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# THE RELATIVE CONTRIBUTIONS OF TIME AND EGGS TO THE COST OF REPRODUCTION

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*Abstract.*—Whether the trade-off between current and future reproduction in insect parasitoids is mediated by the costs of time or eggs remains an issue of contention. Life-history models predict that parasitoids have some risk of exhausting their lifetime supply of oocytes. I develop a simple conceptual model that assesses the relative contributions of time and eggs to the cost of reproduction by placing them in a common currency: foregone future fitness returns. Although rates of egg limitation observed in nature are modest, eggs still often make the dominant contribution to the overall cost of oviposition. Therefore, models of parasitoid reproduction must recognize the costliness of both time and eggs.

*Key words.*—Cost of reproduction, egg limitation, life-history trade-offs, oviposition, parasitoids, sex allocation.

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Parasitoids have been widely employed as model systems to develop and test theory in behavioral and evolutionary ecology. Parasitoids are useful as model systems because much of their reproductive behavior is intimately associated with readily measurable fitness returns, which facilitates the construction and testing of optimality and evolutionary models (Godfray 1994). It is perhaps surprising, then, that one of the most fundamental constraints on reproductive effort, the trade-off between current and future reproduction, remains poorly characterized for parasitoids. In particular, whether this trade-off is mediated by time costs or by the costs of the eggs deposited by ovipositing females remains an issue of great contention.

A primary manifestation of this disagreement is the discrepancy between the two basic approaches used to model parasitoid reproductive behavior. One school has constructed optimality models that employ the rate of fitness gain as the "currency" in which the costs and benefits of different behavioral options are evaluated (e.g., Charnov and Skinner 1984; Parker and Courtney 1984; Skinner 1985; Ives 1989; Janssen 1989; Strand and Godfray 1989; Visser et al. 1992; van Dijken et al. 1993); proponents of this approach argue implicitly and often explicitly that time is the sole mediator of the cost of reproduction. That is, these models assume that parasitoids do not exhaust their supply of mature oocytes, but that instead realized fitness is constrained by the time available to locate and handle suitable hosts in the environment. Time spent handling the current host is time that cannot be spent searching for and exploiting other hosts; thus, if fitness returns from the current host are small (because the host is already parasitized, because the host is unparasitized but of marginal quality, or because a clutch of eggs deposited by the female has already reached a size where sibling competition for host resources is anticipated to be strong), it may be beneficial to leave the host and search for richer host resources elsewhere. The second school of workers has constructed optimality models that employ lifetime reproductive success (expected number of offspring or grandoffspring produced) as the currency; proponents of this approach argue that either time or eggs can limit reproductive success (reviewed by Mangel 1989; Heimpel and Collier 1996; see also McGregor 1997; Sirot et al. 1997). That is, these workers assume that parasitoids may exhaust their supply of mature oocytes in some cases, while in other cases they die before depositing all their eggs. The models predict that optimal parasitoid behavior may change as a function of parasitoid age, egg load, nutritional status, or other physiological state variables that alter the parasitoid's perception of its own risk of being time versus egg limited. Dynamic optimization models are generally represented as incorporating both time and egg costs of reproduction. However, subtle details of model formulation are critical in this regard, and many models either purposefully or inadvertently preclude the time cost of reproduction (see discussion below), leaving a model that represents only the contribution of eggs to the cost of reproduction. These contrasting modeling approaches have contributed to the polarization of opinion on the cost of reproduction in parasitoids.

Using an optimality approach to the evolution of parasitoid fecundity, I have argued that we should expect a significant risk of egg limitation to be a fundamental feature of parasitoid life histories (Rosenheim 1996). In the absence of egg limitation, directional selection for progressive reductions in fecundity exists because of fitness advantages accrued by producing a smaller number of larger eggs (larger eggs confer fitness benefits to offspring) or by shunting additional resources from oocytes (reproduction) to somatic maintenance, thereby extending longevity. Only when some fraction of the population is egg limited does selection for greater fecundity balance the selection for decreased fecundity, thus producing an evolutionary equilibrium. My models suggested that only when alternate allocations of nutrients present in excess oocytes are ignored does the risk of egg limitation approach zero.

Sevenster et al. (1998) have noted that several features of my models are not realistic. I agree—in an attempt to lay bare the role of life-history trade-offs, my models were explicitly designed to be as simple as possible, not as realistic as possible. By incorporating important features of natural systems, such as heterogeneity in rates of host encounter, Sevenster et al. (1998) have shown that expected levels of egg limitation may decrease (e.g., they contrast a prediction of 28.5% egg limitation in one of my models to a prediction of 2–43% egg limitation in their model, depending on host density). Their insights are important, and along with the recent work of Mangel and Heimpel (1998), they represent a valuable effort to determine which factors will be most important in shaping the magnitude of the risk of egg limitation. I see nothing in the results of these models that I would dispute. Indeed, I see the results as supporting the very same qualitative conclusions that I had drawn earlier. However, Sevenster et al. (1998) argue that the risks of egg limitation predicted by their model are sufficiently small that they are insignificant, and therefore that models of parasitoid behavior that consider only time costs are appropriate. It is here that our disagreement lies.

