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Egg maturation, egg resorption and the costliness of transient egg limitation in insects

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Although there is widespread agreement that the cost of oviposition underlies selective oviposition in insects, there is no consensus regarding which factors mediate the cost of oviposition. Models have suggested that egg costs are often paramount in those insects that do not continue to mature eggs during the adult stage (pro-ovigenic insects). Here we address the hypothesis that egg costs are generally less significant in synovigenic insects, which can replenish oocyte supplies through continuous egg maturation. A dynamic optimization model based on the biology of a highly synovigenic parasitoid, *Aphytis aonidiae*, suggests that the maximum rate of egg maturation is insufficient to balance the depletion of eggs when opportunities to oviposit are abundant. Transient egg limitation therefore occurs, which imposes opportunity costs on reproducing females. Thus, whereas the most fundamental constraint acting on the lifetime reproductive success of pro-ovigenic species is the fixed total number of eggs that they carry at eclosion, the most fundamental constraint acting on a synovigenic species is the maximum rate of oocyte maturation. Furthermore, the ability of synovigenic species to reverse the flow of nutrients from the soma to oocytes (i.e. egg resorption) has a dramatic influence on the cost of oviposition. Whereas females in host-rich environments may experience oviposition-mediated egg limitation, females in host-poor environments may experience oosorption-mediated egg limitation. Both forms of egg limitation are costly. Contrary to initial expectations, the flexibility of resource allocation that typifies synovigenic reproduction actually appears to broaden the range of conditions under which costly egg limitation occurs. Egg costs appear to be fundamental in mediating the trade-off between current and future reproduction, and therefore are an important factor favouring selective insect oviposition.

Keywords: cost of reproduction; cost of oviposition; current versus future reproduction; egg limitation; time limitation; egg resorption

1. INTRODUCTION

Herbivorous and parasitic insects are selective when choosing hosts upon which to deposit eggs. Hosts that offer a non-zero probability of supporting successful offspring development but which are suboptimal in some way are often rejected. Why? Williams (1966) was the first to recognize the pivotal importance of the cost of reproduction, and specifically the trade-off between current and future reproduction, to the evolution of reproductive strategies. There is widespread agreement that Williams' thesis explains selective oviposition in insects: the benefits from ovipositing on a marginal-quality host can be too small to offset costs in the form of decreased opportunities for future reproduction. But what factors mediate the trade-off between current and future reproduction in insects? Here there has been no consensus.

Extensive research has been devoted to developing a mechanistic understanding of the cost of reproduction in different groups of animals (Clutton-Brock 1991; Ylönen *et al.* 1998). The exact nature of such costs often depends critically upon the specific biology of the animal being considered. For insects, which generally do not exhibit parental care following oviposition, different schools of thought have emerged regarding the factors mediating the cost of reproduction, and in particular the 'cost of oviposition', which includes only those costs that are incurred by accepting a host and averted by rejecting a host (Rosenheim 1996, 1999*a*; Sevenster *et al.* 1998). One school has argued that these costs are mediated entirely by the time required to deposit eggs (e.g. Charnov & Skinner 1984; Visser *et al.* 1992; Glaizot & Arditi 1998; Kraaijeveld 1999). Another school has argued that the finite lifetime supply of eggs is also often important in mediating the cost of oviposition (e.g. Iwasa *et al.* 1984; Mangel 1989; Mangel *et al.* 1994; Collier 1995*a*; McGregor 1997). In either case, the cost of oviposition can be viewed as an opportunity cost: time or eggs that are devoted to exploiting a current host cannot be used in the future to exploit another, potentially higher-quality, host.

In an attempt to resolve the differences between these two competing schools, Rosenheim (1999*a*,*b*) developed models that place the time and egg costs of oviposition in a common currency (foregone future fitness returns) so that their relative magnitudes could be directly compared. The models showed that even when only a small fraction of individuals in a population exhaust their lifetime supply of eggs, egg costs often continue to make an important contribution to the overall cost of oviposition. Time costs, however, may still be important, especially when hosts are scarce and therefore virtually all females have more oocytes than they will ever have a chance to deposit. Thus, the general conclusion that emerged was that both time and eggs can make important

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contributions to the cost of oviposition, with egg costs predominating when hosts are abundant and time costs predominating when hosts are rare.

For the sake of maximum transparency, these models assumed that egg maturation was pro-ovigenic, i.e. that all oocyte maturation occurs prior to adult eclosion. Pro-ovigeny is a life-history pattern that incorporates a rigid one-time allocation of resources between somatic maintenance and reproduction. Many insects, however, continue to mature oocytes during the adult stage (i.e. synovigeny; Volkoff & Daumal 1994; Boggs 1997*a*,*b*; Rivero & Casas 1999*a*). A natural objection, therefore, to the earlier analyses is that many insects retain substantial flexibility in allocating resources to reproduction versus somatic maintenance during the adult stage, thereby minimizing the risk that egg supplies would be exhausted, even when hosts are abundant. Insects are noteworthy relative to many other animals for the speed with which eggs can be fully provisioned with yolk and readied for deposition (Papaj 2000). No insect, however, can mature oocytes instantaneously. Furthermore, some synovigenic insects have limited abilities to store mature oocytes and, therefore, may carry only a few mature eggs in their ovaries at any time (Iwata 1964). Therefore, even synovigenic insects may experience transient bouts of egg limitation, when they exhaust their supply of mature oocytes and must await further egg maturation before they can resume reproduction (Charnov & Skinner 1988; Heimpel & Rosenheim 1998; Casas *et al.* 2000).

