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Characterizing the cost of oviposition in insects: a dynamic model

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Abstract. The development of a consensus model of insect oviposition has been impeded by an unresolved controversy regarding the importance of time costs versus egg costs in mediating the trade-off between current and future reproduction. Here I develop a dynamic optimization model that places time and egg costs in a common currency (opportunity costs expressed as decreased lifetime reproductive success) so that their relative magnitudes can be compared directly. The model incorporates stochasticity in host encounter and mortality risk as well as behavioral plasticity in response to changes in the age and egg load of the ovipositing female. The dynamic model's predictions are congruent with those of a simpler, static model: both time- and egg-mediated costs make important contributions to the overall cost of oviposition. Modest quantitative differences between the costs predicted by the static versus dynamic models show that plasticity of oviposition behavior modulates the opportunity costs incurred by reproducing females. The relative importance of egg-mediated costs increases substantially for oviposition events occurring later in life. I propose that the long debate over how to represent the cost of oviposition should be resolved not by advocating the pre-eminence of one sort of cost above all others, but rather by building models that represent the complementary roles of different costs. In particular, both time and egg costs must be recognized to produce a general model of insect oviposition that incorporates a realistic representation of the cost of reproduction.

Key words: *Anagrus sophiae*, cost of reproduction, current versus future reproduction, dynamic optimization model, egg limitation, herbivore, life history trade-off, oviposition, parasitoid, time limitation

Introduction

A considerable research effort has been devoted to the development of a general model of insect oviposition (Godfray, 1994; Heimpel and Collier, 1996; Mayhew, 1997). A sound understanding of insect oviposition is important because insects are useful as model systems in the exploration of reproductive behavior in general, because insect oviposition behavior is central to the evolution of insect-plant and host-parasitoid associations (Jaenike and Papaj, 1992; Bernays and Wcislo, 1994; Janz and Nylin, 1997; Carrière, 1998), and because oviposition behavior is tied directly to reproduction, and thus is critical to attempts to link behavior with population and community dynamics (Murdoch *et al.*, 1997). Although the theoretical literature on insect oviposition has burgeoned in the last 15 years, there has been a surprising lack of consensus regarding the appropriate conceptual framework for model building. This lack of consensus stems from our lack of understanding of one of the most fundamental constraints on reproductive effort: the trade-off between current and future reproduction.

A historical perspective is useful in framing the question that I will address: what factors mediate the trade-off between current and future reproduction? The earliest models of insect oviposition behavior attempted to explain diet breadth in insect herbivores, and considered fitness returns from only a single bout of egg laying; these models did not, therefore, address the trade-off between current and future reproduction (Levins and MacArthur, 1969; Jaenike, 1978; Ward, 1987). The first models to treat this trade-off explicitly were instead motivated by a consideration of parasitoid reproduction. In one of the earliest models, Charnov and Skinner (1984) and Skinner (1985) reasoned that the lifetime reproductive success of insect parasitoids is generally limited by the time available to search for hosts (which may be cryptic and widely dispersed in the environment). Thus, Charnov and Skinner argued that time costs are likely to mediate the trade-off between current and future reproduction; that is, time spent depositing eggs on a current host is time that cannot be spent searching for other, potentially higher quality, hosts. This suggestion was adopted by many theoreticians both because of its appealing logic and because models based upon time costs could use the rate of fitness returns as a currency for assessing different behavioral options. The rate maximization currency often leads to models that are amenable to simple, transparent, and heuristic analytical solutions, a very desirable quality.

Although empirical studies of parasitoids (Freeman, 1976; Freeman and Ittyeipe, 1993; Weisser *et al.*, 1997; Rosenheim, 1999) and herbivores (Dempster, 1983; Courtney and Duggan, 1983; Courtney, 1984; Freeman and Geoghagen, 1989; Freese and Zwölfer, 1996; Dixon, 1998) support the importance of time constraints on reproductive success, many workers were immediately concerned that time costs might not be the sole mediator of the trade-off between current and future reproduction. They argued that lifetime reproductive success might also be constrained by the finite supply of eggs, and that therefore egg limitation might also contribute to the cost of oviposition (Weis *et al.*, 1983; Iwasa *et al.*, 1984; Mangel, 1987). This idea led to another family of models emphasizing the costliness of eggs (reviewed in Heimpel and Collier, 1996; Mayhew, 1997). Because these models produced predictions quite different from the predictions of models based upon rate maximization (e.g., compare Turlings *et al.*, 1985; Glaizot and Arditi, 1998; Kraaijeveld, 1999, with Mangel, 1992; Roitberg *et al.*, 1993), it became clear that the differences between them were substantive rather than merely stylistic.

Attempts to resolve the competition between the two modeling approaches focused first on the importance of egg costs. Egg costs would not be realized unless reproducing females faced some risk of exhausting their supply of eggs ('egg limitation'), and thus attention became focused on the question: Do females ever experience egg limitation? Models of the evolution of insect life histories suggested that some risk of egg limitation was likely to be present, because a population that never experienced egg limitation would be selected to reallocate resources from excess oocytes to other functions, such as enhanced somatic maintenance or the production of a smaller number of larger, more yolk-rich eggs (Rosenheim, 1996; Mangel and Heimpel, 1998; Sevenster *et al.*, 1998). Field studies also consistently revealed evidence of low to moderate levels of egg limitation in parasitoid populations (Driessen and Hemerik, 1992; Cronin and Strong, 1996; Heimpel *et al.*, 1996, 1998; Heimpel and Rosenheim, 1998; Ellers *et al.*, 1998; Casas *et al.*, 1999). Together these results strongly suggested that egg limitation was a real phenomenon, and therefore that egg costs were also real.

Rather than resolving the controversy in favor of models incorporating egg costs, however, these theoretical and empirical results instead focused attention on a new question: Is egg limitation sufficiently common that egg costs are important relative to time costs? To address this question, we must move from an evolutionary time frame to an ecological time frame, and place time costs and egg costs into a common currency so that their magnitudes can be compared directly. In an attempt to do this, I earlier presented a simple model of the costs incurred by a parasitoid in depositing a single egg in a host, given that the parasitoid faces some risk, $P_{\text{egg-lim}}$, of permanently exhausting her lifetime supply of eggs:

$$\begin{aligned}\text{Cost of oviposition} &= \text{lost opportunities for fitness returns from}\\ &\qquad \text{hosts to be parasitized in the future}\\ &= (\text{cost mediated by the egg})\\ &\qquad + (\text{cost mediated by time})\\ &= 1 \cdot P_{\text{egg-lim}} \cdot \Delta W + [(T_{\text{ovip}} - T_{\text{rej}}) \cdot r_{\text{ovip}}]\\ &\qquad \cdot P_{\text{time-lim}} \cdot \Delta W, \qquad (1)\end{aligned}$$

