

Intraguild predation in larval parasitoids: implications for coexistence

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Summary

1. Many coexisting parasitoids interact via intraguild predation (IGP); however, in IGP theory without stage structure the intraguild predator and intraguild prey coexist via this mechanism over only a relatively narrow region of parameter space. A recent formulation of IGP theory with a stage of the intraguild prey species that is invulnerable to attack by the intraguild predator shows that coexistence between guild members can occur across a much broader range of resource productivity than is predicted by IGP theory without stage structure. These general theoretical predictions are used to explore the implications for coexistence of *Aphytis melinus* (DeBach) and *Encarsia perniciosi* (Tower), a pair of parasitoids that coexist on California red scale.

2. Reanalysis of a published laboratory competition experiment between two parasitoid species suggests that *Aphytis*, an ectoparasitoid, survives at a lower rate when the reparasitized host contains a more developed juvenile endoparasitoid (*Encarsia*). This pattern is contrary to a common assumption that ectoparasitoids always consume endoparasitoids in a shared host, and may affect coexistence. The experiment covered only the first ~30% of the *Encarsia* development period and did not describe the outcome for *Encarsia*, so the dynamic effects of this interaction in the context of IGP remain unclear. In addition, *Encarsia* is capable of parasitizing much younger hosts than is *Aphytis*, which the experiment did not examine.

3. The experiment was repeated, and extended to cover the full developmental duration of *Encarsia*. An additional experiment was performed to explore whether *Encarsia* could pre-empt *Aphytis* by attacking younger hosts. *Aphytis* juvenile survival was found to decrease as a function of the age of the juvenile *Encarsia* onto which it was laid. When *Encarsia* parasitized very young hosts, it was increasingly invulnerable to attack by *Aphytis* and increasingly more likely to survive to emergence. However, until the formation of an invulnerable pseudomolt, *Encarsia* was always killed in larger hosts, regardless of its age at the time of *Aphytis* attack.

4. According to stage-structured IGP theory, the decline in *Aphytis* success combined with an invulnerable *Encarsia* stage may promote coexistence in this system.

Key-words: *Aphytis*, biological control, ectoparasitoid, *Encarsia*, endoparasitoid.

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Introduction

Intraguild predation is common in ecological systems (Polis, Myers & Holt 1989; Fig. 1). Smith (1929) argued that coexistence occurred in many biological control systems via a balance between species' in-host pred-

atory ability (i.e. intraguild predation, IGP), and extrinsic exploitative ability (i.e. ability to find hosts and produce progeny). This trade-off incorporating IGP has recently received general theoretical treatment in unstructured and stage-structured models (Briggs 1993; Holt & Polis 1997; Diehl & Feissel 2000; Mylius *et al.* 2001).

Theory has shown that the trade-off in systems with IGP works to promote coexistence as follows. As in simple competition theory, the better resource exploiter reduces the resources below the point at which

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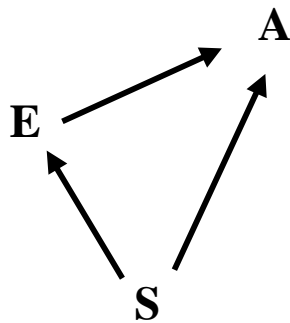


Fig. 1. Intraguild predation is a combination of exploitative competition by guild members for a shared resource (S) and predation on one guild member (E) by the other (A). For coexistence to occur in a moderately productive system, E must be a superior exploiter of S (relative to A), and to compensate for its poorer exploitative ability, A must be capable of using E as a second resource.

the worse exploiter can replace itself. Without a trade-off, this would drive the worse exploiter to extinction. Coexistence can occur in systems with IGP because the worse exploiter (A in Fig. 1) uses the better exploiter, or 'intraguild prey' (E in Fig. 1), as a second resource. But the outcome of this interaction is dependent upon resource productivity: coexistence will occur only at intermediate productivity (Holt & Polis 1997). Theory predicts that only the intraguild prey species will persist at low productivity because it can successfully produce progeny on fewer resources, while the intraguild predator will drive the intraguild prey to extinction at high productivity via a combination of competition and predation (Holt & Polis 1997).

A review of biological control communities reveals that parasitoids that are resource specialists but have differing larval feeding strategies, endoparasitic and ectoparasitic, may often interact via some form of IGP (e.g. Flanders 1971). (Endoparasitoids lay their eggs inside the host body, ectoparasitoids lay their eggs on the host body.) In the entomological literature, it is generally accepted that when eggs of an ectoparasitoid and an endoparasitoid are laid in the same host, the ectoparasitoid will always emerge, having consumed the endoparasitoid (e.g. Flanders 1971; Godfray 1994). Studies have shown that the exploitative ability of endoparasitoids is comparatively higher than that of ectoparasitoids in many systems, as well (e.g. Flanders 1971; Force 1971). Taken together, these observations suggest that IGP is a possible mechanism for coexistence in many parasitoid communities.