In this paper, I will argue that the continuing disagreement regarding the relative importance of egg limitation stems from our failure to ask the right question. Specifically, rather than continuing to ask "What proportion of the parasitoid population is time limited versus egg limited?" we need to ask "What are the relative contributions of time and eggs to the overall cost of oviposition?" By developing a simple conceptual model and applying the model to published studies of parasitoid foraging in the field, I will attempt to show that observed rates of egg limitation, although generally modest, are still sufficiently large that they often translate into the dominant share of the total cost of oviposition. To understand parasitoid reproductive behavior (host acceptance, superparasitism, clutch size, host feeding, etc.), we therefore should not rely uncritically on rate-maximizing models that exclude the costs of eggs; these models will often lead us astray when realistic representations of the cost of reproduction are important. Instead, our models must recognize that both eggs and time costs can be important constraints to parasitoid reproduction.

## THE COST OF REPRODUCTION

To analyze a behavioral trait within a functional context, we need to quantify the costs and benefits of the various behavioral options available. The cost of reproduction for parasitoids can be divided into two parts (Fig. 1). One part of the cost is incurred prior to the moment at which an oviposition decision is reached (henceforth, the preoviposition costs of reproduction). These costs include the physiological costs of producing and maintaining the reproductive apparatus (ovaries and associated glands, mature oocytes, etc.) as well as the time and energy invested in searching for a host and that portion of host handling time that is devoted to assessing host quality. The second part of the cost of reproduction is that which is incurred if the host is accepted for oviposition and avoided if the host is rejected (henceforth, the cost of oviposition). The behavioral options to be compared are simply to lay an egg or not; for parasitoids that lay clutches of eggs, the choice of a clutch size can be seen as a series of these dichotomous decisions. It is the cost of oviposition that will be the focus of this manuscript. The earlier-incurred preoviposition costs of reproduction may be substantial, but cannot be avoided through any option available to a parasitoid that has discovered a host. Thus, to include them as costs in our cost-benefit analysis would be to apply the misguided logic that has been termed the "Concorde fallacy" since it was explicated by Dawkins and Carlisle (1976). This is not to say that we can ignore the time costs of searching for a new host; as explained below, it is the ratio of oviposition time to the expectation of future searching time requirements that shapes the time cost of reproduction. Thus, search time provides the context for evaluating the opportunity cost of devoting time to oviposition.

The benefits of laying an egg are a function of the likelihood of producing an offspring on a given host and the expected fitness of that offspring. In the most general case, the costs are some combination of (1) the opportunity cost of the time required to handle the host (i.e., the time could be spent searching for a higher-quality host); and (2) the opportunity cost of the egg (again, the egg could be saved for oviposition on a better host). In some cases, additional factors may contribute to the cost of oviposition, such as enhanced risks of predation and additional physiological costs associated with oogenesis; these will be addressed later (see Discussion).

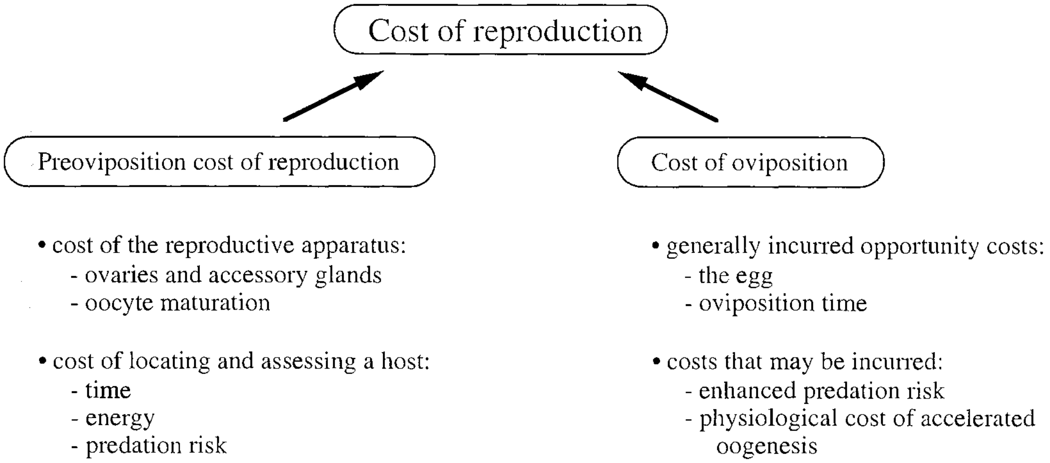

FIG. 1. The total cost of reproduction in insect parasitoids can be decomposed into two components: the preoviposition cost of reproduction and the cost of oviposition. Preoviposition costs may be substantial, but are incurred before the parasitoid makes a decision to oviposit. Therefore, they are not included as costs in the cost-benefit analysis of oviposition behavior.

