

# Egg Size, Intrinsic Competition, and Lethal Interference in the Parasitoids *Encarsia pergandiella* and *Encarsia formosa*

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**Recent population dynamic theory predicts that disruption of biological control may occur when one parasitoid species' superiority in intrinsic competition is associated with a lower ability to find and exploit hosts (i.e., ability in extrinsic competition). One might expect such a trade-off, for instance, if parasitoids with larger (and fewer) eggs are more likely to prevail in intrinsic competition than species with smaller (and more numerous) eggs. We tested the idea that relative egg size could be used to predict the outcome of intrinsic competition in two closely related endoparasitoids, *Encarsia pergandiella* Howard and *Encarsia formosa* Gahan. Contrary to expectation, the parasitoid species with smaller eggs, *E. pergandiella*, prevailed in intrinsic competition, regardless of the order that hosts were exposed to the two species. In a literature survey, we found four studies of competing pairs of endoparasitoid species for which: (a) egg size estimates were available and (b) one species was consistently superior in intrinsic competition. In three of the four studies, the small-egged species prevailed in intrinsic competition, as we also found. Although *E. formosa* lost in intrinsic competition, this species negatively affected *E. pergandiella*'s progeny production by host feeding on and killing hosts containing *E. pergandiella* eggs. *E. formosa* females also host fed on conspecific-parasitized hosts. As a mechanism of both intra- and interspecific interference competition, host feeding on parasitized hosts contradicts assumptions about the nature of interference competition in existing population dynamics models.** © 2002 Elsevier Science (USA)

**Key Words:** Aphelinidae; *Bemisia tabaci*; biological control; counter-balanced competition; host feeding; multiparasitism; *Trialeurodes vaporariorum*.

## INTRODUCTION

Classical biological control is essentially a process of building or rebuilding natural enemy communities *de novo* (Ehler, 1990). Parasitoids (and predators) are collected, reared, and then released with the goal of sup-

pressing pest densities below economically damaging levels. Two crucial questions in classical biological control are how many parasitoid species should be released and how do competitive interactions among introduced parasitoid species affect pest suppression? Some authors have argued that competitive interactions should be beneficial to successful biological control and that the more species that are introduced, the greater the suppression of the pest (Smith, 1929; DeBach, 1966; Huffaker *et al.*, 1976). Other authors have argued that competitive interactions may reduce or disrupt effective biological control (Pemberton and Willard, 1918; Turnbull and Chant, 1968; Kakehashi *et al.*, 1984; Briggs, 1993; Rosenheim *et al.*, 1995; Murdoch *et al.*, 1998). Theory predicts that disruption may occur when parasitoid species interact directly via lethal interference competition, for example, intrinsic competition (multiparasitism) or facultative hyperparasitism (e.g., Briggs, 1993). "Intraguild predation," predators eating other predators in addition to prey, is an analogous phenomenon that is also potentially disruptive of biological control (Rosenheim *et al.*, 1995). The latter view argues that multiple enemy species may not be more effective than a few. Also, biological control agents should be carefully screened to avoid the potentially disruptive effects of interference competition.

The second view also begs the question of how parasitoids ought to be chosen for introduction. How might the possibility of disruption of pest suppression be minimized? One suggestion has been to use the idea of "counter-balanced competition" to screen parasitoid species for release (Zwolfer, 1971). Zwolfer (1971) proposed that parasitoids (and other insects that exploit a discrete resource) might be characterized by their abilities in *extrinsic* and *intrinsic* competition. Extrinsic competition refers to exploitation of the host population (i.e., a parasitoid species' efficiency at finding and parasitizing hosts). Intrinsic competition refers to interactions among immature parasitoids, which occur when female parasitoids of different species oviposit in the same host individual ("multiparasitism"). Counter-

balanced competition proposes that, because of life history trade-offs, species that tend to win in intrinsic competition should lose in extrinsic competition and vice versa.