Although many parasitoids interact via some form of intraguild predation, several aspects of host-parasitoid systems are not incorporated in a unified way into current IGP theory. In particular, endoparasitoids often can attack younger hosts than can ectoparasitoids (Askew 1974), and many developing endoparasitoids mummify their hosts (Godfray 1994), in some cases creating a hard shell invulnerable to re-parasitism (Taylor 1935).

California red scale and its parasitoids provide an example of a system in which the pattern of both ectoparasitoid success and endoparasitoid invulnerability may not follow current IGP model formulations. My reanalysis of data on these parasitoids (data from Yu, Luck & Murdoch 1990; see below, Reanalysis of a Prior Study), suggests that, in addition to (a) early endoparasitoid attacks and (b) an invulnerable endoparasitoid moult stage (c) the ectoparasitoid's probability of survival decreases, at least initially, as the endoparasitoid's age increases. These results suggest that the endoparasitoid may have an increasing probability of survival if attacks by the ectoparasitoid are delayed, although these data were not presented in this study.

The relative timing of attacks by ectoparasitoids and endoparasitoids that can lead to invulnerable refuges for endoparasitoids and declining survival of ectoparasitoids may have important ramifications for coexistence in parasitoid systems. (a) In a host-parasitoid IGP formulation, an advantage is gained, under most circumstances, by attacking younger host stages, so that, all other parameters being equal, the species attacking younger hosts would extirpate the species attacking later host stages (Briggs 1993). (b) In a stage-structured IGP model of lake fish, Mylius *et al.* (2001) show that an invulnerable stage in the intraguild prey species leads to coexistence between guild members across a much broader range of resource productivity than in unstructured models. In addition (c) general IGP theory suggests that, as the intraguild predator's conversion efficiency from attacks on the intraguild prey declines, the coexistence region shrinks (Holt & Polis 1997).

Here I focus on the details of intraguild predation in the California red scale system because, as IGP models suggest, the specific details of this interaction may have broad implications for our understanding of competitive coexistence and resource dynamics. I assess the outcome of direct interaction between the ectoparasitoid *Aphytis melinus* and the endoparasitoid *Encarsia perniciosi*, and their shared resource, California red scale. I report on a laboratory investigation to address three questions. (1) Can the endoparasitoid ever survive parasitism by the ectoparasitoid? (2) Can the endoparasitoid render a host unavailable to the ectoparasitoid by parasitizing very young scales? (3) Does the outcome of IGP depend on the age of the endoparasitoid when the ectoparasitoid attacks?

NATURAL HISTORY

Aonidiella aurantii (Maskell), California red scale, is a homopteran armored scale. It was introduced accidentally into the United States in the late 1800s and rapidly became a pest of citrus crops (Clausen 1978). It is capable of infesting all above-ground parts of a citrus tree, and can cause mortality in extreme infestations. Details of red scale biology can be found in Ebeling

(1959) and Bodenheimer (1951). Development from crawler to crawler-producing female takes $\sim 620^\circ$ days (i.e. ~ 48 days at 25°C , Yu 1986). Juvenile females develop through three instars and two intervening moult stages prior to fertilization. Males develop through two instars and a moult followed by a pupal stage. Males emerge as winged adults after $\sim 350^\circ$ days (~ 27 days at 25°C), concurrent with the female third instar. The diameter of a red scale grows with increasing age.

Aphytis melinus (DeBach) is an introduced natural enemy of red scale. Its natural history is described in detail in Rosen & DeBach (1979). It is a hymenopteran ectoparasitoid that can successfully produce progeny in red scale host individuals older than $\sim 180\text{--}200^\circ$ days (early 2nd instar stage, ~ 14 days at 25°C), though it does not attack hosts during either moult or mature scale stages (Yu & Luck 1988). Development from egg to adult takes $\sim 200^\circ$ days (~ 2 weeks at 25°C , Yu 1986). *Aphytis* first injects a toxin to paralyse the host and then lays an egg on the host body, under the cover. The larva then consumes the host's body from the outside.

Encarsia perniciosi (Tower) is another introduced natural enemy of red scale. Less is known about this species, although developmental and life-history information can be found in DeBach & Sundby (1963), Yu *et al.* (1990), McClain, Rock & Stinner (1990) and Baroffio (1993, 1997). *Encarsia* is a solitary hymenopteran endoparasitoid that can successfully parasitize all juvenile red scale stages older than $\sim 50^\circ$ days (1st instar stage, ~ 4 days at 25°C). This is notably earlier than *Aphytis*, and this advantage represents approximately 40% of the entire *Encarsia* juvenile period ($\sim 320^\circ$ days or ~ 24 days at 25°C). *Encarsia* lays an egg within the host body, and the larva consumes the host from the inside. It does not paralyse the host: its larval development depends on the host's physiology and development. At $270\text{--}300^\circ$ days *Encarsia* causes the host to form a 'pseudomoult', a hard shell inside of which the larva pupates and completes its development to adult.