The purpose of this paper is to analyse the cost of oviposition for an insect that exhibits a very high level of flexibility in reproductive allocations, the parasitoid *Aphytis aonidiae*. *A. aonidiae* feeds as an adult on host and non-host foods, and can use the nutrients obtained thereby to continue to mature eggs. Furthermore, like many synovigenic insects, *Aphytis* spp. can reverse the allocation of nutrients to reproduction by resorbing oocytes during times of metabolic stress (Collier 1995*b*; Heimpel & Rosenheim 1995; Heimpel *et al.* 1997). Specifically, we ask the following questions: (i) Does synovigeny eliminate the opportunity costs of depositing eggs (or, on the contrary, do opportunity costs remain because of constraints on the rate of egg maturation and the capacity to store eggs), and (ii) does the ability to resorb oocytes influence the relative importance of time versus egg costs?

2. METHODS

We use a dynamic optimization model to analyse the cost of oviposition in *A. aonidiae*. This model has been described in detail elsewhere (Heimpel *et al.* 1998), so we begin with only a synopsis of its primary features. We then describe how the model was modified to estimate the time- and egg-mediated costs of oviposition. Finally, we incorporate the dynamics of egg resorption into the model to explore their influence on the trade-off between current and future reproduction.

(a) *The dynamic optimization model*

A model of the feeding and oviposition behaviour of *A. aonidiae* was previously developed to explore factors limiting the lifetime reproductive success in this minute parasitoid wasp (Heimpel *et al.* 1998). The key features of the model are as follows. Parasitoids emerge as adults with both mature oocytes and protein reserves derived from larval feeding. Adult parasitoids then search in the environment for hosts, the armoured scale *Quadraspidiotus perniciosus*, upon which they can feed (to augment their protein reserves, which are used to mature additional eggs and for somatic maintenance) or oviposit (garnering reproductive success). (Note that a model with more parameters would be needed for a parasitoid that feeds on one set of hosts and oviposits on a different set of hosts.) Host encounter is represented as a stochastic process. Hosts exist in three quality classes defined by the number of eggs a daughter developing on that host would carry at emergence (7, 10 and 12 eggs, respectively; we will refer to these as 'grand-eggs'). Mortality, due entirely to predation, is also represented as a stochastic process. The model follows the lifetime of a female parasitoid, calculating the optimal behaviour at each time step as a function of the parasitoid's age, protein reserves and supply of mature eggs ('egg load'). The model also calculates the expectation of future reproduction in units of grand-eggs produced, $F(x, y, t, T, d)$, for females with x eggs and y units of protein reserves at a given time-step, t, on day d, where T is the maximum female longevity. Parameter values describing ecological processes were measured in field studies (Heimpel *et al.* 1996; Heimpel & Rosenheim 1998) and parameters describing physiological processes were measured in laboratory studies of a congeneric species, *Aphytis melinus* (Collier 1995*b*; Heimpel & Rosenheim 1995; Heimpel *et al.* 1997). Here we adopt the central estimates of all parameter values (see Heimpel *et al.* 1998) as our base set of parameters (table 1).

The egg load and protein-reserve levels of newly emerged adult *A. aonidiae* are not known. As discussed in Heimpel *et al.* (1998), simulations in which initial egg loads were distributed uniformly between 0 and 10 (the maximum egg capacity) produced an egg-load distribution that closely approximated the distribution observed in the field, so we again adopt this assumption here. Initial protein reserves were set at 15 minus the initial-egg-load to reflect the observation that adult parasitoids can mature approximately 15 total eggs without any additional protein meals (Heimpel *et al.* 1997; see § 2(c)). Although there is some uncertainty regarding the egg-load distribution at emergence, the egg-load distributions become less sensitive to initial assumptions as the parasitoids forage over the course of a few days; thus, we report results for the first oviposition of the third day of the parasitoid's life (see § 2(b)). The qualitative results of the model are, however, extremely robust to which oviposition event is examined.

(b) *Calculating the opportunity costs of time and eggs*

A. aonidiae generally deposits a single egg per host attacked, and oviposition requires an average of *ca.* 10 min (two time-steps in the model). To inspect and reject a host of marginal quality requires an average of *ca.* 5 min. Thus, each host that is accepted incurs opportunity costs of one egg and 5 min (the difference between host acceptance and rejection times). The dynamic optimization model can be used to translate these two costs into terms of foregone future fitness returns, by comparing appropriate values of $F(x, y, t, T, d)$. This was done with a computer 'experiment', in which three treatments were established for female parasitoids that were about to accept a host. Ignoring for a moment the changes in egg load and protein reserves due to egg maturation and/or resorption (which are treated in § 2(c)), females in the 'control' group performed a normal oviposition, which changes the expectation of future fitness returns from $F(x, y, t, T, d)$ to $(e^{-2\mu}) \times F(x-1, y, t+2, T, d)$. The first term in this expression is

