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# Why are so few parasitoid wasp species pro-ovigenic?

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## ABSTRACT

A recent survey of egg maturation strategies among parasitoid wasps showed strict pro-ovigeny (emergence with the entire potential lifetime complement of eggs mature) to be confined to a small number of species. This finding raises the following important question: Why is strict pro-ovigeny such a rare strategy? Using a dynamic programming model, we show that three traits – small body size relative to travel costs, large eggs relative to the total allocatable resources, and uniformity in host spatial distribution (which translates into extremely low stochasticity in the number of patch encounters) – either by themselves or in combination, may lead to the evolution of strict pro-ovigeny. Turning next to the empirical evidence, we conclude that the prevalence of host patchiness over spatial uniformity has been particularly important in constraining the incidence of strict pro-ovigeny among the world's parasitoid wasp fauna. Model predictions aside, the *empirical* finding that strict pro-ovigeny is a rare egg maturation strategy suggests that theoreticians should – unless evidence indicates otherwise – assume synovigeny (emergence with only part of the lifetime egg complement mature upon emergence) to be the case when considering parasitoid behavioural strategies and parasitoid–host population interactions.

*Keywords*: body size, egg size, habitat stochasticity, life-history strategy, ovigeny index, resource allocation, trade-offs.

## INTRODUCTION

Parasitoid biologists have long assumed a fundamental dichotomy in egg maturation strategies among parasitoids. In some species, all or very nearly all of the lifetime complement of eggs is mature (ready to lay) before the start of oviposition, whereas in others only a fraction of the lifetime egg complement is mature, and the female continues to mature the remaining eggs during the remainder of her reproductive life (Flanders, 1950).

To examine this assumption, Jervis *et al.* (2001) devised an 'ovigeny index' (OI) – the proportion of the lifetime fecundity that exists as mature eggs when the female emerges – and surveyed the egg maturation characteristics of 638 parasitoid wasp species. As well as showing there to be a continuum (rather than a dichotomy) in the ovigeny index, they also

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found strict pro-ovigeny (OI = 1) to be a rare strategy. Only 1.8% of the 638 species were strictly pro-ovigenic. Furthermore, 66% of the species displaying strict pro-ovigeny belonged to only two of the 28 families surveyed: the Mymaridae and the Eucoilidae. This survey may provide a somewhat biased picture. For example, strict pro-ovigeny is thought to be exhibited by all Mymaridae and most, if not all, Eucoilidae (and also all Eucharitidae) (Jervis *et al.*, 2001); these would amount to several hundred species. Nevertheless, this number is likely to be very small compared with the total number of all kinds of parasitoid wasp (estimated to exceed 1 million; Godfray, 1994). This situation contrasts strongly with what is known for other insects. For example, among moths strict pro-ovigeny is common (M.A. Jervis, C.L. Boggs and P.N. Ferns, unpublished manuscript), and among Ephemeroptera it is apparently the sole egg maturation strategy.

Theoretical work on egg maturation strategies predicts that the ovigeny index should vary with body size, host dispersion and host density. Ellers and Jervis (2003), using a dynamic programming model, showed that the ovigeny index declines with increasing body size because the proportionate increase, with increasing body size, in initial egg load (the numerator of the index) is less than that in lifetime potential fecundity (the denominator of the index). Optimal initial egg load shows a weaker relationship with body size because for small (and short-lived, due to the smaller total amount of energy allocated to stored reserves) wasps, the environment is experienced as more stochastic – small females typically sample only a few patches when compared with larger females. In more stochastic environments (host distribution less uniform), the optimal initial egg load exceeds the expected number of hosts found (as shown by the models of Ellers *et al.*, 2000b), so small parasitoids must allocate a larger proportion of their total resources to initial egg load than larger parasitoids, even though small and large parasitoids encounter patches from the same host distribution. For large individuals, the optimal initial egg load also exceeds the expected number of hosts found; however, especially in low-quality habitats (habitat quality being defined as the mean number of patches encountered per resource unit multiplied by the mean number of hosts per patch), it only slightly exceeds that of smaller individuals. The latter allocation strategy ensures the maximum probability of finding a patch, and maintains reproductive plasticity. The model of Ellers and Jervis (2003) confirmed the positive empirical correlation between initial egg load and habitat quality, an effect that manifests itself as an increase in the ovigeny index (in the model, when stochasticity in host availability is low) (Ellers and van Alphen, 1997).

Despite shedding light on the relationship between the ovigeny index and both parasitoid- and habitat-related factors, neither the modelling done by Ellers *et al.* (2000b) nor that of Ellers and Jervis (2003) identified the conditions under which strict pro-ovigeny is the optimal egg maturation strategy.