When eggs of both species are laid on the same host, at most one parasitoid species will successfully emerge from the contested scale. Finally, each of the three species in this system has a developmental threshold at $10\text{--}12^\circ\text{C}$ (Yu 1986; McClain *et al.* 1990; Baroffio 1993), so degree-days per degree C are similar for each species.

REANALYSIS OF A PRIOR STUDY

Yu *et al.* (1990) performed an experiment to determine the ability of *Aphytis* to successfully reparasitize hosts containing a developing juvenile *Encarsia*. On each successive day of the experiment, they watched *Aphytis* females parasitize a subset of hosts that had been previously parasitized by *Encarsia* as well as unparasitized control hosts of the same age, and measured juvenile

Aphytis mortality rates. *Aphytis* were given hosts containing *Encarsia* juveniles that had developed for 0, 1, 2, 4, 6 or 7 days at 27°C . The results yield the probability of *Aphytis* emergence from scales containing an endoparasitoid vs. the probability for emergence in previously unparasitized scales.

The authors did not calculate the changing probability of *Aphytis* success when faced with increasingly older *Encarsia* juveniles. In a reanalysis of these data, I found that the probability an *Aphytis* will emerge decreased when it attacked scales containing older *Encarsia* juveniles (Fig. 2a, Statistical Analysis, below). This result suggests that the endoparasitoid can have a negative effect on the success of the attacking ectoparasitoid if it can parasitize a host even a few days prior to the ectoparasitoid.

While the data from this study suggest an interesting pattern that is contrary to the simplifying assumptions in IGP theory for parasitoid systems, some important details are missing. For example, no data are available on the effect of *Encarsia* age on its subsequent emergence after *Aphytis* attack. In addition, this study assessed *Aphytis* success after a maximum *Encarsia* development of $\sim 100^\circ$ days which is only $\sim 30\%$ of *Encarsia* juvenile development. Finally, the results of this study do not determine whether *Encarsia* can pre-empt *Aphytis* if *Encarsia* capitalizes on its ability to successfully parasitize very young hosts.

Methods

I ran two concurrent $2 \times k$ factorial experiments in which *Aphytis* females were presented with scale. The factors were scale state (previously parasitized by *Encarsia* and not previously parasitized), and scale age (and *Encarsia* larval age) at the time of presentation. The response variables were the survival of *Aphytis* and *Encarsia*. The '1st instar experiment' examined whether *Encarsia* could fully preempt *Aphytis* by laying eggs in extremely young hosts and gaining a developmental advantage before *Aphytis* was capable of parasitizing these hosts. In this experiment, *Encarsia* parasitized red scales when the scales were 4 days old ($\sim 50^\circ$ days at 25°C), and subsets of these parasitized scales were reparasitized by *Aphytis* at 13, 14, 15, 16, 17, 19 and 21 days (Table 1). On each day, *Aphytis* also parasitized previously unparasitized scales of the same age. The '2nd instar experiment' repeated the Yu *et al.* (1990) study, but covered the entire *Encarsia* developmental period. Half of the scales on a lemon were parasitized by *Encarsia* at 14 days ($\sim 180^\circ$ days at 25°C), and subsets of these were reparasitized by *Aphytis* at 14, 15, 16, 18, 20, 23, 24, 26 and 28 days (Table 1). *Aphytis* also parasitized a subset of the previously unparasitized scales on each of these days.

The 1st instar experiment consisted of 10 replicate lemons each containing all treatments and controls (Table 1). The number of scales per treatment on each lemon was variable because of experimental logistics;