Counter-balanced competition is directly related to the classic idea of r-selection versus K-selection in life history theory, which Force (1972) applied to parasitoids and biological control. Force (1972) suggested that parasitoid species subjected to r-selection should be superior in extrinsic competition but inferior in intrinsic competition relative to species subjected to K-selection. Applying these ideas to biological control, Zwolfer (1971) and Force (1972) suggested that r-selected, extrinsically superior parasitoids should be introduced for biological control, while K-selected, intrinsically superior species—those predicted to be most likely to disrupt control—should be withheld.

This idea might be further operationalized by focusing on easily measured life history traits, such as egg size and number. Parasitoid species with many, small eggs might be expected to be better extrinsic competitors than species with relatively few, large eggs (Pschorn-Walcher, 1987). On the other hand, parasitoid species with relatively small eggs might be expected to be inferior in intrinsic competition than larger-egged species. One reason for this may be that small-egged species tend to develop endoparasitically (inside the host) and lose in intrinsic competition to larger-egged ectoparasitoids (which develop outside the host) (e.g., Godfray, 1994). When the two species are endoparasitoids, the larger-egged species might tend to win in intrinsic competition if it hatches earlier or at a larger size relative to the smaller-egged species. Based on these assumptions, one might select parasitoids for biological control using relative egg size as a criterion, releasing species with small eggs and withholding species with large eggs.

Although this approach has a basis in life history theory (e.g., Godfray, 1994) and recent population dynamic models (e.g., Briggs, 1993), empirical tests are few. Yet, at least two key assumptions of the approach may be empirically tested. First, intrinsic competition is assumed to be unidirectional and the only important direct interaction in the system. In other words, interactions are limited to one parasitoid killing the offspring of the other species, e.g., through intrinsic competition (Zwolfer, 1971; May and Hassell, 1981; Kakehashi *et al.*, 1984; Briggs, 1993). Second, intrinsic competitive ability is assumed to reflect differences in egg size. Larger-egged species should consistently “win” in intrinsic competition.

We tested these assumptions using the endoparasitoids *Encarsia formosa* Gahan and *Encarsia pergandiella* Howard as a model system. These species attack the whitefly pests, *Bemisia tabaci* Gennadius and *Trialeurodes vaporariorum* Westwood. *E. formosa* has eggs that are a little less than twice as long as the eggs

of *E. pergandiella* ( $0.127 \text{ mm} \pm 0.001$  (SE) versus  $0.070 \text{ mm} \pm 0.001$  (SE); T.R.C., unpublished data). The eggs of these species are similar in shape at oviposition, so egg length is a reasonable measure of size. We evaluated the hypothesis that *E. formosa* should be a better intrinsic competitor than *E. pergandiella* by testing three specific predictions. First, *E. formosa* should have strong negative effects on *E. pergandiella* progeny production but not vice versa. Second, *E. formosa* should emerge from a majority of multiparasitized hosts, regardless of oviposition order. We initially tested these predictions using *B. tabaci* as a host. However, *B. tabaci* may be less suitable for development of *E. formosa* than the greenhouse whitefly, *Trialeurodes vaporariorum*. *E. formosa* has had a long association with the latter host species (Henter and van Lenteren, 1996). We therefore tested the third prediction that the outcome of intrinsic competition would be the same when *T. vaporariorum* was the host as when *B. tabaci* was the host.

Last, we investigated “host feeding” as mechanism of interference competition. *E. formosa* females kill whitefly nymphs by probing with their ovipositors and feeding on host hemolymph. This may lead to intraspecific lethal interference competition if conspecific-parasitized hosts are fed upon and killed (Collier and Hunter, 2001). *E. formosa* is known to host feed on conspecific parasitized hosts (van Roermund and van Lenteren, 1995; Netting and Hunter, 2000). Feeding on hosts parasitized by heterospecific parasitoids, in this case by *E. pergandiella*, would represent a mechanism of lethal interspecific interference competition (Collier and Hunter, 2001). We investigated host feeding on parasitized hosts by *E. formosa* as a mechanism of both intra- and interspecific interference and as an exception to the simple interaction web assumed by the counter-balanced competition model.