Table 1. *Model parameters describing the dynamics of egg maturation and resorption in the parasitoid* A. aonidiae

(Scenario (i) (no egg resorption) is included only as a point of reference. Scenario (ii) (slow egg resorption) is appropriate for populations that consume sugar-rich foods as adults, and therefore can use sugars to support most of their somatic maintenance requirements. Scenario (iii) (rapid egg resorption) is appropriate for populations, like the one studied in a California almond orchard (Heimpel *et al.* 1998), that do not feed on sugars, and therefore must use protein reserves (pr) to support more of the costs of somatic maintenance.)

parameter	description	estimate
all scenarios		
m	eggs matured per time-step	0.011
$\mathrm{pr}_{\mathrm{egg}}$	protein reserves used per time-step for egg maturation	0.00878
scenario (i): no egg resorption		
$\mathrm{pr}_{\mathrm{soma}}$	protein reserves used per time-step for somatic maintenance	0.00222
scenario (ii): slow egg resorption		
$\mathrm{pr}_{\mathrm{soma}}$	protein reserves used per time-step for somatic maintenance	0.00222
$\mathrm{pr}_{\mathrm{thresh}}$	threshold level of protein reserves below which egg maturation ceases and egg resorption begins	2.0
r	eggs resorbed per time-step	0.00347
$\mathrm{pr}_{\mathrm{res}}$	protein reserves accrued per time-step from egg resorption	0.00222
scenario (iii): fast egg resorption		
$\mathrm{pr}_{\mathrm{soma}}$	protein reserves used per time-step for somatic maintenance	0.0148
$\mathrm{pr}_{\mathrm{thresh}}$	threshold level of protein reserves below which egg maturation ceases and egg resorption begins	4.0
r	eggs resorbed per time-step	0.0232
$\mathrm{pr}_{\mathrm{res}}$	protein reserves accrued per time-step from egg resorption	0.0148

the probability of avoiding predation during two time-steps (μ is the predation rate). Females in the 'no time cost' treatment experienced the normal egg cost of oviposition (one egg) but did not incur the time cost; thus their future expectation of fitness returns after oviposition was $(\mathrm{e}^{-\mu}) \times F(x-1, y, t+1, T, d)$. Females in the 'no egg cost' treatment experienced the normal time cost of oviposition (an extra 5 min) but did not incur the egg cost; thus their future expectation of fitness returns after oviposition was $(\mathrm{e}^{-2\mu}) \times F(x, y, t+2, T, d)$. For the base parameter set, these 'treatments' were applied to females preparing to accept their first host on their third day of foraging. The distributions of female age, egg load and protein reserves for females encountering the first host on the third day of foraging were obtained with a Monte Carlo simulation in which the physiological states of females (1000 per replicate; $n = 5$ replicate runs) that expressed the optimal behaviour identified by the dynamic model were followed over their lifetimes (see Mangel & Clark 1988; Rosenheim 1999*b*). The Monte Carlo simulation used parameter values identical to those used in the dynamic optimization model. Time cost could then be calculated as the difference between expected future reproduction in the 'no time cost' treatment and the 'control' treatment, and egg cost could be calculated as the difference between the 'no egg cost' treatment and the 'control' treatment.

(c) *Oocyte maturation and resorption*

Aphytis spp. parasitoids are flexible in their allocation of metabolic resources between the functions of somatic maintenance and oocyte maturation. The host scale insect is the sole food resource for the developing parasitoid larva, and larvae store proteins and other nutrients, which can subsequently be used during the adult stage to mature approximately 15 eggs without any additional protein meals. The adult parasitoid may have access to two primary types of foods in the environment. First, adults may feed on sugar-rich foods, including floral nectar, extrafloral nectar, or honeydew. Sugars support substantial adult longevity, suggesting that most of the requirements for somatic maintenance are met by sugars, but carbohydrates are insufficient for egg maturation. Carbohydrate-rich foods may be abundant in some habitats but scarce or inaccessible in others (Jervis *et al.* 1996). Second, adult females may feed on host scale insects ('host feeding') by probing the scale with the ovipositor and then drinking the haemolymph that exudes from the puncture site. Host feeding provides adult parasitoids with a protein-rich meal, the nutrients from which support ongoing egg maturation. Host feeding also extends longevity beyond that observed on a diet rich in sugars only, suggesting that some aspects of somatic maintenance require the expenditure of protein. Host insects may be abundant in some environments, providing essentially unlimited protein resources. However, in environments where hosts are rare, protein reserves may dwindle under the dual demands of somatic maintenance and egg maturation. In these cases, females can halt egg maturation and resorb eggs to reclaim proteins and other nutrients needed for somatic maintenance. Protein-starved *Aphytis* adults resorb eggs until their egg supply is exhausted, and death then rapidly ensues (Collier 1995*b*); this observation for *Aphytis* supports the generally held (but difficult to test) view that one of the key functions of oosorption is to avert starvation during times of nutrient stress (Bell & Bohm 1975; Boggs & Ross 1993; Ohgushi 1996). In some insects, resorption may also serve to maintain a constant supply of freshly matured eggs (e.g. Rivero-Lynch & Godfray 1997) but we do not examine this function in this study.