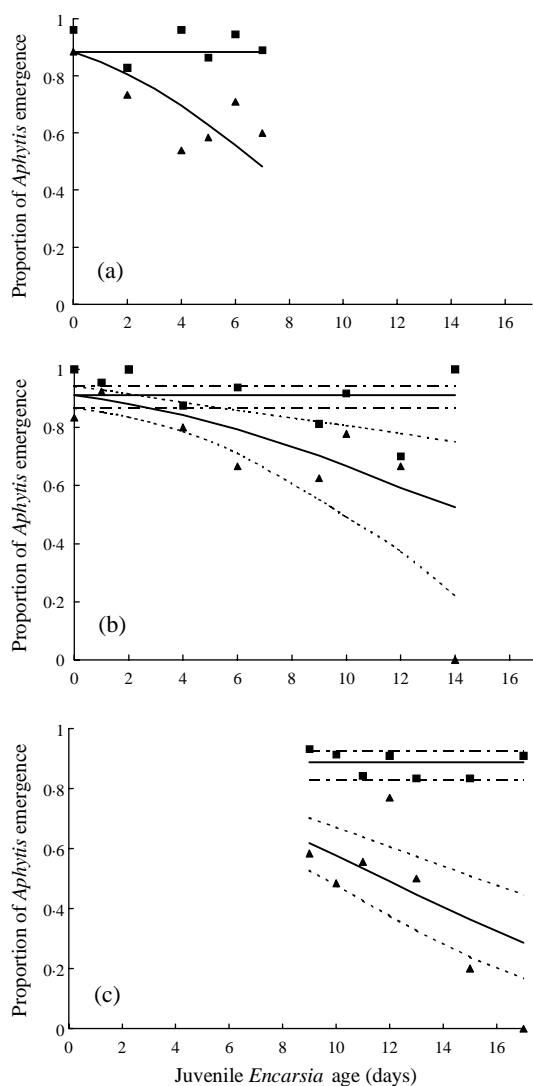


Fig. 2. *Aphytis* probability of emergence from hosts previously attacked by *Encarsia* (▲) declines with the age of the *Encarsia* at the time of *Aphytis* attack relative to *Aphytis* developing alone in a host of the same age (■). The first panel (a) shows a reanalysis of previously published results (Yu *et al.* 1990). In the current experiment, *Aphytis* probability of emergence from scales attacked by *Encarsia* later in development (i.e. 14 days or ~180° days, (b), ▲, *n* = 67) is initially unaffected by *Encarsia* presence, but declines with time compared to *Aphytis*-control scales ((b), ■, *n* = 146). In contrast, *Aphytis* probability of emergence from scales attacked by *Encarsia* early in development (i.e. 4 days or ~50° days; (c), ▲, *n* = 85) is initially > 25% lower than *Aphytis* developing alone in a scale ((c), ■, *n* = 115). Dotted lines represent the 95% CI for the logistic regression model, and each symbol represents the proportion emergence across all replicates.

however, overall there were a total of 1118 scales followed throughout the course of this experiment. The 2nd instar experiment had 9 replicate lemons each containing all treatments and controls (Table 1). As in the 1st instar experiment, the number of scales in each treatment was variable among lemons; however, I tracked a total of 886 scales through the course of this experiment. On each lemon, adjacent scales were grouped, and scale groups were randomly assigned to treat-

ments. Individual scales within each group were treated as repeated measures (see Statistical Analysis, below).

Scale were grown on lemons at 25 °C (~13–15° days day⁻¹) until the day of the *Encarsia* introduction at which point the lemons were moved into the experimental chamber. Both experiments were conducted at 29 °C (±0.74 °C) (~17–19° days day⁻¹) and r.h. 49.3% (±4.3%) in a walk-in constant temperature chamber. Temperature and humidity were recorded each minute throughout the study using a HOBO Pro RH/temp logger (Onset Computer Corporation, Pocasset, MA). Because degree-days for all three species are similar, I will present results in terms of days, rather than degree-days, for simplicity.

ENCARSIA INTRODUCTIONS

A 2-day-old honey-fed female *Encarsia* was placed in an arena on a lemon with about nine adjacent scales. I recorded each scale parasitized by an *Encarsia* female. When she parasitized at least five scales within a treatment or showed a lack of interest in parasitism, she was removed from the lemon. Any scales remaining unparasitized in the treatment group also were removed. All *Encarsia* parasitism on a lemon took place on a single day thus all *Encarsia* juveniles on each experimental lemon were the same developmental age. Scale were 4 days older than the *Encarsia* juvenile they contained in the 1st instar experiment and 14 days older in the 2nd instar experiment (Table 1).

APHYTIS INTRODUCTIONS

Scales containing *Encarsia* ('IGP' scales) were exposed to a 2-day-old, mated, honey-fed *Aphytis* female a known number of days after the *Encarsia* parasitism (Table 1), and the *Aphytis* female was observed as she parasitized each scale. I refer to the difference between *Encarsia* larval age and *Aphytis* larval age as the 'Lag'.

Because scale hosts, as well as *Encarsia* larvae, were ageing throughout the experiment, it also was necessary to track the probability for successful *Aphytis* emergence in the absence of *Encarsia*. Every time I introduced *Aphytis* onto scales containing *Encarsia* larvae, I also introduced *Aphytis* onto a set of previously unparasitized scales of the same age ('*Aphytis*-control' scales) to observe the *Aphytis* emergence rate from parasitized and unparasitized hosts at each scale developmental stage. For comparison with the IGP scales, I refer to the control scales by 'Lag' as well.