## MATERIALS AND METHODS

Our *E. pergandiella* culture was established using insects obtained from the USDA/APHIS Mission Biological Control Laboratory, Texas (Quarantine No. M94055). This population of *E. pergandiella* was originally collected in Brazil on *B. tabaci*. The *E. formosa* culture was established from insects obtained from a commercial insectary (CIBA Bunting, Colchester, UK). Females of both of these populations are thelytokous and produce only female offspring. Parasitoid cultures were reared on *T. vaporariorum* (Aleyrodidae; Hemiptera) and maintained at ca. 27°C and 14:10 (L:D) h of fluorescent and incandescent light. Whitefly cultures were maintained under greenhouse conditions on tobacco (*Nicotiana tabacum* L.), beans (*Phaseolus vulgaris* L.) and/or cotton (*Gossypium hirsutum* L.).

### Progeny Production

This experiment was designed to detect the effect of interference competition on *E. pergandiella* or *E. formosa* progeny production. Female parasitoids were presented with hosts in arenas on individual cotton leaves. Leaves were excised from cotton plants grown in a greenhouse, placed in clear plastic "leaf boxes" (22 × 82 × 125 mm), and held with their petioles in water. The cotton leaves were later infested with 100–200 adult *B. tabaci*. After 16–20 days, an adhesive, ring-shaped, foam callous cushion (Walgreens Co., Deerfield, IL) was affixed to the underside of the leaf. All but 15 early fourth instar nymphs were removed from the area inside the callous cushion arena (inside diameter: 16 mm). The arena opening was covered with a fine-mesh polyester fabric, held in place with soft ski wax (Swix Sport, 2601, Lillhammer, Norway). Arenas were assigned to one of the following treatments: (1) exposure to an individual female *E. formosa*, (2) exposure to an individual female *E. formosa* followed immediately by a female *E. pergandiella*, (3) exposure to an individual female *E. pergandiella*, or (4) exposure to an individual female *E. pergandiella* followed immediately by a female *E. formosa*. All wasp exposures lasted 4 h. Thus, for each species there was an "alone treatment," that species alone on a patch of hosts for 4 h, and a "competition treatment," that species alone on a patch for 4 h followed by a heterospecific competitor for 4 h. In addition, there were two separate alone treatments for each species. Females were introduced to the arenas at different times (morning or afternoon), concurrent with the introduction of either the first or the second females in the competition treatments. After the wasps were removed, the leaf was kept alive until the number and identity of wasp pupae could be recorded (10–14 days).

One of the key comparisons for this experiment is the fraction of progeny produced by each species as the first versus the second female in the arena. We expected that *E. formosa* would consistently win in intrinsic competition and therefore produce a greater fraction of progeny, independent of the order of exposure. A second key comparison is the absolute number of progeny produced by the first female in the alone treatment versus the competition treatment. An effect of interference competition by the second species should appear as a reduction in the number of progeny produced by the first female in the competition versus alone treatments. We expected that *E. formosa* females should reduce the progeny production of first-ovipositing *E. pergandiella* but not vice versa. Because the data are counts or fractions, statistical analyses used Poisson (for counts) or binomial (for fractions) error distributions in the statistical package GLIM (Generalized Linear Interactive Modeling; McCullough and Nelder, 1983; Crawley, 1993).

### Outcome of Intrinsic Competition

We conducted a second set of experiments that combined behavioral observations and host dissections to more directly evaluate the outcome of intrinsic competition in these species. Female parasitoids were offered individual fourth instar *B. tabaci* nymphs in smaller foam callous cushion arenas (inside diameter ca. 4 mm) on individual seedling cotton plants. Seedling cotton plants were grown in clear plastic "cup-cages" (for details, see Collier and Hunter, (2001)). Once the plants had reached about 10 cm in height, one true leaf was infested with ca. 50 *B. tabaci* adults for 48 h. After 16–20 days, a callous cushion arena was affixed to the leaf and all but one early fourth instar *B. tabaci* nymph was removed from the area inside the arena.