where ΔW is the expected fitness returns per host attacked in the future, T_{ovip} is the time required to accept a host and deposit an egg, T_{rej} is the time required to reject a host, r_{ovip} is the expected future rate of oviposition, and $P_{\text{time-lim}} = (1 - P_{\text{egg-lim}})$ is the female's risk of being time limited (i.e., dying with eggs remaining in her ovaries) (Rosenheim, 1999). The first term in the model, the cost mediated by the egg $(1 \cdot P_{\text{egg-lim}} \cdot \Delta W)$, is the product of three factors: (i) the number of hosts that cannot be attacked in the future because an egg was deposited in the current host, assuming that the parasitoid eventually becomes egg limited (i.e., 1 host), (ii) the probability that egg limitation eventually occurs (the model assumes fixed oviposition behavior, and thus egg costs are not realized unless the parasitoid subsequently runs out of eggs), and (iii) the expected fitness returns per host attacked in the future. The second term in the model $((T_{\text{ovip}} - T_{\text{rej}}) \cdot r_{\text{ovip}} \cdot P_{\text{time-lim}} \cdot \Delta W)$ is again the product of three factors: (i) the number of hosts that cannot be attacked in the future because of time allocated to depositing an egg in the current host, assuming that the parasitoid eventually becomes time limited (this equals product of the time taken to deposit an egg and the expected future rate of oviposition), (ii) the probability of eventual time limitation, and (iii) the expected fitness return per host attacked. I evaluated the model using field-estimated parameter values, and concluded that although egg limitation is generally a minority condition in parasitoid populations, egg costs are still a major (and often the dominant) contributor to the overall cost of oviposition. Furthermore, although the time required to deposit an egg is often small relative to the time required to locate a suitable host, time costs of oviposition are still generally significant. Thus, the simple, static model suggested that both time and egg costs must be considered if the trade-off between current and future reproduction is to be represented meaningfully.

A primary shortcoming of Equation (1) is that it assumes that the reproductive behavior of the ovipositing female is static (i.e., the parameters ΔW and r_{ovip} are treated as constants). This is a particularly undesirable assumption to have to make, because a central insight derived from models that recognize the dual contributions of time and eggs to the cost of oviposition is that female reproductive behavior should be fundamentally dynamic, responding to changing external (environmental) and internal (physiological) conditions. The goal of this paper, therefore, is to develop an analogue of Equation (1) that incorporates plasticity of reproductive behavior. Dynamic optimization modeling is one means of approaching this objective. Mangel and Clark (1988) have suggested that a valuable application of dynamic optimization modeling is to assess the robustness of simpler analytical models; here I employ dynamic optimization modeling with just such a goal. I explore whether or not an independent modeling framework, one incorporating flexible insect behavior and other key biological features excluded from the static analytical model (Equation (1)), produces predictions that are concordant with those derived from the static model. I will show that indeed the dynamic and static models are in complete qualitative agreement and substantial quantitative agreement. Furthermore, I will argue that the quantitative differences between the predictions of the two models are instructive, helping to illuminate the ways in which finite egg and time resources contribute to the cost of oviposition.

Methods

The modeling investigation is presented as follows. First, I develop a simple model of insect reproductive behavior using dynamic optimization (Iwasa *et al.*, 1984; Mangel and Clark, 1988; Mangel, 1992; McNamara and Houston, 1996). The model incorporates stochasticity in the processes of survival and reproduction and calculates the expected lifetime reproductive success of a female insect whose behavior is plastic, responding optimally to environmental conditions and her internal state (her age and inventory of mature eggs). In an attempt to keep the model rooted in real biology, I use the well-characterized reproductive biology of the parasitoid *Anagrus sophiae* to frame the model and establish a base set of parameter values. The model is then used in a 'computer experiment' in which the requirement to expend time and an egg to complete the act of oviposition are experimentally eliminated. The predicted costs of oviposition time and eggs are derived by comparing the expected lifetime reproductive success of insects subjected to different 'treatments' in the computer experiment. These predicted costs are compared with the predictions of the static model (Equation (1)). Finally, a sensitivity analysis is performed to assess the robustness of the model results (Gladstein *et al.*, 1991) and as a means of understanding the quantitative differences between the predictions of the dynamic and static models.

The dynamic optimization model

The model is motivated by the biology of the parasitoid *Anagrus sophiae* (Cronin and Strong, 1990, 1993a, b; Trjapitzin and Strong, 1995). This parasitoid is solitary (only one offspring can develop successfully per host, and I will assume that the female lays at most one egg per host per encounter) and strictly proovigenic (i.e., the adult parasitoid emerges with its full lifetime complement of eggs already matured). The model calculates optimal host acceptance decisions (i.e., should an encountered host be accepted, in which case a single egg is laid [$c = 1$], or should it be rejected, in which case no egg is laid [$c = 0$]) and sums the reproductive pay-offs from oviposition over an individual's lifetime.

Time is measured discretely in the model. The basic time unit, Δt, reflects the duration of the shortest host handling behavior, which is host rejection. In this way at most one host may be encountered per time step, and the extra time costs of host acceptance relative to host rejection can be incorporated in the model. For *A. sophiae*, females require an average of 62.2 s to reject a host and 5.5 min to oviposit in a host (both behaviors may involve multiple probes; Cronin and Strong, 1993a, b; J.T. Cronin, pers. comm.). Thus, setting $\Delta t = 62.2\,\mathrm{s}$, the approximate time requirements for host rejection and oviposition can be expressed in terms of the time units as $\tau_{\text{reject}} = 1$ and $\tau_{\text{oviposit}} = 5$ (time requirements for behavior b coded as τ_b; Table 1).

During each time step, the model first applies a constant risk of mortality to each female, such that the probability of survival is $\exp(-\mu)$. In the laboratory *A. sophiae* females with access to hosts and water exhibit a mean longevity of 2 days (none survived beyond day 5), with the distribution of longevities closely approximating the exponential distribution (Cronin and Strong, 1990). Assuming that *A. sophiae* females forage for 8 h per day, we have 462.7 time steps per day, the mean longevity for females is 925.4 time steps, and $\mu = 1/(\text{mean longevity}) = 0.001081$ per time step. I set the maximum female longevity, T, equal to 7 days (or 3239 time steps). (Although 3% of females live to reach the age of 7 days with $\mu = 0.001081$, virtually all of these very old females will have exhausted their eggs before that time, and thus the model predictions are insensitive to further increases in T.) An age-independent mortality risk like that employed here is appropriate for (i) species like *A. sophiae*, whose basic mortality schedule appears to be age-independent in the laboratory, and (ii) parasitoid populations that exhibit senescence in the laboratory, but which are subject to strong predation pressures in the field that prevent most females from living long enough to experience substantial senescence. Predation pressures are intense for many natural parasitoid populations (Rosenheim, 1998). Mortality rates that increase with age are explored in the sensitivity analyses below.