Parasitized scales were examined under the microscope daily for *Encarsia* and *Aphytis* pupae. The most rapidly developing *Encarsia* juveniles emerged after 18 days, so all scales with visibly developing *Encarsia* and *Aphytis* pupae were recorded and removed before this time, then stored until emergence. For scales in which the outcome was not clear at 17 days, I observed them (without manipulating them) each day until I could clearly determine the outcome (e.g. *Aphytis*

Table 1. Experimental design for both experiments. Mature *Encarsia* females parasitized all IGP and *Encarsia*-control scales on Lag 0 of both experiments. *Aphytis* females parasitized a random subset of IGP and *Aphytis*-control scales on each Lag listed. Scale age represents the number of days of host development since settling, and approximate developmental stage of both female and male red scale hosts is tabulated

Scale age (days)	Female scale stage	Male scale stage	Lag*	
			1st instar experiment	2nd instar experiment
13	2I	2I	9	
14	2I	2I	10	0
15	2I/2M	2I	11	1
16	2M	2I	12	2
17	2M	2I/PP	13	–
18	2M	PP	–	4
19	2M/3I	PP/PU	15	–
20	2M/3I	PU	–	6
21	3I	PU	17	–
23	3I	WG		9
24	3I	–		10
26	3I	–		12
28	3I/MF	–		14

*Age (in days) of *Encarsia* larva at the time of *Aphytis* parasitism. *Aphytis*-control scales (no *Encarsia* present) that were exposed to *Aphytis* attack on the same day are referred to using 'Lag' as well.

pupal development, *Encarsia* pseudomolt formation, scale mortality, etc.). By the end of the experiment, I had recorded the fate of each scale (live, both scale and parasitoid(s) dead, *Aphytis* emerged, *Encarsia* emerged).

STATISTICAL ANALYSIS

To determine the probability of *Aphytis* emergence in my own experiments as well as that of Yu *et al.* (1990), I included only scales parasitized by both *Aphytis* and *Encarsia* (IGP scales) or scales parasitized by *Aphytis* alone (*Aphytis*-control scales). Host mortality (from causes other than parasitism) was low ($11.7 \pm 3.2\%$), and those that died during the course of the experiment without producing a parasitoid were excluded from the analyses, as I could not gain insight into final outcome from these individuals. I also included scales parasitized by *Encarsia* alone (*Encarsia*-control scales) to determine *Encarsia*'s probability of emergence in the absence of IGP. For all statistical analyses, I used SAS (SAS Institute, Cary, NC).

I classified both *Aphytis*'s and *Encarsia*'s probability of success using the logistic regression model:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \beta_{i0} + \beta_{i1}L + \beta_{i2}E + \beta_{i3}L \times E, \quad \text{eqn 1}$$

where p_i is the conditional probability of species i emerging from each Lag and IGP treatment, L represents the number of days of development that *Aphytis* lagged *Encarsia* (Lag), E represents whether or not an *Encarsia* was present, and β_{ij} is the j th regression coefficient for species i . *Encarsia*'s probability of emergence was determined by only the intercept and Lag terms

because both species were present in all scales of this analysis (E always = 1), so the last two terms do not vary and effectively dropped out of this analysis.

In my analyses, I counted each set of up to 10 IGP and control scales on each lemon as repeated measures within a single sample unit. Thus each sample unit produced multiple repeated binomial estimates of emergence success. Because variance in a binomial distribution is known, the ratio between actual data variance and expected variance can be calculated to adjust for measured over- or under-dispersion (McCullagh & Nelder 1989, §4.5). In my analyses the dispersion was always < 1 (under-dispersed).

I examined all nested models for the probability of *Aphytis* success, and selected the most parsimonious model using Atkinson's criterion (McCullagh & Nelder 1989, §3.9). This general criterion for model selection uses the dispersion parameter to modify the deviance function derived from the likelihood statistic. The familiar AIC is a special case of this criterion when dispersion is 1. This criterion provides a quantitative method by which nested models with increasing numbers of parameters can be compared and discounted for parameter inclusion.

Results

EGG-LAYING

While I could not conclusively (destructively) determine whether *Aphytis* or *Encarsia* were laying eggs in the treatment scales, I do have evidence of the magnitude of error in my observation accuracy (i.e. accuracy of correctly identifying egg-laying events) from the control scales. Control scales for *Encarsia* parasitism

had high emergence rates: 88% when attacking 1st instar hosts and 89% when attacking 2nd instar hosts. So, at most, background mortality and observation inaccuracies for *Encarsia* parasitism were 12%.