Individual heterospecific females were introduced to the arena in sequence, 4 h apart, and in both oviposition orders. Females were observed until they "attacked" the host (i.e., probed and walked off the host) or "failed to attack" the host (i.e., sat motionless for 5 min, antennated the host twice without probing, or did not encounter the host within 10 min). Females that failed to attack were replaced by a second conspecific female, and trials in which the two conspecific females failed were discarded. Hosts attacked by a female of both species were randomly assigned to be dissected in Insect Ringer's solution on the following day or were reared to parasitoid pupation. The identity of eggs or pupae was noted. We repeated this experiment, without dissecting a fraction of the hosts, using fourth instar *T. vaporariorum* nymphs.

### Host-Feeding on Parasitized Hosts by *E. formosa*

In the observations described above, naïve *E. formosa* females were observed to feed on hosts that had been previously encountered and probed by *E. pergandiella*. In a second set of observations, we investigated host feeding on parasitized hosts by *E. formosa* in more detail. We addressed the following: (a) do "experienced" *E. formosa* females host feed on previously parasitized hosts? (b) do "experienced" female *E. formosa* show differential propensities to host feed on unparasitized hosts versus parasitized hosts and on conspecific-parasitized hosts versus heterospecific-parasitized hosts? and (c) do parasitized hosts that are fed upon produce progeny or inevitably die? *E. pergandiella* were also observed to host feed; however, they did so very rarely: twice in almost 100 observations. Given the infrequency of this behavior, we argue that host feeding on parasitized hosts by *E. pergandiella* is unlikely to be an important mechanism of interaction in this species.

Focal female *E. formosa* were first given experience with a single early fourth instar *B. tabaci* nymph in small arenas, as described above. Females that probed the host but did not host feed were gently forced with a paint brush into a 0.9-ml (quarter dram) glass vial

TABLE 1

Effects of Competition on the Progeny Production of the First Parasitoid Species on the Patch in the Alone Treatment (No Competitor) and the Competition Treatment (Heterospecific Competitor)

First species	Alone treatment				Competition treatment				Analysis of deviance		
	Mean No. progeny	Mean -SE	Mean +SE	<i>n</i>	Mean No. progeny	Mean -SE	Mean +SE	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>
<i>E. pergandiella</i>	11.21	10.61	11.85	29	8.89	8.23	9.60	19	6.07	1	0.014
<i>E. formosa</i>	9.93	9.38	10.52	31	1.95	1.65	2.30	19	131	1	<0.0001

after they had walked off the host. Focal females were then transferred to a callous cushion arena containing either (a) an unparasitized fourth instar nymph, (b) a nymph that had been antennated and probed by a female *E. pergandiella* 4 h earlier (as in the previous experiment), or (c) a nymph that had been antennated and probed (but not host fed) by a female *E. formosa* 4 h earlier. Previous results suggested that hosts in categories "b" and "c" would be consistently parasitized. Focal female *E. formosa* were observed until they attacked or failed to attack the host (as before). In this experiment, an observation was terminated if the focal female failed to attack (i.e., no second female was introduced). All "attacked" hosts were reared for an additional 14 days, a period sufficient for whiteflies and/or parasitoids to reach the pupal stage.

## RESULTS

### Progeny Production

There was no effect of time of exposure (morning or afternoon) on progeny production of females in the alone treatment, so the data for these trials were pooled. In the alone treatments, *E. pergandiella* produced slightly more progeny (1.3 offspring) than did *E. formosa*, although the difference was not statistically significant (Table 1; analysis of deviance,  $\chi^2 = 2.29$ , *df* = 1, *P* = 0.13). On the basis of egg size and number, we might expect that *E. pergandiella* would be a more effective extrinsic competitor than *E. formosa*. However, because host densities were purposely low in this experiment to maximize the strength of interference competition, it is difficult to interpret this result in the context of extrinsic competition.