During each time step surviving females encounter one of i host types with probability λ_i. The probability of encountering a host is considered to be time-independent, which is approximately correct for *A. sophiae* because hosts (leafhopper eggs) are continuously recruited into the population (when adult leafhoppers oviposit), balancing their losses from the population (due to hatch or parasitism; e.g., Murphy *et al.*, 1998). Because there are no published data on host quality variation for *A. sophiae*, I incorporate such variation in a simple manner: I assume that there are two equally common host types, which differ in their quality (g_i, as measured by the fecundity of the progeny – or the number of 'grand-eggs' – that the insect can expect to produce by ovipositing on that host). Host quality variation can be thought of as reflecting either the probability that the host will support successful development of offspring, or the size/quality of resulting offspring. In the base parameter set, I let $g_1 = 34$ and $g_2 = 17$; note that only the relative magnitudes (and not the absolute values) of g_1 and g_2 are important to the model. Although there are no field data on rates of host encounter for *A. sophiae*, approximate values can be inferred from observed levels of egg depletion in field-collected females. Cronin and Strong (1996) reported that 7% of field-collected, mixed-age parasitoids had completely exhausted their lifetime supply of eggs. Although it is difficult to extrapolate from this observation to an estimate of the fraction of females who would eventually exhaust their lifetime supply of eggs at some time before death (Rosenheim, 1999), it seems likely that this risk of egg limitation would exceed 7%. Here, I assume that 10% of the parasitoids eventually run out of eggs (a value similar to the mean egg limitation reported in two other studies of parasitoids [Driessen and Hemerik, 1992; Ellers *et al.*, 1998]). Under this assumption, we can back-calculate values for λ_i; in the base parameter set I let $\lambda_1 = \lambda_2 = 0.00965$.

The model follows two state variables for each female: her inventory of eggs, x, and her age, t. Females eclose with 34 mature eggs. The maximum expected future reproductive success (measured in terms of grand-eggs produced) of a female of age t with egg load x is denoted $F(x, t, T)$. Using a simple computer algorithm (Mangel and Clark, 1988) these fitness values and the fitness-maximizing host-acceptance behavior can be calculated using backward iteration. The backward iteration begins at time T (the maximum longevity), at which time future fitness increments are defined as 0 (the 'terminal fitness function'). For all other time steps, fitness is defined as the sum of potential fitness accrued during the current time step given that a host of type i is encountered, $W_i(c) = c \cdot g_i$, plus future fitness increments to be accrued from oviposition from time steps $t + \tau_b$ to T. The dynamic programming equation is:

$$\begin{aligned} F(x, t, T) = {} & (1 - \lambda_1 - \lambda_2)\exp(-\mu)F(x, t+1, T) \\ & + \sum_{i=1}^{2} \lambda_i \max_{c=0,1}\{W_i(c) + \exp(-\mu\tau_b)F(x - c, t + \tau_b, T)\} \end{aligned}$$

The first term on the right-hand side of the equation represents the future fitness associated with not encountering a host; it is the product of the probability of not encountering a host $(1 - \lambda_1 - \lambda_2)$, the probability of survival to the next time step, $\exp(-\mu)$, and the residual fitness value for a parasitoid reaching the next time step, $F(x, t+1, T)$. The second term represents the fitness associated with encountering a host of type i. It is the product of the probability of encountering a host of type i, λ_i, and the sum of the immediate fitness returns, $W_i(c)$, and the residual fitness value, $\exp(-\mu\tau_b)F(x - c, t + \tau_b, T)$, for a parasitoid that chooses to either reject the host ($c = 0$) or accept the host ($c = 1$), depending on which behavior maximizes its lifetime fitness.

The model predicts that parasitoids should always accept the higher-quality host (host type 1); this is an intuitive result, as there can be no better reproductive opportunities in the future. Parasitoids may, however, reject the lower-quality host (host type 2), depending on their age and egg load (Fig. 1a). The model predicts that parasitoids with small egg loads and who are not closely approaching their maximum possible longevity (time T) should reject the lower quality host, thereby avoiding the opportunity costs of oviposition and saving their time and eggs to search for a higher quality host (i.e., host type 1) in the

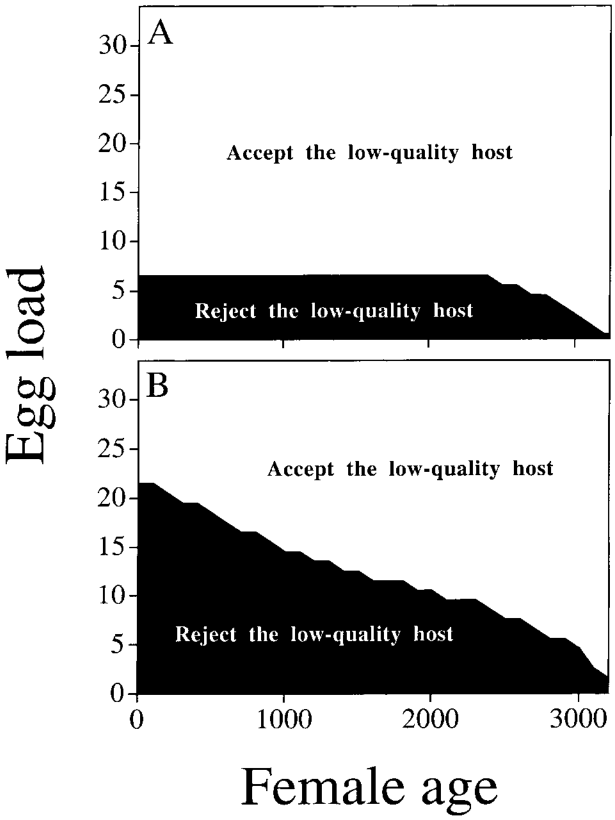

Figure 1. Influence of a female parasitoid's egg load and age on her optimal host acceptance behavior, as identified by the dynamic optimization model. In the shaded region the low-quality host should be rejected, whereas in the unshaded region the low-quality host should be accepted. The high-quality host should always be accepted. (A) Base parameter set, derived from biological studies of *Anagrus sophiae*, and assuming a mortality rate that is independent of female age (see Table 1). (B) Parameters modified to include a mortality rate that is an increasing function of female age. [$\mu = 0.0001 + (0.0000007) \cdot$ (female age, in time steps); also $g_1 = 34$, $g_2 = 6$].

future. Note, however, that although parasitoid behavior varies as a function of egg load across nearly all ages, behavior does not vary as a function of age until females closely approach the 'time horizon', T. Thus, all other things being equal, we expect to see greater contributions to the expression of behavioral plasticity made by egg load than by age (e.g., Heimpel and Rosenheim, 1995). This is an example of the familiar 'stationarity' property of many dynamic optimization problems (Mangel and Clark, 1988), and will be important when interpreting the differences between the predictions of the dynamic and static optimization models.