$$
\begin{aligned}
\text{Cost of oviposition} &= \text{lost opportunities for fitness returns from hosts to be parasitized in the future}\\
&= \begin{pmatrix}\text{Costs mediated by}\\ \text{the use of an egg}\end{pmatrix} + \begin{pmatrix}\text{Costs mediated by the use}\\ \text{of time to deposit the egg}\end{pmatrix}\\
&= \begin{pmatrix}\text{Number of hosts}\\ \text{that cannot be attacked}\\ \text{because the egg was}\\ \text{used, assuming egg}\\ \text{limitation}\end{pmatrix} \bullet \begin{pmatrix}\text{Fitness returns}\\ \text{per host attacked}\end{pmatrix} \bullet \begin{pmatrix}\text{Probability of}\\ \text{egg limitation}\end{pmatrix} + \begin{pmatrix}\text{Number of hosts}\\ \text{that cannot be attacked}\\ \text{because the time was}\\ \text{used, assuming time}\\ \text{limitation}\end{pmatrix} \bullet \begin{pmatrix}\text{Fitness returns}\\ \text{per host attacked}\end{pmatrix} \bullet \begin{pmatrix}\text{Probability of}\\ \text{time limitation}\end{pmatrix}\\
&= (1)\cdot(\Delta W)\cdot(P_{egg\text{ - }lim}) + (T_{ovip} - T_{rej})\cdot(r_{ovip})\cdot(\Delta W)\cdot(P_{time\text{ - }lim})\\
&= \left\{P_{egg\text{ - }lim} + \left[(T_{ovip} - T_{rej})\cdot(r_{ovip})\right]\cdot(P_{time\text{ - }lim})\right\}\cdot(\Delta W)
\end{aligned}
$$

FIG. 2. Derivation of an equation describing the relative contributions of eggs and time to the cost of oviposition for an insect parasitoid.

To develop a simple conceptual model for the contribution of time and eggs to the cost of oviposition, I will make a number of simplifying assumptions. The effects of relaxing these assumptions will be addressed later (see Discussion), but the goal here is to develop a model that is as straightforward as possible. First, I will assume that our parasitoid is strictly proovigenic, that is, all eggs are matured prior to reaching the adult stage. For such a parasitoid, once the full complement of eggs is exhausted, there is no ability to mature additional oocytes; the risk of egg limitation can therefore be defined simply as the risk of exhausting the lifetime supply of oocytes prior to death. Although the model developed below is for the proovigenic case, it also has relevance for those parasitoids that continue to mature eggs during the adult stage ("synovigenic" parasitoids). For synovigenic species, there are two ways in which egg limitation can occur (Ellers 1998; Heimpel and Rosenheim 1998). First, parasitoids may temporarily exhaust their supply of eggs and be forced to delay further reproduction until additional oocytes are matured. Second, synovigenic species, like proovigenic species, may experience a permanent form of egg limitation. Synovigenic species generally exhibit egg maturation rates that decline with age, and in many cases eventually exhaust their ability to mature additional oocytes, thus entering a postreproductive period during which their ovaries may atrophy (Jervis et al. 1994). The model developed below quantifies the fitness costs associated with the permanent, but not the transient, type of egg limitation. Thus, it will estimate the full opportunity cost of egg use for proovigenic species, but underestimate the opportunity cost of egg use for synovigenic species, making my argument more conservative for these species.

Additional simplifying assumptions are as follows. First, assume that the parasitoid population density is stable, so that we do not need to adjust the relative values of current and future reproduction. Second, assume that the parasitoid lays only a single egg per host. Finally, assume that parasitoid oviposition behavior is shaped by an evolutionarily adjusted expected risk of becoming egg versus time limited, but is not adjusted conditionally as a result of parasitoid experiences during foraging.

The cost of oviposition can now be viewed as the fitness foregone through lost opportunities for future reproduction (Fig. 2). To assess the relative contribution of eggs and time to this lost reproduction, we need to put them into a common currency. We can do this by translating both costs into terms of foregone fitness returns from hosts that will not be parasitized in the future because of the current reproductive decision. How does the egg contribute to this cost? An egg laid on the current host represents exactly one host that cannot be parasitized in the future. Of course, it is only if the parasitoid eventually becomes egg limited (i.e., exhausts its egg supply before dying) that this cost is realized. Thus, the total contribution of the egg to the cost of oviposition is (1 host) × (expected fitness returns per host parasitized in the future) × (probability of egg limitation). How does the time required to lay an egg contribute to the cost of reproduction? We must calculate the expected fitness returns from hosts that would be parasitized if the current host were rejected and the parasitoid instead invested the oviposition time to seek out alternative host resources. This expected value is the product of the time savings ([time to accept the host] − [time to reject the host]), the overall rate of oviposition achieved in the environment, and the mean quality (in terms of fitness returns) of hosts parasitized. Again, it is only if the parasitoid eventually becomes time limited (i.e., cannot locate and handle enough hosts before it dies to exhaust its supply of eggs) that this cost is realized. Thus, the total contribution of time to the cost of reproduction is ([time to accept the host] − [time to reject the host]) × (oviposition rate) × (expected fitness returns per host parasitized in the future) × (probability of time limitation). In this model, once an individual parasitoid dies, it can be categorized as having been either purely egg limited or purely time limited (depending upon whether it exhausted its egg supply prior to death), and the proportions of parasitoids in these two categories must sum to 1.0. A newly emerged parasitoid adult, however, may face a risk of either fate.

