* (Hymenoptera, Aphidiidae) – factors influencing reproductive allocation to hosts and host patches. *Annals of the Entomological Society of America*, **88**, 220–226.

Mondor, E.B. & Roitberg, B.D. (2000) Individual behaviour and population dynamics: lessons from aphid parasitoids. *Entomologia experimentalis et applicata*, **97**, 75–81.

Murdoch, W.W., Briggs, C.J. & Nisbet, R.M. (1996) Competitive displacement and biological control in parasitoids: a model. *American Naturalist*, **148**, 807–826.

Murdoch, W.W., Nisbet, R.M., Gurney, W.S.C. & Reeve, J.D. (1987) An invulnerable age class and stability in delay-differential parasitoid–host models. *American Naturalist*, **129**, 262–282.

Nechols, J.R. & Kikuchi, R.S. (1985) Host selection of the spherical mealybug (Homoptera: Pseudococcidae) by *Anagyrus indicus* (Hymenoptera: Encyrtidae): influence of host stage on parasitoid oviposition, development, sex ratio and survival. *Environmental Entomology*, **14**, 32–37.

Nicol, C.M.Y. & Mackauer, M. (1999) The scaling of body size and mass in a host parasitoid association: influence of host species and stage. *Entomologia experimentalis et applicata*, **90**, 83–92.

Rauwald, K.S. & Ives, A.R. (2001) Biological control in disturbed agricultural systems and the rapid re-establishment of parasitoids. *Ecological Applications*, **11**, 1224–1234.

Sequeira, R. & Mackauer, M. (1987) Host instar preference of the aphid parasite *Praon pequodorum* (Hymenoptera, Aphidiidae). *Entomologia Generalis*, **12**, 259–265.

Sequeira, R. & Mackauer, M. (1992a) Covariance of adult size and development time in the parasitoid wasp *Aphidius ervi* in relation to the size of its host, *Acyrthosiphon pisum*. *Evolutionary Ecology*, **6**, 34–44.

Sequeira, R. & Mackauer, M. (1992b) Nutritional ecology of an insect host–parasitoid association: the pea aphid–*Aphidius ervi* system. *Ecology*, **73**, 183–189.

Sequeira, R. & Mackauer, M. (1993) The nutritional ecology of a parasitoid wasp, *Ephedrus californicus* Baker (Hymenoptera, Aphidiidae). *Canadian Entomologist*, **125**, 423–430.

Takahashi, S., Inaizumi, M. & Kawakami, K. (1993) Life-cycle of the soybean aphid *Aphis glycines* Matsumura in Japan. *Japanese Journal of Applied Entomology and Zoology*, **37**, 207–212.

Völkl, W. & Mackauer, M. (2000) Oviposition behaviour of aphidiine wasps (Hymenoptera: Braconidae): morphological adaptations and evolutionary trends. *Canadian Entomologist*, **132**, 197–212.

Wang, C.L., Siang, N.I., Chang, G.S. & Chu, H.F. (1962) Studies on the soybean aphid, *Aphis glycines* Matsumura. *Acta Entomologica Sinica*, **11**, 31–43.

Wang, X.G. & Liu, S.S. (2002) Effects of host age on the performance of *Diadromus collaris*, a pupal parasitoid of *Plutella xylostella*. *Biocontrol*, **47**, 293–307.

Weisser, W.W. (1994) Age-dependent foraging behavior and host-instar preference of the aphid parasitoid *Lysiphlebus cardui*. *Entomologia experimentalis et applicata*, **70**, 1–10.

Weisser, W.W. (1995) Within-patch foraging behaviour of the aphid parasitoid *Aphidius funebris*: plant architecture, host behaviour and individual variation. *Entomologia experimentalis et applicata*, **76**, 133–141.

Weisser, W.W., Houston, A.L. & Völkl, W. (1994) Foraging strategies in solitary parasitoids: the trade-off between female and offspring mortality risks. *Evolutionary Ecology*, **8**, 587–597.