To describe the survival and reproduction of a cohort of parasitoids expressing optimal host acceptance behavior, I performed a Monte Carlo

Table 1. Description of parameters in the dynamic optimization model and estimates, derived from studies of *Anagrus sophiae*, used in the base parameter set

Parameter	Description	Estimate
Δt	Single time step	62.2 s
τ_b	Handling time for behavior b	$\tau_{\text{reject}} = 1$; $\tau_{\text{oviposit}} = 5$
μ	Mortality rate per time step	$\mu = 0.001081$
T	Number of time steps per lifetime	$T = 3239$
λ_i	Probability of encountering a host of type i during a single time step	$\lambda_1 = \lambda_2 = 0.00965$
g_i	Grand eggs obtained per host i	$g_1 = 34$; $g_2 = 17$

simulation (Mangel and Clark, 1988) using the same parameter values that were used in the optimization model (Table 1). The simulation tracks the lives of each of $N = 7000$ parasitoids beginning at age $t = 1$ with 34 mature eggs. At each time step, random numbers are drawn to implement a fixed probability of mortality and host encounter. Hosts are rejected or accepted for oviposition following the rule described in Figure 1a, and the simulation records the changing egg loads of parasitoids and their residual inventory of eggs at their time of death (Fig. 2). The simulation demonstrates that the stochastic nature of host encounters generates substantial variation in egg loads for same-aged parasitoids. The distributions of egg loads at the time of parasitoid death declines monotonically from egg load values of 34 to 7, at which point there is a small increase, due to the slowed rate of oviposition at these lower egg loads (lower quality hosts now generally being rejected). As desired, the simulation results in 10% of the parasitoid cohort accumulating in the absorbing state of permanent egg limitation (i.e., egg load at death $= 0$).

The static model

I calculated the egg and time costs of oviposition predicted by the static model (Equation (1)) to compare them with the predictions of the dynamic model. The goal of comparing the static and dynamic models was two-fold. First, if the models agree, then the static model could be used to provide a quick, approximate estimate of the costliness of time and eggs for reproducing females (time costs are important in a number of contexts beyond those analyzed in this paper; e.g., see Bernays (1998) on the evolution of resource specialization and Glaizot and Arditi (1998) on information gathering for host quality assessment). Second, I argue below that differences between the static and dynamic models can help us understand how behavioral plasticity shapes the costs experienced by reproducing females.

The parameters of the static model have been estimated for a number of insects in the field (Rosenheim, 1999). However, previous studies of *A. sophiae*

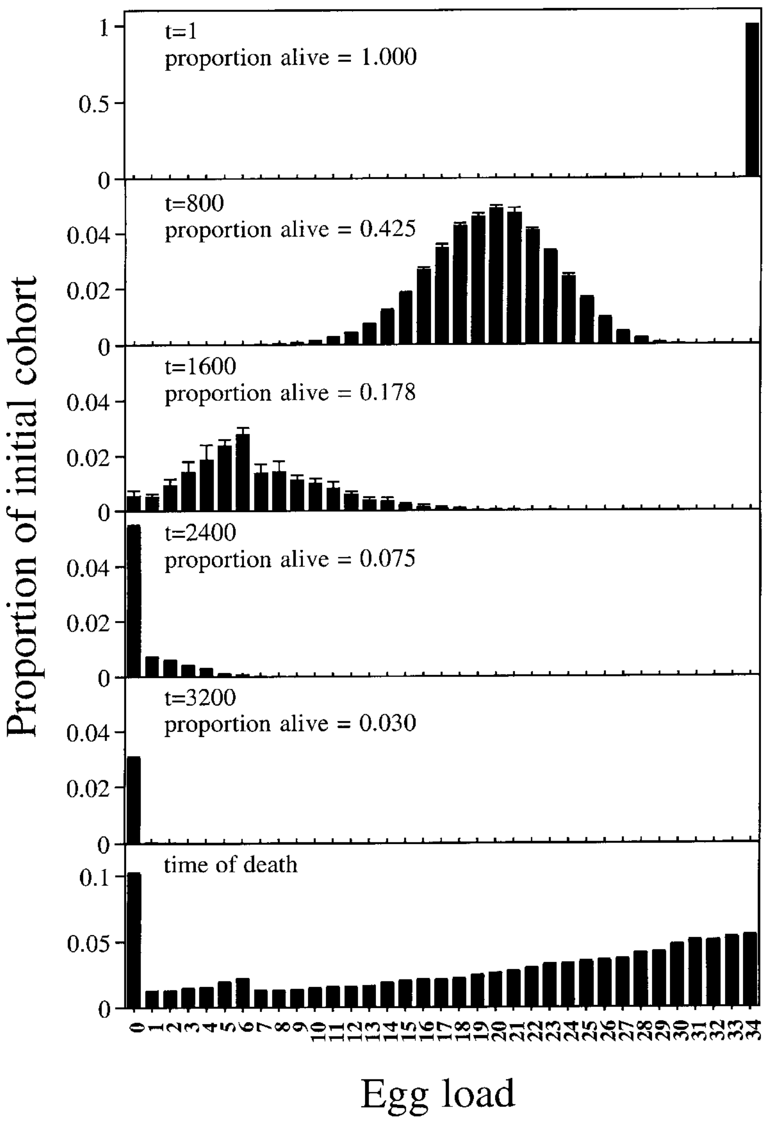

Figure 2. Dynamics of egg load distributions in a cohort of proovigenic parasitoids exhibiting the optimal host acceptance behavior identified by the dynamic model. Shown is the mean ± 1SE proportion of an initial cohort of parasitoids ($n = 7000$; replicated 5 times) at the beginning of the adult stage (time step = 1), at time steps 800, 1600, 2400, and 3200, and at their time of death (which could occur at any age, and which occurred at the time 'horizon', time step 3239, for any parasitoids that lived that long).

were not conducted with this goal in mind, and as a result we lack direct estimates of the model's parameters. For this reason, the static model was parameterized using the values obtained from the Monte Carlo simulations just described. The Monte Carlo simulations provide estimates of the parameters that directly mirror what would be measured in the field, and thus are well-suited for this surrogate role. Each replicate run of $N = 7000$ parasitoids in the 'control' treatment contributed a single estimate of (*a*) mean lifetime number of eggs laid per female, and (*b*) mean female longevity (the quotient of a/b provided an estimate of r_{ovip}); the proportion of females exhausting their total supply of eggs before death ($P_{\text{egg-lim}}$); and the mean quality of hosts accepted for oviposition (ΔW). The probability of time limitation, ($P_{\text{time-lim}}$) was calculated as $(1 - P_{\text{egg-lim}})$, except as noted below. Because the static model estimates costs incurred by a single female making an immediate oviposition decision, whereas the dynamic model estimates the average costs experienced across a cohort of newly-emerged females (some of whom will die before they encounter a host), I used the static model's predictions with projections of within-cohort mortality to obtain cohort-wide mean cost predictions that were directly comparable to the dynamic model's predictions (see Table 2 for the equations used). Multiple runs ($n = 5$ for the base parameter set and $n = 3$ for all other runs) of the Monte Carlo simulation provided replicate estimates of the static model's predictions, from which means ±1SE are reported below (standard errors are given only to illustrate the precision of the reported means).