The key point of this model is that we cannot calculate the relative contributions of time and eggs to the cost of oviposition with just the probabilities of time and egg limitation. We must also consider detailed aspects of oviposition behavior (i.e., how much time is required to deposit an egg on a host once the host has been assessed) and local ecological conditions (i.e., what rate of oviposition the parasitoid can realize if it quits the current host). If we can estimate time requirements for depositing eggs and rates of oviposition, we can calculate the number of oviposition opportunities foregone by virtue of the time spent ovipositing on the current host (this is the term $[T_{ovip} - T_{rej}] \times r_{ovip}$ in Fig. 2). Under the usual expectation that the time required to accept a host is greater than the time required to reject a host, the value of $(T_{ovip} - T_{rej}) \times r_{ovip}$ must be greater than zero. Noting that $r_{ovip}$ can be rewritten as $(1/[T_{search} + T_{ovip}])$, where $T_{search}$ is defined broadly to include all activities that occur between successive oviposition events (i.e., searching, resting, feeding, rejecting low quality hosts, etc.), it can also be seen that the maximum value of $(T_{ovip} - T_{rej}) \times r_{ovip}$ is 1.0 (this maximum value is approached when host abundance is so high that search times are near zero $[T_{search} \approx 0]$ and when hosts can be rejected rapidly $[T_{rej} \approx 0]$). Ignoring the term $(T_{ovip} - T_{rej}) \times r_{ovip}$ in Figure 2 (i.e., trying to evaluate the relative importance of eggs and time by examining only the probabilities of time versus egg limitation) is equivalent to assuming that it is always present at its maximum value (1.0). What is the value of this term? That is, what is the expected number of host attacks that are foregone because of time spent depositing an egg on the current host?

## FIELD ESTIMATES OF TIME COSTS AND REALIZED OVIPOSITION RATES

Estimates of $(T_{ovip} - T_{rej}) \times r_{ovip}$ can be extracted from the handful of studies that have quantified realized rates of parasitoid oviposition under field conditions (Table 1). What these studies show is that the time required to deposit eggs (oviposition time) is a small fraction of the total time required to locate and exploit a host (search time + total handling time). For 11 parasitoid species for which data are available, the number of oviposition opportunities foregone because of time spent ovipositing ranged from 0.0024 to 0.187 (median: 0.022). Thus, in all cases studied to date, the value of $(T_{ovip} - T_{rej}) \times r_{ovip}$ is much closer to its theoretical minimum (0.0) than to its theoretical maximum (1.0). This is the first of the two critical pieces of empirical evidence needed to evaluate the relative contributions of eggs and time to the overall cost of oviposition.

## FIELD ESTIMATES OF THE RISK OF EGG LIMITATION

We now need one more parameter estimate to calculate the relative contributions of eggs and time to the cost of oviposition: the parasitoids' risk of egg limitation. There are two possible ways to estimate this parameter. First, we could derive estimates from optimality models of life-history evolution; however, this would be an ill-advised approach. Optimality models should not be expected to produce quantitatively useful predictions when the fundamental relationships and parameter values with which the models are constructed are poorly characterized (Abrams 1999; Clark and Mangel 1999). For example, the levels of egg limitation predicted by optimality models are dependent on trade-offs between egg number and fitness benefits associated with larger eggs, but the function relating egg size to offspring fitness has never been measured for a parasitoid. Further complicating this trade-off, the functional significance of egg size may prove to be conditional on the quality of the host, as has been found for some herbivores that have parasitoid-like biologies (e.g., seed beetles; Fox and Mousseau 1996; Fox et al. 1997) or perhaps on the likelihood that there will be competition for resources on superparasitized hosts. The trade-off between egg production and parasitoid longevity is also critical to predicted levels of egg limitation, but this relationship is only now beginning to be characterized (Ellers and van Alphen 1997). The trade-off between fecundity and longevity may again vary with changing ecological conditions, in this case as a function of the availability of nutrients to reproductive females (Tatar and Carey 1995). The trade-off between reproduction and longevity can, in principle, be studied experimentally by manipulating access of parasitoids to hosts. However, such experiments will tell us little about the cost of reproduction for proovigenic species (e.g., Kopelman and Chabora 1992) and, as noted by Heimpel and Collier (1996), will be difficult to interpret for many synovigenic species that can also feed on hosts, thereby confounding effects of reproduction with effects of nutrition (e.g., Bai and Smith 1993). Furthermore, inferring microevolutionary trade-offs from the results of phenotypic manipulations may also be difficult (Reznick 1985; Stearns 1992). Given our lack of knowledge of the importance of central life-history trade-offs under field conditions, we cannot currently build models that produce quantitatively meaningful estimates of the risk of egg limitation.

The second approach is to measure levels of egg limitation in real populations of parasitoids foraging in the field. The most direct way to do this would be to capture proovigenic parasitoids as they die and dissect them to see if they have exhausted their egg supply. This, however, has never been done. Instead, there are two types of studies that we can use to provide relatively direct estimates of the risk of egg limitation (for less direct approaches see Heimpel and Rosenheim 1998). First, female parasitoids of unknown age collected in the field can be dissected to establish the proportion of females that have exhausted their supply of eggs. Cronin and Strong (1996) dissected field-collected individuals of the proovigenic parasitoid *Anagrus delicatus* and recorded that 7% had laid all their eggs. We expect that a field sample of mixed-age females taken from a proovigenic species may be a poor estimate of the proportion of females that eventually exhaust their eggs prior to death. Given that *A. delicatus* has many overlapping generations, the assumption of a stable age distribution may be roughly appropriate. However, to project from a mixed-age sample to an estimate of egg limitation at death, we need two pieces of information that we currently lack: the distribution of parasitoid longevities and the age-dependence of the probability of exhausting the egg supply. Because it seems likely that the 7% value represents an underestimate, I will retain this value as a conservative measure of egg limitation for *A. delicatus.*