We explored three scenarios for nutrient dynamics (table 1).

(i) No egg resorption. This scenario was included as a point of comparison only, given that the ability to resorb eggs appears to be widespread among highly synovigenic insects (Bell & Bohm 1975; Boggs & Ross 1993; Ohgushi 1996;

Lopez-Guerrero 1996). Egg maturation occurred at rates observed in laboratory and field studies (Collier 1995*b*; Heimpel *et al.* 1997; Casas *et al.* 2000; table 1). One unit of stored protein was sufficient to mature one egg (an egg was assumed to contain 0.8 units of protein) and to fulfil the protein demands of somatic maintenance incurred over the time required to mature one egg (0.2 units of protein). Egg maturation continued regardless of protein reserves or egg loads.

(ii) Carbohydrate-rich foods present; slow egg resorption. When parasitoid populations have ample access to sugar-rich foods, oosorption occurs slowly (approximately one egg per day) when females are protein starved (Collier 1995*b*; Heimpel & Rosenheim 1995; Heimpel *et al.* 1997; table 1). We assume that parasitoids mature eggs when protein reserves are above a threshold (which we set at two units of protein) and cease egg maturation and initiate egg resorption below this threshold. Parasitoids starve to death if their protein reserves fall below one unit. We assume that the recovery of protein from resorbed eggs is 80% efficient (i.e. the egg yields 0.64 units of protein) and that the observed rate of egg resorption provides protein resources that satisfy metabolic demands. Although this scenario is not appropriate for the population of *A. aonidiae* that we studied, because they apparently did not have access to sugar-rich foods in the field, it should describe the ovarian dynamics of other *Aphytis* populations that feed as adults on sugary foods. We note, however, that because the physiology of egg resorption is still poorly understood, aspects of our depiction of resorption in the model (e.g. the thresholds for initiation of resorption and the efficiency of nutrient recovery) are necessarily somewhat speculative.

(iii) Carbohydrate-rich foods absent; rapid egg resorption. When *Aphytis* spp. cannot consume sugar-rich foods, they resorb eggs rapidly (approximately 6.7 eggs day^{-1}; Heimpel *et al.* 1997) to stay alive. Direct observations and biochemical assays of *A. aonidiae* foraging on almond trees suggest that these parasitoids are unable to find sugar-rich foods in their environment (Heimpel *et al.* 1998; G. E. Heimpel, unpublished data). Therefore, this scenario is the one that best describes our focal population. The efficiency of protein recovery was maintained at 80%. The threshold level at which egg maturation ceased and resorption began was raised to four units of protein (so that females would not need to switch from egg maturation to oosorption during a single night-time resting period).

In all scenarios, egg maturation or resorption occurred during both day and night hours and eggs matured in excess of abdominal capacity (ten eggs) were assumed to be lost.

3. RESULTS

(a) *Model without egg resorption: base parameter set for the observed field population*

The base parameter set reflected a key feature of the ecology of the observed *A. aonidiae* population: the rate of host encounter (1.00 host h^{-1}) was substantially in excess of the rate of egg maturation (0.132 eggs h^{-1}). Most of the encountered hosts were accepted for oviposition, leading to a substantial frequency of transient egg limitation: many females exhausted their supplies of mature oocytes during each day's foraging period and matured additional oocytes during the overnight resting period (Heimpel *et al.* 1998). Under these conditions, and assuming that there is no opportunity to resorb eggs, the total cost of oviposition is high (4.92 ± 0.03 grand-eggs; figure 1*a*) and a very large fraction of this total cost is contributed by the cost of the egg (97.56 ± 0.04%; figure 1*b*). This is not to say that no females were time limited; because predation rates were high (Heimpel *et al.* 1997), some females were killed before they could exhaust their egg supply. Nevertheless, time costs contributed only the remaining 2.44% of the total cost of oviposition. Under these conditions female reproductive success is strongly constrained by egg supply, thus the opportunity costs of depositing an egg are high. Egg costs thus appear to be much more important than time costs for the field population of *A. aonidiae* that was studied in California. This result from the dynamic optimization model reinforces and extends the result of a simpler, analytical model (Rosenheim 1999*a*). Optimization models that consider only time-mediated costs of oviposition, including many rate-maximization models, would not be appropriate for analysing the reproductive behaviour of this parasitoid population.

(b) *Model without egg resorption: sensitivity analysis for host density*

Parasitoids in the observed population foraged in an almond orchard with a moderately high density of scale insect hosts (Heimpel & Rosenheim 1998). Because previous models have emphasized the importance of host density in determining the relative importance of egg versus time costs and because many almond orchards harbour much lower densities of the host scale insect *Q. perniciosus* (J. A. Rosenheim, personal observation), we performed a sensitivity analysis in which the rate of host encounter was varied. Both the total cost of oviposition and the proportional contribution of egg costs to the overall cost of oviposition decreased as host encounters became less frequent (figure 1*a*,*b*). This result parallels that obtained for pro-ovigenic insects (Rosenheim 1999*b*). When hosts are abundant, eggs become the limiting resource and egg costs therefore dominate the cost of oviposition. The total cost of oviposition is high, and therefore insects are predicted to be highly selective in choosing hosts (Iwasa *et al.* 1984; Mangel 1989). When hosts are rare, time to find hosts becomes the limiting resource, and time therefore dominates the cost of oviposition, at least in this simple model without egg resorption. The total cost of oviposition decreases when hosts are rare, and therefore insects are predicted to be more catholic in host acceptance.