Results

The computer experiment

The dynamic optimization model was used in a computer experiment to calculate the contributions of time and egg costs to the overall cost of a single oviposition. This was accomplished by establishing four 'treatments'. In the 'control' treatment, the normal time and egg costs associated with oviposition were retained (i.e., each oviposition required 5 time steps and 1 egg to be expended). In the 'no time cost' treatment each female was allowed to oviposit on the first accepted host by expending one egg (i.e., the normal egg cost) but only a single time step (i.e., no additional time costs beyond those required to reject a host). All subsequent oviposition was associated with the normal costs. In the 'no egg cost' treatment each female was allowed to oviposit on the first accepted host by expending 5 time steps (i.e., the normal time cost) but without expending an egg (i.e., egg load was not decremented). Again, all subsequent oviposition was associated with the normal costs. In the 'neither time nor egg cost' treatment each female was allowed to oviposit on the first accepted host by expending only a single time step and without expending an egg (i.e., no additional time or egg costs beyond those required to reject a host). Again, all subsequent oviposition was associated with the normal costs. The model reveals how eliminating the time and egg requirements of a single oviposition event influences the expected lifetime number of hosts parasitized, quality of hosts parasitized, and fitness (Table 2). The time costs of a single oviposition can be calculated as [(Fitness in the 'no time cost' treatment) – (Fitness in the 'control' treatment)], and the egg costs of a single oviposition can be calculated as [(Fitness in the 'no egg cost' treatment) – (Fitness in the 'control' treatment)]. The total cost (time + egg) of oviposition can be calculated as [(Fitness in the 'neither time nor egg cost' treatment) – (Fitness in the 'control' treatment)]; interactions between time and egg costs can be examined by asking if the total cost of oviposition is as predicted by the sum of the time and egg cost calculated separately.

The most important results of this study are obtained by considering the time and egg costs predicted by the dynamic model and by comparing them to

Table 2. Contributions of oviposition time and the deposited egg to the cost of oviposition. Shown are the expected lifetime number of hosts parasitized, mean quality of hosts parasitized, and fitness (expected number of grand-eggs produced) of a female parasitoid that employs the optimal host acceptance behavior identified by the dynamic optimization model. Model output is shown for four 'treatments': a control, treatments in which time costs or egg costs of a single oviposition event are eliminated, and a treatment in which both the time and egg costs are eliminated. Predictions from a static oviposition model (Equation (1)) are also presented for comparison. Base parameter set for *Anagrus sophiae* (Table 1)

Treatment	Expected lifetime number of hosts parasitized	Expected mean quality of hosts parasitized	Lifetime reproductive success (grand-eggs)	Cost components predicted by the dynamic model	Cost components predicted by the static model; mean (1SE)
Control	14.201	25.980	368.954		
No time cost	14.259	25.980	370.448		
No egg cost	14.338	25.948	372.047		
Neither time nor egg costs	14.396	25.948	373.554		
Time cost				1.494	1.391 (0.003)[a]
Egg cost				3.093	2.623 (0.040)[b]
Time + Egg costs				4.600	4.014 (0.029)

[a] Predicted time cost estimated as: $P_{\text{surv}(t=\text{1st oviposition})} \cdot (T_{\text{ovip}} - T_{\text{rej}}) \cdot r_{\text{ovip}} \cdot P_{\text{time-lim}(t=\text{1st oviposition})} \cdot \Delta W$, where $P_{\text{surv}(t=\text{1st oviposition})}$ is the probability that a female will survive from emergence until the first oviposition (when the 'treatments' were applied), $P_{\text{time-lim}(t=\text{1st oviposition})} = [1 - P_{\text{egg-lim}(t=0)}/P_{\text{surv}(t=\text{1st oviposition})}]$ is the probability of time limitation for females that are still alive at the time of the first oviposition, and $P_{\text{egg-lim}(t=0)}$ is the probability of egg limitation for a newly-emerged female (i.e., the fraction of the initial cohort that will eventually run out of eggs). All parameter values derived from the Monte Carlo simulations for 'control' treatment females.

[b] Predicted egg cost estimated as: $P_{\text{surv}(t=\text{1st oviposition})} \cdot P_{\text{egg-lim}(t=\text{1st oviposition})} \cdot \Delta W$, where $P_{\text{egg-lim}(t=\text{1st oviposition})}$ is the probability of egg limitation for those females that are still alive at the time of the first oviposition.

costs calculated with the static model. First, despite the fact that egg limitation is a minority condition in the parasitoid population, egg costs are substantial (3.093 grand-eggs, representing 67.2% of the overall cost of oviposition). Second, despite the fact that oviposition is relatively rapid (oviposition requires only 5 time steps, whereas hosts that are accepted for oviposition are encountered only once per 65.2 time steps, on average), time costs are also substantial (1.494 grand-eggs, representing 32.5% of the overall cost of oviposition). Thus, the dynamic model's predictions are concordant with the primary qualitative conclusion from my earlier analysis of the static model (Rosenheim, 1999): both time and egg costs appear to make important contributions to the overall cost of oviposition. Third, time and egg costs do not show important interactions: the total cost of oviposition (4.600) is almost exactly as predicted by the sum of the egg cost and the time cost (3.093 + 1.494 = 4.587; a discrepancy of only 0.3%). Additive time and egg costs were observed to be a robust result in the sensitivity analyses (data not shown); therefore for the sake of brevity the 'neither time nor egg cost' treatment is not addressed further.

Fourth, quantitative cost estimates produced by the dynamic model are relatively similar to those produced by the static model. The time costs predicted by the static and dynamic models are fairly close when the model is run with the base parameter set (Table 2; the values show a discrepancy of 6.9%), and indeed in all subsequent model runs (see below). The modest differences in time cost predictions are generated by small inaccuracies in the way I estimated r_{ovip} and ΔW for the static model. I used average lifetime values for these parameters, but the treatments were applied at a single moment in the female's life, and both r_{ovip} and ΔW will generally change over time as females change their host acceptance behavior and as some females eventually exhaust their supply of eggs. When the models were run with parameter values under which r_{ovip} and ΔW were invariant across a female's life, the time cost estimates of the static and dynamic models were essentially identical (within 0.25%; data not shown). More important than the small differences in time cost estimates, under the base parameter set the dynamic model's estimate of egg costs is 18% greater than the static model's estimate.

Why does the dynamic model produce a somewhat larger estimate of the opportunity cost of using an egg? An answer is suggested by noting that females in the 'no egg cost' treatment differ from females in the 'control' treatment in not only the lifetime number of hosts attacked (which increases), but also in the mean quality of hosts attacked (which decreases, Table 2). This suggests that the host acceptance decisions of these females differ from those of the control females. Of course, it is exactly because dynamic optimization models can illuminate this sort of behavioral response, for which empirical support is now widespread (Bjorksten and Hoffman, 1998; Rosenheim, 1999), that they are preferred for this analysis. The extra egg held by females in the 'no egg cost' treatment prolongs the period during which they accept the lower quality host (the treatment shifts them up one egg on the *y*-axis of Fig. 1a), thereby enhancing the rate of oviposition and decreasing the mean quality of accepted hosts. Behavioral plasticity does not produce a measurable change in the mean quality of hosts accepted by females in the 'control' versus 'no time cost' treatments (Table 2), because optimal host acceptance behavior is only minimally responsive to female age (that is, the optimal host acceptance behavior is 'stationary' across most of the female's life; Fig. 1a). If, however, the model is modified so that host acceptance behavior is no longer stationary, then the 'no time cost' treatment also produces a modest shift in the mean quality of accepted hosts compared to the 'control' treatment (see the sensitivity analysis below). This interpretation of the causal basis for the quantitative differences between the static and dynamic model predictions can be 'tested' with a further computer experiment, which I now present, in which host quality variation is manipulated.