In addition, *Aphytis* emergence from control scales was 86% for the 1st instar experiment and 90% in the 2nd instar experiment, though the range of success among lags was from 100% to 70% (see *Aphytis*-control results, Fig. 2b,c). Therefore, background mortality and observation inaccuracy were 10–15%, at most. In a small destructive laboratory study, when a 10-day-old *Encarsia* juvenile was present in a scale and a 2-day-old honey-fed *Aphytis* female was introduced onto that scale, the behaviour I called 'parasitism' resulted in an *Aphytis* egg being laid in 9 of 10 trials.

These results, taken together, leave me reasonably sure that the decrease in *Aphytis* success in scales previously parasitized by *Encarsia* was due to direct interaction with an *Encarsia* juvenile, not misidentification of parasitism or mortality of *Aphytis* juveniles independent of direct interaction with *Encarsia*.

CONSISTENCY OF RESULTS AMONG EXPERIMENTS

A comparison of Fig. 2a and the first 6 days of Fig. 2b shows a qualitative match between the results of the 2nd instar experiment and the results of the Yu *et al.* (1990) experiment. Both experiments suggest that the probability for *Aphytis* success is depressed by 15–20% compared to its success in control scales of the same age. My results show a somewhat higher success rate by *Aphytis* than do those of Yu *et al.* (1990), in both the presence and absence of *Encarsia* during these first several days. The pattern between experiments is consistent, however: *Aphytis* emergence success decreases with increasing age of the *Encarsia* juvenile developing in the shared host.

EFFECT OF *ENCARSIA* PRESENCE ON *APHYTIS* EMERGENCE

As an *Encarsia* juvenile aged within a host, its presence had an increasingly negative effect on the probability of *Aphytis* emergence (Fig. 2b,c; Appendix 1). *Encarsia* juveniles >5 days old had an appreciably negative effect on *Aphytis*, but by the time a host contained a 9-day-old *Encarsia* juvenile, the probability of *Aphytis* emergence dropped by 20–30%.

After 15–19 days of juvenile development, *Encarsia* caused scales to form pseudomoult, at which point these hosts were no longer available to *Aphytis* for parasitism. Between days 15 and 17, *Aphytis* success dropped substantially, and by day 19 *Aphytis* was unable to parasitize any scales containing *Encarsia*.

The increasingly negative effect imposed by the developing *Encarsia* juvenile appears to be consistent regardless of the scale age initially attacked by *Encarsia*. Together, Fig. 2b and 2c show a clear pattern: *Aphytis*

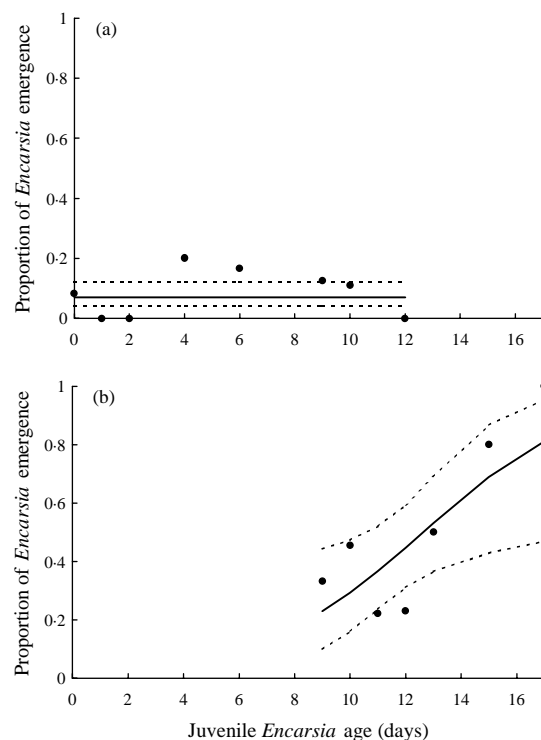


Fig. 3. *Encarsia* survival of predation by *Aphytis* depends on the age of both the host and *Encarsia* at the time of *Aphytis* attack. If *Encarsia* attacks older hosts, its success without interspecific competitors is 89% ($n = 46$), but with competitors (a) its success is always extremely poor ($n = 85$). In contrast, if *Encarsia* attacks young hosts, its success without interspecific competition is 88% ($n = 226$), while its success with competition (b) increases with increasing *Encarsia* larval age at the time of *Aphytis* attack ($n = 67$). Dotted lines represent the 95% CI for the logistic regression model, and each symbol represents the proportion emergence across all replicates.

has a high and consistent probability of survival when *Encarsia* is not present in a scale, and its probability declines continuously with the age of its competitor in scales previously attacked by *Encarsia* regardless of the age of the host.