(c) *Model with egg resorption*

The influence of egg resorption on the cost of oviposition varied with host availability (figure 1). At very high host densities, neither the total cost of oviposition nor the proportional contributions of egg and time costs were sensitive to the inclusion of egg resorption in the model. This is not surprising because when hosts are abundant host feeding opportunities are also abundant, and therefore protein reserves do not fall below the threshold at which resorption is initiated. However, when hosts are scarce, the inclusion of egg resorption in the model

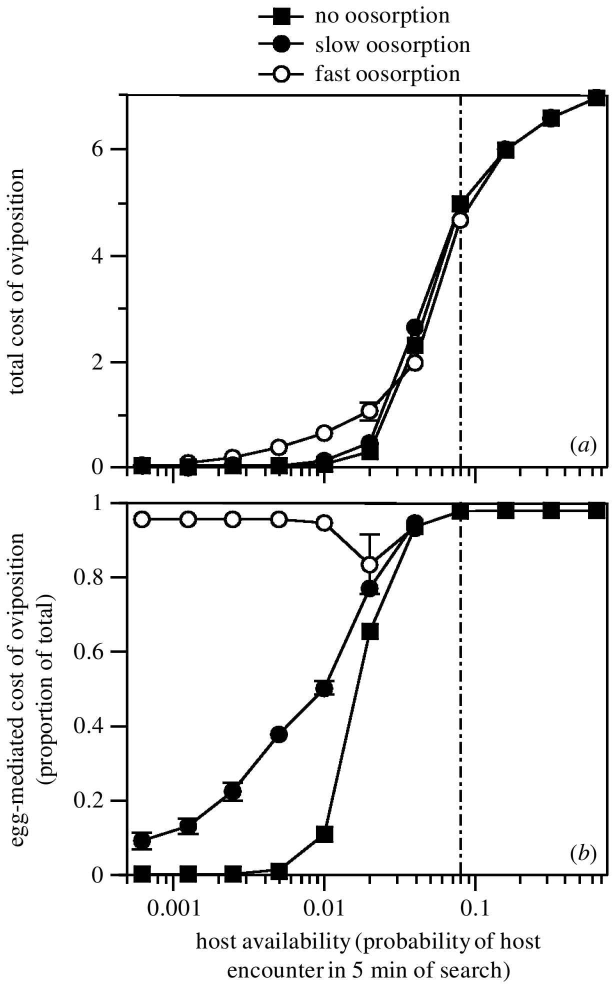

Figure 1. Influence of host availability on the total cost of oviposition and the proportion of the total cost that is contributed by the egg cost. Host availability is measured as the probability of encountering a host during a single 5-min time-step; the vertical line indicates the level of host availability observed in the field (probability of host encounter during 5 min of search = 0.08). (*a*) Total cost of oviposition, measured in terms of the number of eggs carried by the emerging adult offspring of the focal female ('grand-eggs'). To put the absolute values of these costs into perspective, note that the expected 'benefit' of oviposition on a low-quality host equals the product of the probability that the deposited egg will develop successfully to the adult stage (0.61) and the expected fecundity of the resulting daughter (7.0), or 4.27 grand-eggs. The expected benefits of ovipositing on a medium- and high-quality host are 6.1 and 7.32 grand-eggs, respectively. (*b*) The proportional contribution of egg costs to the total cost of oviposition (the remaining proportion is contributed by the time costs of oviposition).

elevated the total cost of oviposition and had a dramatic influence on the relative importance of egg and time costs.

Why is this result observed? Has the inclusion of egg resorption somehow changed the fundamental challenge faced by parasitoids that must spend time in extensive searching for rare hosts? No. Egg resorption instead allows parasitoids to translate egg resources into additional search time. The protein that can be recovered from a single egg through resorption (0.64 units of protein) represents a substantial amount of search time (up to a maximum of 43 time-steps, or 3.6 h when parasitoids are sugar starved, and 288 time-steps, or 24 h when parasitoids can feed on sugars). Thus, the opportunity costs associated with depositing an egg can be large if the egg would otherwise support additional search time. The amount of time at stake is large relative to the immediately incurred cost of the 5.0 min required to deposit the egg.