In the competition treatments, *E. pergandiella* produced the greatest fraction of progeny, and this fraction was independent of the order of exposure of parasitoids (i.e., 0.77 (first) versus 0.82 (second); binomial analysis of deviance,  $\chi^2 = 0.43$ , *df* = 1, *P* = 0.51). This suggests that *E. pergandiella*, not *E. formosa*, consistently prevailed in intrinsic competition. Nevertheless, both *E. formosa* and *E. pergandiella* negatively affected each other's progeny production. When *E. for-*

*mosa* followed *E. pergandiella* on the patch, *E. pergandiella*'s progeny production was significantly reduced, dropping by about 2.3 offspring or 20% (Table 1). When *E. pergandiella* followed *E. formosa* on the patch, the mean number of *E. formosa* progeny dropped by 8 offspring or 80%, a highly statistically significant difference (Table 1).

### Outcome of Intrinsic Competition

The previous experiment documented the effect of one or more mechanisms of interference competition on progeny production and suggested that *E. pergandiella* had prevailed in intrinsic competition. In this experiment, we evaluated the outcome of intrinsic competition directly by estimating the frequency of multiparasitism and comparing this estimate to emergence data. Hosts that had been antennated and probed or "attacked" by a female of both species but not host fed upon were randomly assigned to be dissected or reared until parasitoid emergence.

In observations in which hosts had been dissected, all first-ovipositing females laid one egg (*E. formosa*: *n* = 18; *E. pergandiella*: *n* = 14). Moreover, all second-ovipositing *E. formosa* laid a single egg (*n* = 14). Two of 18 second-ovipositing *E. pergandiella* females, however, failed to oviposit (though they antennated and probed the host). We accounted for these failures to oviposit by *E. pergandiella* in calculating the expected frequency with which each species should win in intrinsic competition. Our null hypothesis was that each species had a 50% probability of emerging from hosts that produced a parasitoid. Given this, and that *E. pergandiella* failed to oviposit in 2/18 hosts, *E. formosa* could be expected to emerge from  $(0.5)(16/18) + (1.0)(2/18)$  of the hosts in the *E. formosa*-followed-by-*E. pergandiella* trials. Likewise, *E. formosa* could be expected to emerge from  $(0.5)(12)$  hosts in the *E. pergandiella*-followed-by-*E. formosa* trials.

*E. formosa* emerged from fewer than expected hosts (Table 2). The deviation of observed and expected frequencies was statistically significant both when *E. formosa* was followed by *E. pergandiella* and when *E. pergandiella* was followed by *E. formosa* (Table 2).

TABLE 2

Outcome of Intrinsic Competition between *E. formosa* and *E. pergandiella* When an Individual Fourth Instar *B. tabaci* or *T. vaporariorum* Was the Host

Host species	Order first/second	Outcome	<i>E. formosa</i> pupae	<i>E. pergandiella</i> pupae	Dead pupae	Goodness of fit
<i>Bemisia tabaci</i>	<i>E. pergandiella</i> / <i>E. formosa</i>	Observed	0	13	3	$G = 18$
		Expected	6.5	6.5	—	$P < 0.001$
<i>Bemisia tabaci</i>	<i>E. formosa</i> / <i>E. pergandiella</i>	Observed	1	10	4	$G = 10.6$
		Expected	6.1	4.9	—	$P = 0.001$
<i>Trialeurodes vaporariorum</i>	<i>E. pergandiella</i> / <i>E. formosa</i>	Observed	1	13	2	$G = 11.78$
		Expected	7	7	—	$P < 0.001$
<i>Trialeurodes vaporariorum</i>	<i>E. formosa</i> / <i>E. pergandiella</i>	Observed	2	10	4	$G = 5.59$
		Expected	6	6	—	$P = 0.02$

Note. Shown are the observed and expected frequencies of *E. formosa* and *E. pergandiella* progeny (see text).  $G$  values are adjusted by William's correction (Sokal and Rohlf, 1981).