A second relatively direct means of estimating egg limitation is to combine field data, including observed egg loads, with an estimate of projected future opportunities for oviposition prior to death. Ellers et al. (1998) dissected field-collected individuals of the synovigenic parasitoid *Asobara tabida* and estimated the total number of eggs laid prior to capture by subtracting observed egg loads from laboratory estimates of the full initial egg complement. Future opportunities for oviposition were estimated from residual fat reserves (an indicator of future longevity) to produce an estimate of 7.3% permanent egg limitation in the population. Driessen and Hemerik (1992) studied reproduction of the

TABLE 1. Empirical studies quantifying the time costs of oviposition. The criterion for inclusion of a study was that the parasitoid oviposition rate was quantified in the field with natural populations of hosts. Parasitoids observed were either members of wild populations or laboratory-reared individuals that were released and then tracked. Oviposition and rejection times were derived from either field or laboratory observations.

| Parasitoid | Host | Rejection time[1] ($T_{rej}$) | Oviposition time: first egg ($T_{ovip}$) | Oviposition time: subsequent eggs | Oviposition rate[2] (eggs/h) ($r_{ovip}$) | $(T_{ovip} - T_{rej})(r_{ovip})$ | Reference |
|---|---|---|---|---|---|---|---|
| *Aphytis aonidiae* (Aphelinidae) | *Quadraspidiotus perniciosus* (Diaspididae) | 4.9 min | 9.5 min | (solitary) | 0.40 | 0.031 | Heimpel et al. (1996, 1998) |
| *Aphytis vandenboschi* (Aphelinidae) | *Quadraspidiotus perniciosus* (Diaspididae) | 17.6 min | 20.6 min | (solitary) | 0.43 | 0.022 | G. E. Heimpel (pers. comm. 1997) |
| *Comperiella bifasciata* (Encyrtidae) | *Aonidiella aurantii* (Diaspididae) | 55.0 sec | 203.0 sec | 94.8 sec | 2.04 | 0.084 | P. J. Ode (pers. comm. 1997); Rosenheim and Hongkham (1996) |
| *Anicetus beneficus* (Encyrtidae) | *Ceroplastes rubens* (Coccidae) | n/a | 5.3 min | (solitary) | 2.10 | 0.187 | Itioka and Inoue (1996); T. Itioka (pers. comm. 1997) |
| *Asobara tabida* (Braconidae) | larval *Drosophila* spp. (Drosophilidae) | ≈ 4.0 sec | 29.8 sec | (solitary) | 1.78 | 0.013 | Janssen (1989) |
| *Leptopilina heterotoma* (Eucoilidae) | larval *Drosophila* spp. (Drosophilidae) | ≈ 4.0 sec | 29.2 sec | (solitary) | 2.89 | 0.020 | Janssen (1989) |
| *Leptopilina clavipes* (Eucoilidae) | larval *Drosophila* spp. (Drosophilidae) | 1.8 sec | 40.0 sec | (solitary) | 0.88 | 0.009 | Driessen and Hemerik (1992); Driessen et al. (1991) |
| *Aphaereta minuta* (Braconidae)[3] | larval Diptera | n/a | ≈ 22.5 sec | ≈ 22.5 sec | 2.31 | 0.014 | Visser (1994, 1996) |
| *Pauesia unilachni* (Braconidae) | *Schizolachnus pineti* (Aphidae) | 59.0 sec | 234.0 sec | (solitary) | 2.00 | 0.097 | W. Völkl (pers. comm. 1997); Völkl and Kraus (1996) |
| *Lysiphlebus cardui* (Braconidae) | *Aphis fabae* (Aphidae) | 19.0 sec | 57.0 sec | (solitary) | 13.30 no ants<br>21.60 w/ants | 0.140 no ants<br>0.228 w/ ants | W. Völkl (pers. comm. 1997); Völkl (1990) |
| *Aphidius rosae* (Braconidae)[4] | *Sitobion fragariae* (Aphidae) | n/a | ≈ 1.5 sec | (solitary) | 5.80 | 0.002 | Völkl (1994) |

[1] Rejection times on hosts that were examined carefully. (In some cases, hosts that are completely unsuitable for oviposition are rejected more rapidly, but the time cost is most appropriately measured for hosts that are accepted under at least some conditions.) In cases where rejection times were not available in the literature, they were assumed to be zero, thus potentially leading to an overestimate of the time costs of oviposition.

[2] For the species studied with direct field observations, within-patch oviposition rates are the rates recorded in the literature. These rates may overestimate the global oviposition rate because they exclude between-patch travel times.

[3] A mark-release-recapture experiment.

[4] Parasitoids were outplanted.

TABLE 2. Estimates of the relative contributions of eggs and time to the overall cost of oviposition in parasitoids.

| Parasitoid | Proovigenic versus synovigenic | $P_{egg\text{-}lim}$ estimate | Percent of total cost contributed by eggs | Percent of total cost contributed by time |
|---|---|---|---|---|
| *Aphytis aonidiae* | synovigenic | 0.09[1] | 76 | 24 |
| *Aphytis vandenboschi* | synovigenic | 0.09[1] | 82 | 18 |
| *Comperiella bifasciata* | unknown | 0.09[1] | 54 | 46 |
| *Anicetus beneficus* | synovigenic | 0.09[1] | 35 | 65 |
| *Asobara tabida* | synovigenic | 0.07[2] | 86 | 14 |
| *Leptopilina heterotoma* | synovigenic | 0.09[1] | 83 | 17 |
| *Leptopilina clavipes* | proovigenic | 0.13[2] | 94 | 6 |
| *Aphaereta minuta* | synovigenic | 0.09[1] | 88 | 12 |
| *Pauesia unilachni* | synovigenic | 0.09[1] | 51 | 49 |
| *Lysiphlebus cardui* | synovigenic | 0.09[1] | 30–41 | 59–70 |
| *Aphidius rosae* | synovigenic | 0.09[1] | 98 | 2 |

[1] Average incidence of permanent egg limitation observed in three field studies analyzed in the text.