A key aspect of the study of parasitoid biology is the use of models to predict parasitoid oviposition behaviour and its influence on population dynamics (Godfray, 1994), and modellers have mainly assumed parasitoids to be strictly pro-ovigenic (e.g. Iwasa *et al.*, 1984; Driessen and Hemerik, 1992; Getz and Mills, 1996; Rosenheim, 1996; Mangel and Heimpel, 1998; Sevenster *et al.*, 1998; West *et al.*, 1999; see also van Baalen, 2000). As strict pro-ovigeny is now known to be very much the exception and limited to particular taxonomic groups, the predictions of behaviour and population dynamics models may not be generally applicable. The interpretation of such models is therefore difficult without knowing what range of ecological conditions favour the evolution of strict pro-ovigeny. In this study, we extend our dynamic programming modelling to identify these conditions.

The model of Ellers and Jervis (2003) used combinations of several parameters, and the range of values chosen for body size and lifetime potential fecundity was liberal compared with the empirical data. Despite this, strict pro-ovigeny was found in only one of the many scenarios modelled, and then only when a measure of maximum potential fecundity was used that biased the ovigeny index more towards unity. The mean ovigeny index ranged between 0.04 and 0.84 (near-extreme and weak synovigeny, respectively). Our approach here is therefore to use only extreme values for the parameters of body size (range biased towards small body size), host availability (range biased towards higher habitat richness), a uniform spacing of patches, and a very high degree of stochasticity in the number of hosts per patch. Also, we focus on a previously ignored parameter: egg size, as resource investment per egg is likely to be optimized in relation to body size, and has indeed been established empirically to be positively correlated with body size (see below).

## OVERVIEW OF THE MODEL

In this model, egg production is a function of current energy reserves and egg load for parasitoids of different sizes (Ellers *et al.*, 2000b; Ellers and Jervis, 2003). We recapitulate only the basic features of the model, and indicate the changes made for the purposes of this study.

The model assumes that a parasitoid has a fixed amount of resources that can be allocated to eggs and energy reserves. It optimizes the initial egg load and the number of eggs subsequently matured by females following each host patch visit, and it assumes there is a linear trade-off between the initial egg load and the remaining energy reserves (Tatar *et al.*, 1993; Ellers *et al.*, 2000a):

$$Q = a \cdot E_i + R$$

where $Q$ is the fixed amount of resources, $E_i$ is the initial egg load and $a$ is the amount of resources per egg (i.e. egg size). The parasitoid is assumed to lay one egg in all hosts present in the patch, within the limits of its current egg load. The remaining energy resources $R$ can be used for fuelling travel costs to host patches or for maturing more eggs. However, egg maturation is not instantaneous, so eggs cannot be produced and laid immediately after finding a host. Thus, the cost of egg maturation consists of missed oviposition opportunities – that is, egg-limitation (Heimpel and Rosenheim, 1998). Also, empirical research suggests the existence of an upper limit to the number of eggs matured ($E_{\max}$) at the time-scale of consecutive patch visits (Collier, 1995).

We simulated differences in body size by varying the amount of resources, $Q$. In insects, many studies have shown an increase in both energy reserves, such as protein, glycogen and lipids, and fecundity in larger individuals (Honek, 1993; Blanckenhorn, 1994; Visser, 1994; Ellers *et al.*, 1998; Briegel *et al.*, 2001), indicating an increase in the total amount of resources ($Q$) to be allocated. Because a negative relationship between body size and the ovigeny index is predicted (see above), we included extremely small values of $Q$. The model does not contain any size-related differences in performance other than the amount of resources to be allocated. Differences in egg size were simulated by varying the amount of resources allocated per egg ($a$). Larger eggs were assumed to be more resource-costly (Table 1), as has recently been shown to be the case (Giron and Casas, 2003).

The parasitoid's habitat was characterized both by mean host availability and by unpredictability in host encounters. The mean host availability of the habitat was generated