Thus, *E. pergandiella* appeared to "win" in cases of multiparasitism regardless of oviposition order.

The outcome of intrinsic competition was similar when the host was *T. vaporariorum* instead of *B. tabaci* (Table 2). Here, we calculated expected frequencies based on a 50–50 outcome of competition and the assumption that both parasitoids always oviposited. This provides a conservative test if second-attacking *E. pergandiella* did not lay eggs in all hosts (as in the outcome experiment with *B. tabaci*). Again, *E. pergandiella* emerged from a greater fraction of hosts than would be expected if *E. pergandiella* and *E. formosa* were equal in intrinsic competition.

#### Host-Feeding on Parasitized Hosts by *E. formosa*

In the experiments described above, naive *E. formosa* females were observed to host feed on whitefly nymphs previously probed (and parasitized) by *E. pergandiella* (3 of 36 females). Experienced *E. formosa* females also host fed on *E. pergandiella*-parasitized hosts (5 of 21 females) and on *E. formosa*-parasitized hosts (6 of 21). Moreover, experienced female *E. formosa* treated unparasitized and parasitized hosts differently, selectively ovipositing on unparasitized hosts and host feeding on parasitized hosts; 1 of 20 unparasitized hosts were fed upon versus 11 of 42 parasitized hosts (Fisher exact test,  $P = 0.04$ ). However, *E. formosa* females appeared to host feed on *E. formosa*-parasitized and *E. pergandiella*-parasitized hosts with similar propensities (Fisher exact test,  $P = 0.25$ ). Three antennal rejections by *E. formosa* females were observed (in 24 observations), and in each case it was an *E. formosa*-parasitized host that had been rejected. No *E. pergandiella*-parasitized host was rejected by *E. formosa* after antennation. This difference was not statistically significant, however (Fisher exact test,  $P = 0.14$ ). Finally, no parasitized host that had been fed upon survived to produce a parasitoid offspring. This agrees with earlier reports that *E. formosa* host feeds

"destructively" (c.f., Jarvis and Kidd, 1986; van Lenteren *et al.*, 1980).

#### DISCUSSION

One of our goals was to test the simple interaction web assumed by the counter-balanced competition model (Zwolfer, 1971; May and Hassell, 1981; Kakehashi *et al.*, 1984; Briggs, 1993). In this model of parasitoid interactions, one parasitoid species directly affects the other by consistently winning in intrinsic competition (and killing the other species' progeny). Our results contradict the counter-balanced competition model in at least two ways. First, both species negatively affected the progeny production of the other, one through intrinsic competition and the other through host feeding. Second, *E. formosa* reduced conspecific progeny production by host feeding on and killing hosts containing conspecific eggs. Such direct intraspecific interactions are absent from the counter-balanced competition model but are predicted to have important effects on both coexistence and pest suppression (Briggs and Collier, 2001). Host feeding on conspecific- and heterospecific-parasitized hosts may, in fact, be a common mechanism of interaction among parasitoids; it has been observed in a number of other species, including *Encarsia sophia* Girault (Collier and Hunter, 2001), *Encarsia luteola* Howard (M.S.H. and T.R.C., unpublished data), *Aphytis melinus* DeBach (Yu *et al.*, 1990; T.R.C., pers. obs.), and *Itopectis naranyae* Ashmead (Ueno, 1998, 1999).