[2] Species-specific estimates of the incidence of egg limitation.

proovigenic parasitoid *Leptopilina clavipes*. Field estimates of the natural distributions of realized oviposition rates and longevities were incorporated into a Monte Carlo simulation and produced the estimate that 12.9% of the population is egg limited.

Our three empirical estimates of egg-limitation rates are therefore fairly similar (7%, 7.3%, and 12.9%), and average approximately 9%. Despite the paucity of the data, these estimates of egg limitation rates provide us with insights into trade-offs central to parasitoid reproduction.

## PUTTING IT TOGETHER: THE RELATIVE COSTLINESS OF EGGS AND TIME

We now have field-derived estimates of all the parameters needed to assess the relative contributions of eggs and time to the cost of oviposition. Using the model described in Figure 2, the relative contribution of eggs, $C_{egg}$, can be estimated as:

$$C_{egg} = P_{egg\text{-}lim}/[P_{egg\text{-}lim} + (T_{ovip} - T_{rej})(r_{ovip})(P_{time\text{-}lim})],$$

and the relative contribution of time, $C_{time}$, as:

$$C_{time} = (T_{ovip} - T_{rej})(r_{ovip})(P_{time\text{-}lim})/[P_{egg\text{-}lim} + (T_{ovip} - T_{rej})(r_{ovip})(P_{time\text{-}lim})].$$

These calculations are presented for 11 parasitoid species in Table 2, with relative costs expressed as percentages. The first result is that in both of the parasitoids for which we have species-specific estimates of all the needed parameters (*Asobara tabida* and *Leptopilina clavipes*), eggs make the larger contribution to the total costs of oviposition (86% and 94% of the total cost, respectively). If we apply our rough estimate of 9% egg limitation to the remaining nine species in Table 2, we can see that either eggs or time can make the larger contribution; in no case is either factor's role so small as to be negligible (with the possible exception of time costs for one parasitoid that oviposits very rapidly: *Aphidius rosae*). Thus, this relatively broad-brush analysis suggests that egg limitation, although apparently often a minority condition within parasitoid populations, nevertheless makes a considerable and often the dominant contribution to the cost of oviposition. Models of parasitoid reproductive behavior must, therefore, recognize the contributions of both eggs and time whenever the costs of oviposition are to be incorporated.

## DISCUSSION

Several factors have contributed to the longevity of the debate on the roles of eggs and time in mediating the cost of parasitoid reproduction. The paucity of relevant field data is an obvious one. Competition between alternate modeling frameworks may also have contributed to the polarization of opinion. Another contributor, however, has been our failure to ask the right question. We have been asking, "What is the relative likelihood of egg limitation versus time limitation?" Certainly the answer to this question is germane to the issue of parasitoid reproductive behavior. However, we must also ask, "What are the relative contributions of eggs and time to the total cost of oviposition?" By translating time and egg costs into a common currency (future fitness returns potentially foregone) and evaluating a model of the cost of oviposition with field estimates of oviposition rates and egg limitation, I have attempted to demonstrate that although egg limitation may occur infrequently in parasitoid populations, both eggs and time make important contributions to the trade-off between current and future reproduction.

*Populations and Individuals.*—The data in Table 1 are mean oviposition rates recorded for populations of parasitoids. We are, however, interested in how the costs of reproduction shape behavior at the level of the individual. Both mean tendencies and variation will be potentially important. An adult parasitoid that has just eclosed from the pupal stage, mated, and begun to forage for hosts may not yet have much information about local conditions, and its initial behavior may be regulated by genetically determined rules. However, as the parasitoid forages it may acquire information with which it can adjust its projected risk of egg versus time limitation. Are hosts abundant or rare? Will the availability of carbohydrate-rich food resources (e.g., nectar, honeydew), pressure from predators, and ambient abiotic conditions support a long or a short period of active foraging? Driessen and Hemerik (1992) explored how the risk of egg limitation would change for *L. clavipes* under a range of "good" and "bad" circumstances; across 10 scenarios, predicted levels of egg limitation ranged from 2.6% to 32.0%. Given the oviposition time requirements for this parasitoid (Table 1) and taking into account the influence of changing $r_{ovip}$ on time costs, it appears that eggs will be the dominant contributor to the cost of oviposition in most, if not all, of these scenarios. Nevertheless, in many parasitoids it seems likely that the relative importance of eggs and time may be reversed as ecological circumstances change. A large empirical literature demonstrates that parasitoids adjust their behavior in response to their rate of host contact (e.g., Roitberg and Prokopy 1983; Hardy et al. 1993; Nakamura 1997; Takasu et al. 1997), projected longevity (e.g., Roitberg et al. 1992, 1993; Fletcher et al. 1994; Sirot et al. 1997), and egg load (Rosenheim and Rosen 1991; Minkenberg et al. 1992; Fletcher et al. 1994; Prokopy et al. 1994; Heimpel and Rosenheim

1995; Heimpel et al. 1996; van Randen and Roitberg 1996). These experimental results are consistent with parasitoids that are balancing the risks of egg and time limitation. The plasticity of parasitoid behavior and, in particular, the responsiveness to egg load demonstrate that egg costs have indeed been significant over evolutionary time. In the debate over how to model parasitoid reproductive behavior, the parasitoids themselves have weighed in on the side of models incorporating both egg and time costs.