A closer examination of the model output can help to explain why slow oosorption had a more modest influence on the cost of oviposition than did fast oosorption. The field population of *A. aonidiae* that we studied in California was subject to intense predation pressures from a complex of generalist predators (Heimpel *et al.* 1997), thus, expected longevities were relatively short (1.3 days). Under scenario (ii), parasitoids have access to sugar-rich foods; therefore, metabolic demands placed on protein reserves are modest. Under these conditions, even if opportunities to host feed are rare, protein reserves take several days to dwindle to the dangerously low levels at which egg resorption is initiated (figure 2*a*). For example, a parasitoid that emerges with an average protein reserve, ten units, and fails to secure any host-feeding meals still has enough protein to support egg maturation and somatic maintenance for 2.53 days before she draws her protein reserves down to the threshold at which resorption begins (two protein units). Even infrequent host-feeding meals will delay the onset of egg resorption further. Furthermore, egg resorption must not only be initiated but must continue for long enough that the egg supply can actually be exhausted before the bulk of the opportunity cost of depositing an egg is finally realized. Females with access to sugars resorb eggs slowly (approximately one egg day^{-1}), thus, egg load is drawn down gradually (figure 2*b*). Thus, when predation pressure is intense and demands on protein resources are light, few individuals live long enough to initiate egg resorption and produce a significant risk of oosorption-induced egg limitation (figure 2*c*). Therefore egg resorption has a relatively small influence on the cost of oviposition when parasitoids have access to sugar-rich foods and oosorption is therefore slow.

When parasitoids are sugar starved, however, the metabolic demands made by the soma on protein reserves are intense. Protein reserves can now be depleted more quickly (figure 2*a*). A parasitoid emerging with ten units of protein can now reach the threshold at which egg resorption is initiated (four protein units) in 0.88 days, and the rapid oosorption (6.67 eggs day^{-1}) that ensues when reserves reach dangerously low levels can quickly lead to oosorption-induced egg limitation (figure 2*b*,*c*). Thus, when host densities decline to levels at which host feeding cannot maintain protein reserves, many females resorb all their eggs and starve to death before they are killed by predators, and egg costs are therefore high.

The details of the results displayed in figure 1 are, therefore, sensitive to the potential for female longevity, opportunities for females to feed and oviposit, and the magnitude of protein demands for egg maturation and somatic maintenance. Our general conclusion, however, is that when females must resorb eggs to avoid starvation, egg resources become critical, and therefore the egg-mediated costs can dominate the cost of oviposition.

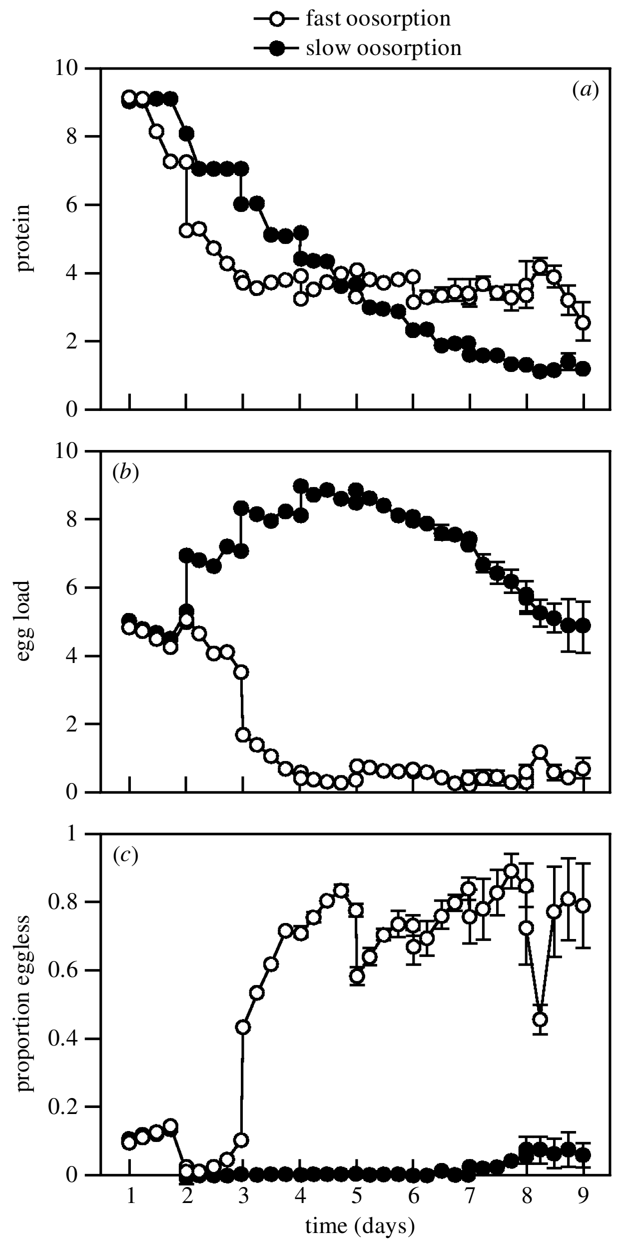

Figure 2. Influence of slow versus fast oosorption on (*a*) the protein reserves, (*b*) egg loads and (*c*) proportion of females who have exhausted their supply of mature oocytes. Data are from Monte Carlo simulations (1000 female parasitoids simulated per replicate; $n = 5$ replicate runs) of female *A. aonidiae* parasitoids that expressed the optimal behaviour identified by the dynamic model. The simulations used the base parameter set (see Heimpel *et al.* 1998; table 1) except that host availability (the probability of finding a host during a 5-min time-step) was set at 0.005, a value that is well below the value observed in the field (0.08). At this low level of host availability, host-feeding opportunities are rare, and egg resorption may therefore occur to satisfy metabolic demands. When parasitoids can feed on sugar-rich foods in the environment, oosorption is initiated when protein reserves fall to two units, and oosorption is slow (scenario (ii) in table 1); when sugar-rich foods are absent, oosorption is initiated when protein reserves fall to four units, and oosorption is fast (scenario (iii) in table 1). Shown are means ± s.e.m.