Our second goal was to determine whether intrinsic competitive ability was related to egg size in these parasitoid species, an idea that is implicit in the counter-balanced competition model (Zwolfer, 1971) and the application of the classic idea of "r- and K-selection" to parasitoid life histories (Force, 1972). We tested the prediction that the larger-egged *E. formosa* would prevail in intrinsic competition. We found the

TABLE 3

Egg Size and the Outcome of Intrinsic Competition from Studies of Competing Endoparasitoids

Species	Egg length (mm)	Outcome
<i>Encarsia formosa</i> (Aphelinidae)	0.13 <sup>a</sup>	Loser
<i>Encarsia pergandiella</i> (Aphelinidae)	0.07 <sup>a</sup>	Winner <sup>a</sup>
<i>Aphelinus asychis</i> (Aphelinidae)	0.22 <sup>b</sup>	Loser
<i>Aphidius ervi</i> (Braconidae)	0.05 <sup>c</sup>	Winner <sup>d</sup>
<i>Praon pequodorum</i> (Braconidae)	0.63 <sup>e</sup>	Loser
<i>Aphidius smithi</i> (Braconidae)	0.10 <sup>f</sup>	Winner <sup>g</sup>
<i>Microplitis demolitor</i> (Braconidae)	0.89 <sup>h</sup>	Loser
<i>Hyposoter didymator</i> (Ichneumonidae)	0.30 <sup>i</sup>	Winner <sup>j</sup>
<i>Microplitis croceipes</i> (Braconidae)	0.76 <sup>k</sup>	Winner
<i>Cardiochiles nigriceps</i> (Braconidae)	0.57 <sup>l</sup>	Loser <sup>m</sup>

<sup>a</sup> This study.<sup>b</sup> Carver and Woolcock (1985).<sup>c</sup> Strand and Grbic (1999).<sup>d</sup> Bai and Mackauer (1991).<sup>e</sup> Chow and Sullivan (1984).<sup>f</sup> Bernal Ruiz *et al.* (1984).<sup>g</sup> Chow and MacKauer (1984).<sup>h</sup> Trudeau and Strand (1998).<sup>i</sup> Bahena *et al.* (1999).<sup>j</sup> Tillman and Powell (1992).<sup>k</sup> Lewis (1970).<sup>l</sup> Chamberlin and Tenhet (1926).<sup>m</sup> DeMoraes *et al.* (1999).

reverse; the species with smaller eggs, *E. pergandiella*, was superior in intrinsic competition. We must recognize, however, that there may indeed be a positive statistical relationship between relative egg size and propensity to win in intrinsic competition. The *E. pergandiella*-*E. formosa* interaction may merely represent a rare exception to the general "rule." We therefore looked to the literature for other examples. We identified studies in which both species were endoparasitoids, like *E. pergandiella* and *E. formosa*, where one parasitoid species won in intrinsic competition regardless of the order of oviposition and for which egg size estimates were available. In three of four examples, the smaller-egged species won (Table 3).

Clearly, there are not enough data to statistically evaluate the relationship between egg size and intrinsic competition, and most cases include one or more parasitoids from a single taxon: the superfamily Ichneumonoidea. Nevertheless, the pattern that we observed raises an interesting possibility—small-egged endoparasitoid species may generally have an advantage in intrinsic competition. One possible mechanism leading to this pattern is that small-egged species may hatch before larger-egged species. This may confer an advantage in physical combat to small-egged parasitoid species. Although this may be true in other sys-

tems, is not so for *E. pergandiella* and *E. formosa*; *E. pergandiella* eggs take longer to hatch than do *E. formosa* eggs (D. Donnell and M. Hunter, unpublished data). Another mechanism by which small-egged species might win in intrinsic competition is preemptive nutrient uptake (c.f., Vinson and Hegazi, 1998). *E. pergandiella* have hydroptic eggs, which swell dramatically in the 24 h following oviposition. *E. formosa* eggs, which are anhydroptic, swell relatively little. *E. pergandiella*'s smaller eggs may rapidly take up nutrients necessary for *E. formosa*'s development, and this may confer a competitive advantage to *E. pergandiella* (D. Donnell and M. Hunter, unpublished data). This phenomenon might be a general mechanism by which small-egged endoparasitoids can prevail over large-egged endoparasitoids in intrinsic competition.