This very plasticity of behavior erodes the distinction between egg and time limitation. As noted by several authors (Driessen and Hemerik 1992, Visser 1994, Mangel and Heimpel 1998), individual parasitoids may fall at any point along a continuum between strict egg limitation and strict time limitation. Some parasitoids will die without exhausting their egg supply, and yet may have foregone some opportunities to oviposit on medium- or low-quality hosts because of a high perceived risk of egg limitation. In some cases, egg limitation may be avoided precisely because the parasitoid reduces its oviposition rate through enhanced host selectivity and/or reduced clutch sizes (Mangel and Heimpel 1998). Thus, when parasitoid behavior is conditional on egg and time budgets, opportunity costs of eggs can be incurred without eventually becoming egg limited. Likewise, costs of time can be incurred without eventually becoming time limited. Dynamic optimization modeling provides a means of exploring how these perceived, but never fully realized, constraints to lifetime reproduction change the costs of oviposition predicted by the static analytical model described in Figure 2. An exploration of a dynamic optimization model for a proovigenic parasitoid supports the predictions of the simple model presented here, and suggests that the model is conservative with regards to the cost contribution from eggs (Rosenheim, unpubl. data). The dynamic optimization model also suggests that the empirically based evaluation of oviposition costs presented in Table 2 is conservative, because it employs values for the risk of egg limitation that are experienced by newly emerged females. A newly emerged cohort of females can be described as having some initial risk of egg limitation (these are the values presented in Table 2), and the time and egg costs presented in Table 2 are roughly appropriate for the first oviposition events in a female's life. However, as females age and reproduce, and some females die, the true risk of egg limitation among the surviving females will increase relative to the true value that they experienced at emergence (the subset of surviving females is enriched for those individuals that will eventually exhaust their supply of eggs); thus, egg costs become increasingly important relative to time costs for oviposition events occurring later in life (Rosenheim, unpubl. data).

*Models.*—For a general model of parasitoid reproductive behavior to represent the central features of the trade-off between current and future reproduction, both time and eggs costs must be recognized. Dynamic optimization modeling is not the only way to do this (e.g., Charnov and Stephens 1988; Hunter and Godfray 1995), but is the most widely employed approach. However, details of model formulation are critical if the role of time costs are not to be excluded inadvertently. Many dynamic optimization models of insect reproduction have assumed that at most a single host can be encountered during one time step; fitness is then maximized over this time step across a range of behavioral options (e.g., reject the host, host feed, or deposit one or more eggs). This model structure applies the same time costs to all behavioral options and thereby eliminates the contribution of time to the cost of oviposition; given the significant role of time costs suggested by the analysis presented in Table 2, this formulation is undesirable. The more sound approach is to make the model's time step correspond to the shortest-duration behavioral option (often host rejection) and assign longer time requirements (i.e., multiple time steps) for other behaviors, such as host feeding or oviposition (e.g., Iwasa et al. 1984, Heimpel et al. 1998; see also Sirot et al. 1997). In this way, both time and egg costs will be accounted for appropriately in the cost of oviposition.

*Other Costs of Oviposition.*—The model developed here to analyze the cost of oviposition has focused on two perhaps nearly universal contributors to the trade-off between current and future reproduction: eggs and time. However, there may be other contributors as well. One potentially important, but still poorly understood, factor is the physiological cost associated with oocyte maturation. In proovigenic parasitoids, these costs are paid before the adult starts ovipositing and therefore are not part of the cost of oviposition (Fig. 1). However, for synovigenic parasitoids, oocyte maturation continues into the adult stage; if accelerated oogenesis is linked obligately to oviposition, then these costs become associated with oviposition decisions. If, however, oviposition only creates an opportunity for additional oocyte maturation (for instance, by creating room in the ovaries), but oogenesis is independently regulated, then the "decision" to mature additional oocytes is distinct from the decision to oviposit, and costs and benefits of oocyte maturation should be considered separately. There is some experimental evidence suggesting a strong association between oviposition rates and rates of oocyte maturation in parasitoids (Rivero-Lynch and Godfray 1997), but whether this reflects an obligate linkage is unclear. Oocyte maturation does appear to be costly for parasitoids (Ellers and van Alphen 1997); mortality may be elevated in the short term due to competing demands for nutrient resources used for both reproduction and survival and in the longer term in the form of accelerated senescence (Tatar and Carey 1995; Carey et al. 1998).

It is also possible that a parasitoid's risk of predation may be enhanced during oviposition, as has been demonstrated for the herbivorous medfly, *Ceratitis capitata,* ovipositing in fruit (Papaj 1994). If this is the case, the time costs of oviposition will be amplified (Iwasa et al. 1984). Although I know of no studies producing strong quantitative estimates of predation risk as a function of parasitoid behavior, it may be that parasitoids with their ovipositors inserted into hosts are less able to escape from an attacking predator (see Heimpel et al. 1997).