Host quality variation and behavioral plasticity

If, as just hypothesized, it is behavioral plasticity in response to egg load that is responsible for the modest quantitative difference between the egg costs predicted by the dynamic versus the static model, then the predictions of the two models should be more nearly equivalent if the opportunities for behavioral plasticity to enhance parasitoid fitness are eliminated. This can be accomplished by eliminating variation in host quality from the model. When all hosts are of equal quality, the dynamic model predicts that any host that is encountered should be accepted, regardless of egg load, and thus no opportunities exist for conditional behavior to shape the model's outcome. When the model is parameterized as in Table 1, but both host types are now equal in quality ($g_1 = g_2 = 34$), the egg costs predicted by the dynamic optimization model (4.362 grand-eggs) do indeed become more similar to those predicted by the static model (4.695 grand-eggs).

Can the remaining discrepancy between the dynamic and static models' predictions (the dynamic model now underestimates the egg cost by 7.6%) be understood? The difference between the models appears to stem from imprecision in the way egg costs are formulated in the static model. The static model assumes that all parasitoids that exhaust their supply of eggs before death pay the cost of egg limitation (even when all hosts are equal in quality). Is this correct? For the cost of egg limitation to be realized, parasitoids that have run out of eggs must actually live long enough to encounter one additional host (in this case, the 35th host of their lives); that is, they must encounter a host that they cannot parasitize because they have no remaining eggs. With the probability of host encounter equal to 0.0193 ($\lambda_1 = \lambda_2 = 0.00965$), the expected time to encounter an additional host is $1/(\lambda_1 + \lambda_2) = 51.8$ time steps. With a mortality rate of 0.001081, the probability of living 51.8 time steps is 0.946. Thus, the predictions of the static model can be improved by discounting the egg cost by a factor of 0.946; the resulting prediction of 4.440 grand-eggs is now very close (within 1.8%) to the value predicted by the dynamic model (4.362 grand-eggs). Thus, the static model (Equation 1) is somewhat imprecise because of the finite fecundity of real insects, the imprecision being more important as fecundity decreases. This point will be especially important when the costs of egg limitation are examined for highly synovigenic insects, which may experience repeated bouts of transient egg limitation, and whose egg inventories may be quite small (often < 10 eggs, e.g., Tatar, 1991; Heimpel *et al.*, 1998; Casas *et al.*, 1999).

Thus far, I have assumed that the probability of egg limitation, $P_{\text{egg-lim}}$, and the probability of time limitation, $P_{\text{time-lim}}$, sum to 1.0. If, then, the static model is slightly overestimating the cost of egg limitation, does that mean that it is necessarily incorporating an error in calculating the cost of time limitation? No. The important observation here is that, ignoring variation in host quality, the finite fecundity of real insects means that it is actually possible for time and eggs to be ‘perfectly’ balanced. This is achieved by those females who deposit their last egg and then die before they encounter another host. The fitness of such females would not be enhanced by either an increase in longevity or an increase in fecundity alone; instead, a simultaneous increase in both would be required to augment female reproductive success. Thus, in the absence of host quality variation, finite female fecundity means that the probability of time limitation and the probability of egg limitation do not sum exactly to 1.0.

Sensitivity analysis: effect of oviposition time requirements

Do the static and dynamic models continue to produce congruent predictions when time and egg costs differ widely in their relative magnitudes? To address this question, I performed a sensitivity analysis examining the role of oviposition time requirements, a variable with a direct influence on time costs of oviposition. This is a biologically relevant variable to examine in a sensitivity analysis, because actual oviposition times can vary widely, from a fraction of a second to many minutes (Godfray, 1994; Quicke, 1997; Rosenheim, 1999); hosts that can escape from, or defend themselves against, an attacking parasitoid are often attacked more rapidly than hosts that are sessile and defenseless. Time and egg costs predicted by the dynamic model are

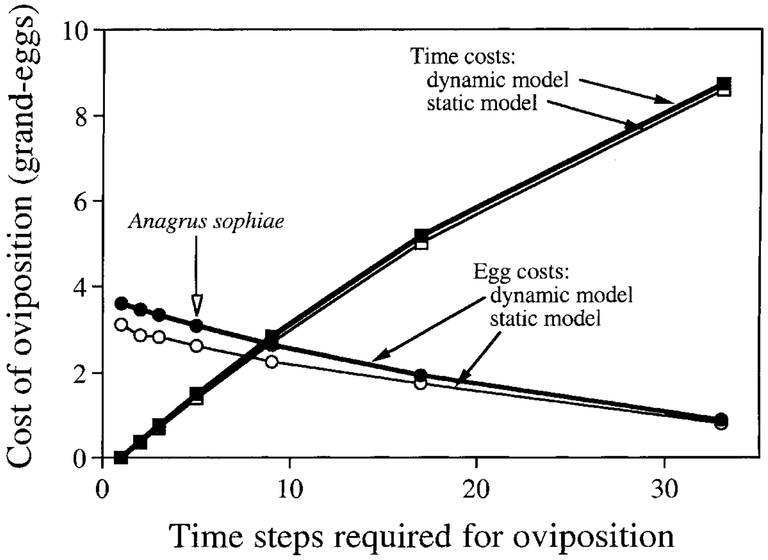

Figure 3. Sensitivity analysis of the effect of oviposition time requirements on the egg-mediated costs (circles) and time-mediated costs (squares) of oviposition predicted by the static model (open symbols) versus the dynamic model (filled symbols). Means are plotted without SE bars, which are too small to discern. The base parameter set, reflecting the biology of *Anagrus sophiae*, includes an oviposition time requirement of 5 time steps.

quantitatively similar to those predicted by the static model across a wide range of oviposition times (Fig. 3). As the time requirement for oviposition is increased, egg costs decrease because the risk of egg limitation declines (from 12.0% when oviposition time = 1 time step to 3.1% when oviposition time = 33 time steps); long oviposition time requirements decrease the realized rate of oviposition, and therefore make it less likely that females will exhaust their entire supply of eggs. The dynamic model predicts that time and egg costs would be equal for *A. sophiae* if oviposition time requirements were increased from 5.5 (the actual value; Cronin and Strong, 1993a, b) to 9.3 min.

Sensitivity analysis: effect of oviposition number

All of the analyses presented thus far have examined the costs associated with ovipositing on the first host that a female accepts during her reproductive lifetime. Do the relative magnitudes of egg and time costs change as a female deposits successive eggs over her lifetime? We might expect that indeed the cost estimates will change, because as females in a cohort age and reproduce while experiencing a constant risk of mortality, the subset of survivors is enriched for those individuals that will live long enough to deposit all their eggs. That is, the probability of egg limitation increases as females deposit successive eggs

(Fig. 4a). To explore the effects of oviposition number, I repeated the computer experiment with the base set of parameters (Table 1), but with the treatments applied to the first oviposition, every fifth oviposition thereafter, and the final (34th) oviposition.