Because oosorption is a general feature of synovigenic insects, it appears likely that egg costs make a substantial contribution to the overall cost of oviposition, even when hosts are rare.

4. DISCUSSION

We draw two primary conclusions from our analysis. First, although the parasitoid *A. aonidiae* can continue to mature eggs as an adult, the finite maximum rate of egg maturation still means that transient egg limitation can occur when hosts, and therefore opportunities to oviposit, are abundant. When the egg supply is temporarily exhausted, females must halt reproduction to await the maturation of additional eggs. In our model of *A. aonidiae*, a halt in reproduction imposes a cost, because there is a risk of mortality during the waiting period. More generally, a halt in reproduction is costly because of immediate risks of mortality, the progression of senescence and, in some cases, loss of opportunities to oviposit on host resources that are available only for a short time. Thus, as has been emphasized by other authors, whereas the most fundamental constraint acting on the lifetime reproductive success of pro-ovigenic species is the fixed total number of eggs that they carry as a newly emerged adult, the most fundamental constraint acting on a synovigenic species is their maximum rate of oocyte maturation (Charnov & Skinner 1988; Rosenheim 1996; Casas *et al.* 2000). Both of these constraints mean that there is a risk of oviposition-mediated egg limitation, which is permanent in the case of a pro-ovigenic species but potentially transient in the case of a synovigenic species.

Second, the ability of synovigenic species to reverse the flow of nutrients from the soma to oocytes has a dramatic influence on the cost of oviposition. Whereas females in host-rich environments may encounter oviposition-mediated egg limitation, females in host-poor environments may encounter oosorption-mediated egg limitation. Both forms of egg limitation are costly. The resorption of eggs allows females to support their basic metabolic requirements, thereby translating egg resources into additional search time. The search time gained from resorbing an egg may be large compared to the time costs associated with depositing an egg; oviposition time requirements are generally small (typically in the order of seconds to minutes), whereas eggs are often provisioned with abundant nutrients, so that a resorbed egg can support the female's metabolic demands for a significant length of time (typically in the order of hours to days) (Godfray 1994; Rosenheim 1999*a*). Eggs are therefore a valuable resource even when hosts are rare, because females who resorb their entire supply of eggs face imminent death due to starvation.

Eggs, therefore, appear to make important contributions to the overall cost of oviposition for highly synovigenic insects, just as they do for strictly pro-ovigenic insects. Contrary to initial expectations, the flexibility of resource allocation that typifies synovigenic reproduction actually appears to broaden the range of conditions under which costly egg limitation can occur. Whereas for pro-ovigenic insects egg costs predominate only when hosts are abundant, for synovigenic insects egg costs may predominate when hosts are abundant or rare. Egg costs appear to be fundamental in mediating the trade-off between current and future reproduction, and are thus basic to the understanding of why insects are choosy about where they oviposit.

(a) *Egg-load dynamics in two highly synovigenic parasitoids*

How generalizable is our result that a highly synovigenic species may still face a costly risk of experiencing transient egg limitation in the field? Although we feel that *A. aonidiae* exhibits traits that are typical of highly synovigenic insects, additional case studies would certainly help us to assess the generality of a basic constraint imposed by the maximum rate of egg maturation. Two recently collected data sets provide useful insights.

Casas *et al.* (2000) studied a field population of another *Aphytis* species, *Aphytis melinus*. Simple but ingenious manipulations showed that during the period of active foraging (10.00–16.00) the rate of egg maturation (measured under semi-field conditions) was 0.25 eggs h^{-1}, whereas the rate of oviposition was 0.58 eggs h^{-1}. Thus, just as was observed for *A. aonidiae*, the rate of oviposition greatly exceeded the rate of egg maturation, and the result was that a substantial fraction (they estimated between one-third and one-half of all females) experienced egg limitation at some time each day. The distribution of egg loads for females collected at the end of the daily foraging period confirmed this inference: many females had no mature oocytes in their ovaries. Their analysis also suggested that as females depleted their egg supply, they slowed their rate of oviposition, a pattern that has been observed for *Aphytis* spp. in the laboratory (Rosenheim & Rosen 1991; Heimpel & Rosenheim 1995) and field (Heimpel *et al.* 1996) and that is predicted by optimality models (Mangel 1987). Although a coupling of the rate of oviposition with egg load can certainly reduce the likelihood of completely exhausting the egg supply, it appears not to eliminate this possibility (Mangel & Heimpel 1998; Rosenheim 1999*b*).