Finally, it has been hypothesized that physical wear of the ovipositor might constrain lifetime oviposition (Jones and Kim 1994; Lalonde and Mangel 1994; Papaj and Messing 1996). If this is demonstrated to be important, then parasitoid reproductive behavior may be shaped in part by the need to minimize the number of times a host is physically pierced with the ovipositor. Such a factor could potentially comple-

TABLE 3. The relative contributions of eggs, hosts, provisions, and time to sex allocation problems found within the Hymenoptera.

| Sex allocation problem | Components of parental investment | Optimal strategy | References |
|---|---|---|---|
| Heteronomous hyperparasitoids: hosts for producing male and female offspring are found in the same habitat | eggs, hosts | If eggs are limiting, proportion males = 0.5<br>If hosts are limiting: accept all hosts encountered; proportion males will then reflect the relative encounter rates with hosts suitable for the development of male and female offspring. | Godfray and Waage (1990); Hunter and Godfray (1995) |
| Heteronomous hyperparasitoids: hosts for producing male and female offspring are found in different habitats | eggs, search time | If eggs are limiting, proportion males = 0.5.<br>If search time is limiting: allocate equal time to searching in each environment; proportion males will then reflect the relative encounter rates achieved in the two habitats. | Godfray and Waage (1990); Hunter and Godfray (1995) |
| Sex allocation in parasitoids that produce single-sex broods, with male and female broods of unequal mean size | eggs, hosts | If eggs are limiting, proportion males = 0.5.<br>If hosts are limiting: produce an equal number of male and female broods; proportion males will then reflect the mean size of all-male broods relative to all-female broods. | Godfray (1994); West et al. (1996) |
| Sex allocation in sexually dimorphic nest-building Hymenoptera | eggs, provisions for offspring | If eggs are limiting: proportion males = 0.5.<br>If provisions are limiting: invest equal provisions in males and females; proportion males will then reflect the mean food requirements of males relative to females. | Rosenheim et al. (1996) |

ment the roles of time and eggs in mediating the trade-off between current and future reproduction.

*Potential Biases.*—The estimates of oviposition rates and risks of egg limitation presented in Tables 1 and 2 may be biased because of operational factors associated with the field studies. First, observational studies may be more likely to be performed at field sites where hosts are relatively abundant, because high host and parasitoid densities facilitate the observations. Studies performed at sites with high host densities will inflate estimates of the rate of oviposition (which will tend to increase the contribution of time to the cost of oviposition) and the incidence of egg limitation (which will tend to increase the contribution of eggs to the cost of oviposition); these biases may be at least partially offsetting in their net influence on the relative contributions of time and eggs to the cost of oviposition. Second, in some cases parasitoids may divide their foraging time between within- and between-patch movement, whereas the field observations generally document only within-patch search, where all the oviposition occurs. This potential bias would inflate the estimate of the rate of oviposition and therefore the contribution of time to the total costs of oviposition.

Estimates of the relative importance of egg and time costs may also be sensitive to our measure of fitness. Our use of lifetime reproductive success as a measure of fitness rests on the assumption of stable population size (Stearns 1992). If instead the population is declining or growing, a measure of fitness that recognizes the age-specific schedule of reproduction may be important to quantifying fitness costs associated with reproduction (e.g., Tatar and Promislow 1997). For example, in a rapidly growing population where offspring produced earlier during the adult stage are more valuable than offspring produced later, the relative importance of time costs will increase, because time costs delay all subsequent reproduction, whereas egg costs are realized only later in life, when and if egg limitation occurs. The reverse is true for shrinking populations.

*Egg Limitation within the Context of Sex Allocation.*—A final factor that has perhaps contributed to the confusion surrounding the potential costliness of egg limitation is that the issue of egg limitation has also been considered in a context (sex allocation) distinct from that analyzed here (the cost of oviposition). Although the same terms have been applied to the costliness of eggs in both contexts, the costs and benefits associated with sex allocation are fundamentally different from those associated with host acceptance and clutch size (Fig. 1), and thus it is probably counterproductive to combine these two contexts without distinguishing them (*mea culpa*: Rosenheim et al. 1996; Heimpel and Rosenheim 1998). In particular, in the case of sex allocation, the evolutionary problem is to find the optimal allocation of the various components of parental investment to male versus female offspring. Parental investment typically includes eggs and the host resource itself; the time required to deposit eggs is no longer important, unless time requirements differ for male versus female eggs (the act of oviposition is a requirement for producing offspring of either sex), although the time spent in searching for hosts can be important in some cases. The biological settings in which this question has arisen, the key components of parental investment, and predictions for the optimal allocation of resources under various limiting factors are outlined in Table 3. Although the relative importance of eggs may be smaller, on average, within the context of sex allocation, because we now have the counterbalancing effect of the host resources, experimental evidence again supports that view that females employ dynamic investment strategies in response to changing risks of egg limitation versus time or host limitation (Hunter and Godfray 1995; Rosenheim et al. 1996; Kim 1997). Thus, whether we are analyzing the deployment of eggs or the assignment of sex to those eggs, we should not assume that eggs are without cost. Egg costs are a fundamental component, along with the time and host costs, in the reproductive behavior of parasitoids and their kin.

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