A third issue is whether egg size yields information about a parasitoid's ability in extrinsic competition, though we did not directly address this possibility in *E. pergandiella* and *E. formosa*. Based on relative egg size and number, we might expect that *E. pergandiella* should be a better extrinsic competitor than *E. formosa* and therefore would be more effective at suppressing *B. tabaci* populations. *E. pergandiella* has approximately three times as many eggs as *E. formosa* 24–48 h after eclosion (i.e., a mean of 30.1 eggs versus *E. formosa*'s 10.4 eggs; T.R.C. unpublished data). Vet and van Lenteren (1981) studied the efficacy of *E. formosa* and a different (Californian) population of *E. pergandiella*, using *T. vaporariorum* as the host. These authors found that lifetime reproduction was actually higher in *E. formosa* than in *E. pergandiella*. *E. pergandiella* had a greater instantaneous rate of increase than *E. formosa*, however, which reflected a shorter development time. *E. pergandiella*'s lower propensity to host feed than *E. formosa* may also give *E. pergandiella* an advantage in extrinsic competition. A parasitoid's efficiency at exploiting the host is often influenced by a number of life history attributes (Murdoch and Briggs, 1996), and these measures of extrinsic competitive ability may conflict. Consequently, it is often difficult to identify a single measure of extrinsic competitive ability. The data available for *E. pergandiella* and *E. formosa* offer little support for the contention that egg size can be used to predict either extrinsic or intrinsic competitive ability.

Other recent case studies similarly provide weak or no support for the counter-balanced competition hypothesis. Takagi and Hirose (1994) recently summarized work on *Coccobius fulvus* Compere and Annecke and *Aphytis yanonensis* DeBach and Rosen, two parasitoid species that attack the arrowhead scale, *Unaspis yanonensis* Kuwana. *C. fulvus* has a greater lifetime fecundity and attacks younger stages of the host than its competitor. Both of these traits would be expected to confer an extrinsic advantage to *C. fulvus* (Murdoch and Briggs, 1996). *C. fulvus* is also inferior to *A. yanon-*

*ensis* in intrinsic competition, as would be predicted based on counter-balanced competition. Nonetheless, *A. yanonensis* has a shorter development time and a more female-biased sex ratio than *C. fulvus*, traits that should confer extrinsic competitive ability to *A. yanonensis*. In another recent case study, DeMoraes *et al.* (1999) found better but mixed support for the counter-balanced competition model in two parasitoids of *Heliothis virescens* Fabricius. In their study, the weaker intrinsic competitor, *Cardiochiles nigriceps* Viereck, was better at finding hosts than *Microplitis croceipes* Cresson (which has larger eggs; Table 3). However, *M. croceipes* had a shorter development time, which should again confer an advantage to this species in extrinsic competition (Murdoch and Briggs, 1996). While a number of classic studies appear to fit the counter-balanced competition model (Zwolfer, 1971; Force, 1972; Pschorn-Walcher, 1987), more recent studies suggest the existence of considerable complexity, much of which does not fall easily into a simple dichotomy between intrinsic and extrinsic competition.

Finally, a recent study that used a comparative rather than a case-study approach also provides mixed support for assumptions of the counter-balanced competition model. Lane *et al.* (1999) examined the biological control record for a positive relationship between parasitoid fecundity and effective biological control, a measure of extrinsic competitive ability. These authors found no such relationship when all pest families were combined. However, parasitoid fecundity was positively correlated with the successful control of lepidopteran pests. This was the only host family for which there was both substantial variation in fecundity and a large sample size. Lane *et al.*'s (1999) study suggests that, for parasitoids of Lepidoptera, egg number might be a reasonable predictor of extrinsic competitive ability. It is also possible that parasitoids of Lepidoptera better fit assumptions of the counter-balanced competition model than parasitoids of other taxa. We argue that more case studies are needed, particularly those that explicitly consider life history variation and mechanisms of intrinsic competition in a diversity of parasitoid and host taxa. Ultimately, information on the relationship between life history and extrinsic and intrinsic competition bears on one of the most fundamental debates in classical biological control.

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