A field experiment by K. R. Hopper (personal communication) showed, however, that a population of the aphid parasitoid *Aphelinus asychis* exhibited no egg limitation: none of the 92 sampled females had exhausted their supply of eggs. The modal egg load was 14, which is approximately the maximum egg load for this species, and only one female had as few as two mature oocytes. Thus, for the females in this population, egg maturation appears to have been more than adequate to offset oviposition and oosorption. The availability of hosts and honeydew, a sugar-rich food, to female parasitoids in this population provides a context for understanding this result. The parasitoids were foraging in a field whose aphid population had recently declined from high levels. Thus, hosts, and hence opportunities to oviposit, were relatively rare (the estimated total number of progeny produced per female wasp was three to five). Honeydew produced by aphids during the earlier dense aphid population can persist on protected leaf surfaces (K. R. Hopper, personal communication), so that females had ample access to sugar meals. In the laboratory, females held without hosts but with access to honey showed little change in egg load for five days, and egg load declined only modestly, from an average of twelve eggs to eight eggs, over the next ten days (Sanchez 1994). In this species, egg resorption may occur at the same time as egg maturation if females are held without hosts; in the studied field population, however, there may have been little or no net decline in egg load due to resorption because females had access to both honeydew and aphids upon which they could host feed to replenish protein reserves. Thus, this population of *A. asychis* underscores the importance of understanding how local ecological conditions, including the availability of hosts and non-host foods, interact with parasitoid physiology to determine levels of egg limitation.

Papaj (2000) has argued cogently that models that treat the rate of egg maturation as a constant are overlooking an important aspect of insect biology, namely plasticity in the level of vitellogenic activity. We concur. Although we have attempted to incorporate some flexibility of ovarian dynamics into our model by incorporating both egg maturation and resorption, we still simplify ovarian function by treating egg maturation as a one-speed process. However, we note that both *A. aonidiae* and *A. melinus* displayed high levels of egg limitation (Heimpel *et al.* 1996; Heimpel & Rosenheim 1998; Casas *et al.* 2000); thus, our expectation is that these parasitoids were displaying their maximum attainable rate of egg production for the environmental conditions that they experienced. It appears, then, that these parasitoid populations experience a fundamental physiological constraint, one which they are incapable of circumventing through short-term metabolic adjustments. Populations subject to such intense losses of reproductive opportunity due to egg limitation might be expected to respond over a longer time-frame through evolution of increased fecundity or accelerated egg maturation (Rosenheim 1996; Sevenster *et al.* 1998).

(b) *Transient versus permanent egg limitation in synovigenic insects*

A factor that has a strong influence on the rate of egg maturation in synovigenic females is age. As females age, their rate of egg maturation generally declines (e.g. Shirota *et al.* 1983; Hoffmann *et al.* 1995; Boggs 1997*b*); whether this degradation of ovarian function increases the likelihood of exhausting the egg supply depends on the extent to which senescence might also diminish the ability of females to forage successfully for suitable oviposition sites. In many species of herbivorous and parasitic insects, vitellogenesis ceases entirely in old females who have experienced rich opportunities to oviposit (e.g. Dunlap-Pianka *et al.* 1977; Jervis *et al.* 1994; Lopez-Guerrero 1996). Thus, highly synovigenic species, in common with pro-ovigenic species, can experience a permanent form of egg limitation, which would augment the egg-mediated cost of oviposition associated with transient egg limitation. Age-dependent declines in ovarian function have been documented in the laboratory, and opportunity costs of permanent egg limitation have been analysed with models (Rosenheim 1999*b*), but field studies of age-dependent changes in female foraging ability, ovarian function and levels of egg limitation are needed before the relative importance of transient and permanent egg limitation will be resolved for highly synovigenic species.

(c) *Environmental heterogeneity and the function of egg resorption*

Our model underscores the value of eggs as a source of nutrients that can be mined during times of metabolic stress. We feel, however, that the true value of egg resorption (and therefore the costs associated with egg limitation during times of nutrient stress) may often be greater than indicated by our model. The reason is that our model assumes constant environmental conditions (i.e. constant availability of foods and hosts), whereas nature is characterized by both temporal and spatial heterogeneity. A female who experiences a short period of host or food scarcity, and who subsequently experiences conditions rich with opportunities to reproduce, may realize very large increases in lifetime reproductive success if she can survive through the period of scarcity by resorbing eggs (e.g. Ohgushi 1996). Additional work, including perhaps both field studies and modelling efforts, are needed to explore this possibility.

(d) *Physiology, behavioural ecology and life-history evolution*

We close by echoing a point recently advanced by Sinervo & Svensson (1998) in their studies of the cost of reproduction in vertebrates: a deeper understanding of reproductive behaviour and the long-term evolutionary trajectories of life-history traits is likely to emerge from an enhanced understanding of the physiological basis of the cost of reproduction. Our model has highlighted the importance of understanding not only the ecology of reproductive opportunity (e.g. the availability of oviposition sites and foods in the local environment, and the intensity of mortality factors) but also the physiology of bi-directional flows of proteins and other compounds between the soma and the developing oocytes. Mechanistic studies of ovarian dynamics (e.g. Boggs 1997*a*,*b*; Rivero & Casas 1999*a*,*b*; Papaj 2000) will contribute greatly to our understanding of insect life-history evolution.

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