EFFECT OF *APHYTIS* ATTACK ON *ENCARSIA* EMERGENCE

The effect on *Encarsia* of in-host interactions with an *Aphytis* juvenile is not consistent between the two experiments. The probability of *Encarsia* emergence depended both on the host stage initially attacked by *Encarsia* and the age of the juvenile *Encarsia* at the time of attack by *Aphytis*. Attack by *Aphytis* had a very strong and consistently negative effect on *Encarsia*'s success in the 2nd instar experiment. *Encarsia* had a constant positive, though extremely low, probability of emergence in hosts attacked by *Aphytis* (Fig. 3a; Appendix 1) which was in marked contrast to *Encarsia* success in hosts not attacked by *Aphytis* (89%). The survival rate for *Encarsia* in IGP hosts of this experiment (6.9%) is smaller than the error rate for *Aphytis*-control

scales (1 – observed probability of *Aphytis* alone = 9.8%). This implies that *Encarsia* survival could be a product solely of *Aphytis* mortality and is not confidently attributable to a low level of *Encarsia* success. *Encarsia* survived exposure to *Aphytis* at high rates in the 2nd instar experiment only after it had formed a pseudomoult (between days 12 and 14, Fig. 3a), a physical barrier preventing predation by *Aphytis*.

In contrast to the 2nd instar experiment, after attacking a 1st instar host, an *Encarsia* juvenile had an increasing probability of emerging with increasing age, in spite of *Aphytis* parasitism (Fig. 3b; Appendix 1). After 15 days, the probability of *Encarsia* success after *Aphytis* attack was similar to that in hosts attacked only by *Encarsia* (88%).

The developmental time of *Encarsia* juveniles that survived to emerge was slightly longer when it laid its eggs on 1st instar hosts than when it laid eggs on 2nd instar hosts. When *Encarsia* initially attacked 1st instar scale, its time to emergence was 24.8 ± 2.3 days (min = 22, max = 37); however, when it attacked 2nd instar scale, its emergence time was 22.3 ± 2.5 days (min = 18, max = 28).

Discussion

My laboratory results have shown that these parasitoid species exhibit strong asymmetry in their abilities to successfully garner host resources. *Aphytis* is not always a successful intraguild predator of *Encarsia*, and conversely, *Encarsia* cannot entirely pre-empt *Aphytis* regardless of how early the *Encarsia* parasitizes a host. Survival of an *Aphytis* juvenile decreases almost entirely as a function of the age of the *Encarsia* juvenile onto which it is laid. In contrast, *Encarsia* survival depends both on its age when *Aphytis* was introduced and on the scale stage in which the *Encarsia* egg was laid.

These data suggest that *Encarsia* becomes increasingly resistant to predation by *Aphytis* with increasing larval age. When *Encarsia* attacks small hosts, this increase in resistance is continuous; however, *Encarsia* mortality prior to pseudomoult formation may be almost complete when faced with an *Aphytis* attacker in larger hosts. Similar gains to the intraguild prey species may occur in many systems with intraguild predation. For example, Kim & DeVries (2001) show that in lake systems, bluegills act as size-selective predators, and in a study of aphid predators, Lucas, Coderre & Brodeur (1998) found that susceptibility to predation decreased with developmental age of the intraguild prey species. Regardless of the host stage attacked by *Encarsia*, it eventually develops into a juvenile stage that is completely invulnerable to *Aphytis* attack.

Endoparasitoid success followed a consistent pattern of increasing invulnerability to ectoparasitoid attack, rather than being a random occurrence as has been suggested previously (Askew 1974). This pattern also has been shown in other parasitoid systems. Sugiura & Takagi (1996) found that if the endoparasitoid in

their system attacked before the ectoparasitoid, it could survive the attack at a low rate. So, in this system and others, the intraguild prey species does not always succumb to predation when attacked.

Encarsia and *Aphytis* maintain red scale on California citrus at a level more than 200 times lower than it would be without parasitoids (DeBach, Rosen & Kennett 1971), suggesting that these species coexist on limited resources. This observation as well as recent field observations and experiments (E. T. Borer unpublished data) suggest that intraguild predation occurs in field populations. Thus, *Encarsia*'s lifetime fraction of invulnerability to predation by *Aphytis* will, in part, determine the likelihood that this is the mechanism by which these two species coexist. The IGP models without an invulnerable stage in the intraguild prey species suggest that coexistence of *Aphytis* and *Encarsia* would be possible only at intermediate host productivity (Holt & Polis 1997). But this coexistence region is relatively narrow: it is bounded between the productivity region in which the basal resource and intraguild prey do not provide enough resource for the intraguild predator to invade and the productivity region in which the predator is too abundant for the intraguild prey to persist. If the invulnerable stage is only a relatively small fraction of the intraguild prey species' lifetime, Mylius *et al.* (2001) found that the model results are qualitatively similar to those predicted for the intraguild prey without an invulnerable stage. However, in this model formulation, a relatively high lifetime fraction of invulnerability in the intraguild prey causes the predicted region of coexistence to expand across a much larger range of resource productivity.