The egg-mediated cost of oviposition is exactly constant if viewed from the perspective of an entire initial cohort of females (Fig. 4b). Although fewer

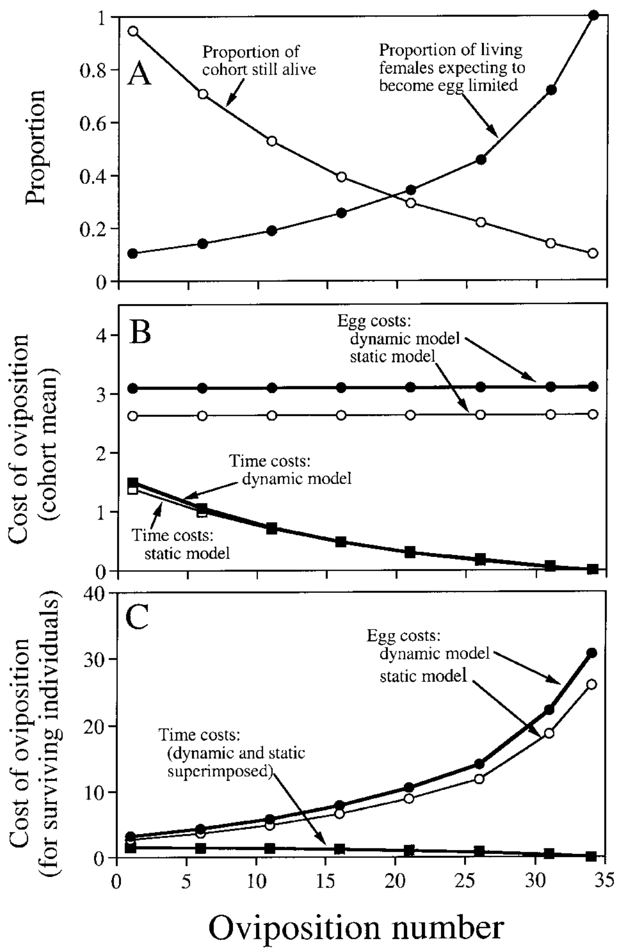

Figure 4. Sensitivity analysis of the influence of successive ovipositions on the relative magnitudes of egg- and time-mediated costs of oviposition. (A) Survivorship of a cohort of ovipositing females, and the proportion of females expected to become egg-limited among sub-cohorts of females who survive to reach the *n*th oviposition. (B) Egg-mediated costs (circles) and time-mediated costs (squares) of oviposition predicted by the static model (open symbols) versus the dynamic model (filled symbols). These values are averaged across all members of the original cohort of females. (C) As in (B), except the costs are averaged across only those members of the original cohort that survive to reach the *n*th oviposition.

females live to reach later oviposition events (and therefore, fewer females pay the egg-mediated cost of this oviposition), this decrease is exactly offset by the increasing risk of egg-limitation and therefore the increasing opportunity cost of egg use experienced by the surviving females (Fig. 4a). This can be understood intuitively as follows. Let $C_{\text{egg-}n}$ be the cohort-wide egg-mediated cost of the nth oviposition, $P_{\text{surv}(t=\text{nth oviposition})}$ be the probability of surviving to the nth oviposition, $P_{\text{egg-lim}(t=n\text{th oviposition})}$ be the probability of egg limitation among females living to the nth oviposition, and ΔW be the expected fitness returns per host. The initial cohort of newly-emerged females anticipates the following egg-mediated cost associated with the nth oviposition:

$$C_{\text{egg-}n} = P_{\text{surv}(t=n\text{th oviposition})} \cdot P_{\text{egg-lim}(t=n\text{th oviposition})} \cdot \Delta W. \tag{2}$$

Note, however, that

$$P_{\text{egg-lim}(t=n\text{th oviposition})} = P_{\text{egg-lim}(t=0)} / P_{\text{surv}(t=n\text{th oviposition})}, \tag{3}$$

where $P_{\text{egg-lim}(t=0)}$ is the probability of egg limitation experienced by newly-emerged females. Substituting (3) into (2) and simplifying, we obtain

$$C_{\text{egg-}n} = P_{\text{egg-lim}(t=0)} \cdot \Delta W.$$

Thus, the cohort-wide expected egg costs are unchanging over successive ovipositions. Cohort-wide time costs, however, decline strongly (Fig. 4b), both because fewer females are alive to incur the costs and because the probability of time limitation decreases as females reach successive oviposition events.

We are also interested in the perspective of the individual female who lives long enough to reach the nth oviposition of her life. The sensitivity analysis demonstrates that the relative importance of egg-mediated costs increases dramatically relative to time-mediated costs for oviposition events occurring later in life (Fig. 4c). This is a critical point that has not been addressed in previous discussions of insect reproduction, but which is entirely congruent with models predicting increasingly selective host use by ovipositing females as their egg load declines (Mangel, 1987; Minkenberg *et al.*, 1992; Heimpel *et al.*, 1998). The subset of females who escape mortality factors for long enough to reach later oviposition events is enriched for those individuals who will eventually exhaust their lifetime supply of eggs. Thus, an inexorable demographic process means that egg costs are most modest early in the female's life (which were the focus of my earlier work; Rosenheim, 1999) and increasingly strong later in life. For example, for the base parameter set, whereas the first oviposition was associated with an egg cost of 3.3 grand-eggs (Fig. 4c), the 34th oviposition cost 30.6 grand-eggs. The mean cost of an egg averaged across all oviposition events during a female's life was 7.4 grand-eggs (mean weighted by $P_{\text{surv}(t=n\text{th oviposition})}$).

Sensitivity analyses: other parameters

I performed sensitivity analyses for a number of additional model parameters or features. First, to test if the congruence of the static and dynamic models was sensitive to the near stationarity of host acceptance behavior (Fig. 1a), I explored a model that incorporated age-dependent mortality rates (see Vaupel *et al.*, 1998). When mortality rates increase linearly with female age, host acceptance behavior is sensitive to age across the entire female lifespan (Fig. 1b). Nevertheless, the predictions of the static and dynamic models remain quantitatively very similar (Table 3); females freed from the normal egg cost show a slight decrease in the mean quality of hosts accepted, whereas females freed from the normal time cost show a slight increase in the mean quality of hosts accepted. Thus, parasitoids adjust their host acceptance behavior in response to their changing risks of becoming egg versus time-limited.

I also examined the effect of varying the mortality rate, the host encounter rates, the basic time step of the model, and the number of time steps until the time horizon was reached. In all cases the static and dynamic models continued to produce similar estimates of both the time and egg costs.