The proportion of the *Encarsia* juvenile lifetime that is invulnerable to *Aphytis* attack primarily depends upon timing of the pseudomoult formation. For example, when *Encarsia* attacked 1st instar scale, the average developmental period was nearly 25 days, while progeny became invulnerable to *Aphytis* attack after ~15 days, suggesting that the invulnerable juvenile fraction for *Encarsia* is ~0.4. The invulnerable fraction was similar when *Encarsia* attacked 2nd instar scale. Though short-lived, *Encarsia* adults are invulnerable to *Aphytis* attack as well, so this proportion is, in reality, somewhat larger. Regardless of the absolute value, however, stage-structured models of IGP (Briggs 1993; Mylius *et al.* 2001) suggest that a relatively long invulnerable stage should act to increase the probability of coexistence of these species. Where this system falls along this continuum depends, of course, on the magnitude of resource productivity and *Encarsia* lifetime invulnerability relative to other system rates (e.g. attack rates).

For *Aphytis*, the most important factor in survival to emergence is the age of the *Encarsia* juvenile already growing in the shared host. This result is contrary to the general belief that ectoparasitoids are always predators of endoparasitoids (e.g. Salt 1961; Flanders 1971; Askew 1974; Godfray 1994; Mills 1994; Sugiura & Takagi 1996). Overall *Aphytis* functions as the

intraguild predator in this interaction; however, it does not always convert attacks on *Encarsia* juveniles into *Aphytis* progeny as does the intraguild predator in Briggs's (1993) stage-structured IGP formulation for parasitoids.

This observation presents another twist in IGP theory that has not yet received a thorough theoretical investigation: the decreasing probability of *Aphytis* emergence when attacking increasingly older *Encarsia* juveniles. Intuitively, if predator mortality is increased, then the predator's ability to convert attacks into female progeny is reduced. Maintenance of the predator population will require more attacks, and hence greater resource productivity. Thus the increased mortality should increase both the productivity required for the predator to invade and the productivity required for it to exclude the intraguild prey. Intuition alone can be a dangerous guide in mathematical modelling, however. A full understanding of the effects of increased predator mortality combined with decreased vulnerability of the intraguild prey, both on coexistence of the two species and the dynamics of their shared resource, requires further theoretical work.

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Appendix

STATISTICAL MODELS FOR FIGS 2 AND 3

In the following models $P(A)$ refers to the conditional probability of *Aphytis* emergence, and $P(E)$ refers to the conditional probability of *Encarsia* emergence. Lag represents the difference in age between the *Encarsia* and *Aphytis* juveniles as well as the age of the host at the time of attack.

1a. Results from the 1st instar experiment show that *Aphytis* has a decreased probability of emergence with increasing *Encarsia* larval development; if *Encarsia* gets in early, *Aphytis* loses a significant advantage. The model is:

$$\ln \left[\frac{P(A)}{1 - P(A)} \right] = 1.9935 - (0.1717 \text{ Lag} \times \text{Encarsia}). \quad \text{eqn 2}$$

2a. Results from the 2nd instar experiment show that, as in the 1st instar experiment, direct interaction with increasingly older *Encarsia* juveniles causes a decreased probability of *Aphytis* emergence. The model including both main effects (*Encarsia* and Lag) and the model with only the interaction term

(Lag \times *Encarsia*) were virtually identical in their parsimony using Atkinson's criterion (McCullagh & Nelder 1989, §3.9), so I present the one-parameter model here. Biologically, both models provide similar interpretation. The model is:

$$\ln \left[\frac{P(A)}{1 - P(A)} \right] = 2.3100 - (0.1578 \text{ Lag} \times \text{Encarsia}). \quad \text{eqn 3}$$

1b. In 1st instar scales, *Encarsia* has an increasing probability of emerging with increasing developmental time prior to *Aphytis* attack. The rapid increase in *Encarsia* probability for emergence is coincident with the rapid decline in *Aphytis* success (Figs 2c and 3b). The model is:

$$\ln \left[\frac{P(E)}{1 - P(E)} \right] = -4.4462 + (0.3536 \text{ Lag}). \quad \text{eqn 4}$$

2b. Unlike the 1st experiment, *Encarsia* has a constant, low, probability for survival regardless of its age when attacked by *Aphytis*. The intercept-only model is:

$$\ln \left[\frac{P(E)}{1 - P(E)} \right] = -2.5985. \quad \text{eqn 5}$$