Discussion

The dynamic model, incorporating behavioral plasticity in host acceptance and stochasticity in host encounter and female mortality, produced results that were congruent with the results of a simpler, static model. Even when egg limitation is a minority condition in a population of ovipositing females, the

Table 3. Comparison of the time and egg costs of oviposition predicted by the static model and the dynamic model for the case where female mortality increases with female age (parameters described in legend of Fig. 1b)

Treatment	Expected lifetime number of hosts parasitized	Expected mean quality of hosts parasitized	Lifetime reproductive success (grand-eggs)	Cost components predicted by the dynamic model	Cost components predicted by the static model; mean (1SE)
Control	20.229	22.548	456.119		
No time cost	20.271	22.561	457.331		
No egg cost	20.611	22.264	458.878		
Time cost				1.212	1.215 (0.006)
Egg cost				2.759	2.095 (0.074)

opportunity cost of egg use is a major contributor to the overall cost of oviposition. Furthermore, even when the act of oviposition is rapid relative to the time requirements of host location, the opportunity cost of the time required to deposit an egg is also a major contributor to the overall cost of oviposition. Therefore, I propose that the long debate over how to represent the cost of oviposition – a debate that has been conducted in parallel by students of parasitoid oviposition behavior (reviewed by Rosenheim, 1996) and by students of herbivore oviposition behavior (reviewed by Mayhew, 1997) – should be resolved not by advocating the pre-eminence of one cost factor above all others, but rather by building models that represent the complementary roles of time and egg costs. Finally, the static model supplied with parameter values measured in the field appears to be a simple but useful tool for researchers wishing to estimate the relative magnitudes of the time- and egg-mediated costs.

Subtle differences were observed in the quantitative cost estimates produced by the static and dynamic models. These differences are instructive, illuminating the nature of the opportunity costs incurred by ovipositing females. As the risk of egg limitation increases, the optimal behavior of ovipositing females is to increase their selectivity, raising the quality threshold below which hosts are rejected (Mangel, 1987); thus, the decrease in egg load that accompanies an oviposition event results in an increase in the mean quality of hosts that are accepted and a concomitant decrease in the overall rate of oviposition. The net result of this behavioral plasticity is that the risk of egg limitation imposes costs that differ from the simplest costs represented in the static model, namely the inability to exploit hosts after the lifetime supply of eggs has been exhausted. The same is true for the opportunity costs experienced by females responding to a risk of time limitation: as the risk of time limitation increases, the optimal behavior of ovipositing females is to decrease their selectivity, lowering the quality threshold below which hosts are rejected; thus, the decrease in time that accompanies an oviposition event results in a subsequent decrease in the mean quality of hosts that are accepted and a concomitant increase in the overall rate of oviposition. The opportunity costs associated with devoting time to egg deposition therefore differ from the simplest costs represented in the static model, namely the loss of time to forage for the next host.

Despite the fact that the dynamic model incorporated behavioral flexibility in response to age and egg load, it produced estimates of time- and egg-mediated costs of oviposition that were broadly congruent with those of the static model. Why? In the base parameter set, oviposition behavior was sensitive to egg load only when egg loads were heavily depleted (<7) and was sensitive to age only when females approached their maximum longevity (age >2400 time steps; Fig. 1a). Thus, only a minority of females deposited enough eggs or lived long enough for their host acceptance behavior to be state-dependent, and this diminished the opportunities for large discrepancies to exist between the two models. However, even when the parameter values were changed in the sensitivity analyses so that female behavior was state-dependent across nearly the full range of egg loads and ages (e.g., Fig. 1b and Table 3), the dynamic and static models continued to be in agreement. The static model ignores a great deal of variability in behavior, but still produces a cost estimate that is approximately correct as a mean expectation of lost future reproduction. For researchers interested in the average cost of oviposition experienced by a cohort of female insects, the static model appears to be a useful tool, because it successfully averages across age- and egg-load driven variability in host acceptance behavior. The dynamic model will be critical in other applications, where the primary emphasis is on the behavioral variability itself.

The view of the cost of oviposition that emerges from this study is one that has been anticipated by a now substantial body of experimental studies. Studies of both herbivores and parasitoids have documented exactly the sort of behavioral plasticity that is predicted for insects that are balancing time and egg costs (see reviews by Minkenberg *et al.*, 1992; Heimpel and Collier, 1996; Mayhew, 1997; Cronin and Strong, 1999; Rosenheim, 1999). Although experimental manipulations have been used to isolate the behavioral effects of egg costs (Rosenheim and Rosen, 1991; Prokopy *et al.*, 1994; Heimpel and Rosenheim, 1995; van Randen and Roitberg, 1996), the same cannot at present be said for time costs (but see Papaj and Alonso-Pimentel, 1997). Studies evaluating the oviposition response to hosts that are similar in quality but different in their handling-time requirements might be especially useful in this regard.

The model that I have analyzed here was guided by a consideration of the biology of *A. sophiae*, a parasitoid that emerges with its full complement of eggs already matured (i.e., a strictly proovigenic species). Does the analysis tell us anything about egg-mediated costs of oviposition for species that continue to mature eggs during the adult stage (i.e., synovigenic species)? For proovigenic species, egg limitation is always permanent; having deposited their last egg, there is no opportunity to mature additional eggs. Thus, my model represents the full opportunity cost of egg use for strictly proovigenic species. For synovigenic species, however, egg limitation may be either permanent or transient (Heimpel and Rosenheim, 1998; Ellers, 1998), and my model incorporates only that contribution to total egg cost that is made by the permanent form of egg limitation. A permanent form of egg limitation appears to occur in most synovigenic species: when females are given rich opportunities to oviposit in the laboratory, the physiological ability to mature additional oocytes appears to degrade before the ovipositing female dies, producing a ‘post-reproductive period’ (Jervis *et al.*, 1994; Carey *et al.*, 1998). In *Drosophila* this reproductive senescence appears to be linked to the finite life span of individual somatic and germline stem cells in the ovarioles (Margolis and Spradling, 1995). Although I know of no formal reviews of the prevalence of a post-reproductive period for either parasitoids or herbivores, an examination of descriptive, life-table studies of parasitoids in the journal *Entomophaga* (1990–1995) revealed 12 relevant laboratory studies, 9 of which documented a post-reproductive period. The incidence of post-reproductive periods under laboratory conditions may be even more widespread than indicated by a survey of the literature, because most published studies report age-specific fecundity and mortality rates averaged across cohorts, which tend to hide short post-reproductive periods (e.g., contrast Table 1 and Fig. 1 in Shirota *et al.*, 1983). However, it should be emphasized that field studies quantifying the incidence of permanent egg limitation in strongly synovigenic species have not yet been performed, and it is possible that permanent egg limitation occurs less often in strongly synovigenic than in proovigenic species. Synovigenic species may also experience transient periods of egg limitation, in which the ovaries are emptied and further oviposition must await the maturation of additional oocytes. Many insects appear to experience substantial risks of transient egg limitation, even on a daily basis (Tatar, 1991; Heimpel *et al.*, 1998; Casas *et al.*, 1999). Further work is needed to quantify the combined costs of transient and permanent risks of egg limitation; the current model, however, presents the full egg-mediated cost for those species experiencing only permanent egg limitation (strictly or predominantly proovigenic species), and a partial or minimum cost estimate for species experiencing both permanent and transient egg limitation (strongly synovigenic species).

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