**Table 1.** Parameterization of the model

| Factor | Parameter | Range | Interpretation of range |
|---|---|---|---|
| **Parasitoid factors** | | | |
| Fixed amount of resources | $Q$ (total resources to be allocated) | 15, 25, 50 | Small *vs* normal body size |
| Egg size | $a$ (amount of resources per egg) | 0.2, 0.7, 1, 2, 5, 10 | Egg cost varies from 0.4% to 66.7% of total resources |
| Egg maturation rate | $E_{\mathrm{max}}$ (maximum number of eggs matured per patch visit) | 20 | |
| **Habitat factors** | | | |
| Patch density | $m_{\mathrm{p}}$ (mean number of patches encountered per resource unit) | 0.1 | Patch density |
| Patch quality | $m_{\mathrm{h}}$ (mean number of hosts per patch) | 10, 100, 200 | Low to very high patch richness |
| Stochasticity in number of patches encountered | $I_{\mathrm{p}}$ (index of dispersion of patches encountered) | 0.25, 1 | Uniform *vs* random (i.e. Poisson) spacing of patches |
| Stochasticity in number of hosts per patch | $I_{\mathrm{h}}$ (index of dispersion of hosts per patch) | 1, 50 | Random *vs* very aggregated distribution of hosts |

by a mean host patch density and a mean number of hosts per patch (patch richness). We chose very high host densities because the model previously predicted a positive relationship between host availability and the ovigeny index (see above). Unpredictability in host encounters was characterized by stochasticity in the number of patch encounters and stochasticity in the number of hosts per patch. Again, we chose extreme parameter values to generate very low stochasticity in host encounters (with uniform distribution of host patches) and very strong stochasticity in host encounters (with highly aggregated host distributions over patches; Table 1). Note two features of our model. First, the foraging parasitoid attacks *all* of the hosts within each patch – that is, the probability of a host being located and attacked by a parasitoid is unity. Secondly, we ignore factors such as superparasitism, the effects of experience on foraging decisions, and extrinsic mortality acting on adults. To include these in the model would require additional untested assumptions and would greatly reduce the transparency of the model.

Using dynamic programming, we solved the optimal initial resource allocation and the predicted egg maturation decisions as a function of the energy reserves and the egg load of the parasitoid. Dynamic models incorporate the physiological state of the organism and allow for changes in the allocation strategy in response to a change in the state of the organism. We obtained the number of eggs matured in each scenario using a forward iteration in which individual parasitoids expressed the optimal initial resource allocation and degree of egg maturation as identified by the dynamic model (Mangel and Clark, 1988).

For each parameter combination we recorded whether strict pro-ovigeny was the optimal strategy. Strict pro-ovigeny occurs if the initial egg load equals the maximum potential lifetime fecundity (OI = 1). In real parasitoids, maximum potential fecundity can be estimated as the mean total egg production by females under the most favourable conditions, such as unlimited food and hosts (Jervis *et al.*, 2001). In the model, we used a variant of this method of estimation: because of stochasticity in the model, females encounter a range of adverse and favourable conditions; therefore, in each size class for each parameter setting, the maximum potential fecundity was taken as the highest number of eggs produced by any of the 1000 females run in the forward iteration model. Increasing the number of females fivefold per run did not significantly affect our estimate of maximum lifetime potential fecundity.

Because the output variable of the model showed a binary response (strict pro-ovigeny or not), we analysed the data using logistic regression.

## RESULTS

The results demonstrate our success in identifying those parameter ranges that are most likely to lead to strict pro-ovigeny: 70.4% of the scenarios led to strict pro-ovigeny, whereas none of the scenarios in our previous study (Ellers and Jervis, 2003) led to this strategy. Figure 1 shows the probability curves of strict pro-ovigeny derived from the logistic model for different egg size and body size. All but two of the scenarios with extremely small body size led to OI = 1 (Fig. 1a). Similarly, all scenarios with very large egg size led to strict pro-ovigeny (Fig. 1c). Logistic regression showed that three parameters significantly influenced the probability of strict pro-ovigeny: body size, egg size and stochasticity in the number of patch encounters (Table 2). These parameters act in combination so that the value of $Q$, the amount of resources available for allocation, needs to be considered in relation to the costs of travel between host patches (patch density) or costs of egg production (egg size), as we shall elaborate in the Discussion.

Neither the number of hosts per patch nor the aggregation of hosts over patches was significant in explaining the incidence of strict pro-ovigeny.

## DISCUSSION

The results show small body size and large egg size, as well as uniformity in host patch distribution, to increase the probability of strict pro-ovigeny being the optimal egg maturation strategy. However, it is neither body size nor egg size *per se* that is responsible for making an ovigeny index equal to 1 more likely. Rather, it is the amount of resources available for allocation *relative to physiological costs* – for example, the cost of travel between host patches (patch density) or the cost of egg production. Why these are key factors determining the optimal reproductive strategy is probably best understood by means of two examples. In the first, we examine the optimal ovigeny index for very small-bodied females with the total amount of resources to be allocated $Q = 15$. In our scenarios, the mean number of patches found per resource unit is $m_p = 0.1$. Accordingly, the average cost of finding one patch is 10 resource units. Females with a very small body size, therefore, only have sufficient resources to allow one patch visit, not more. The egg maturation strategy in

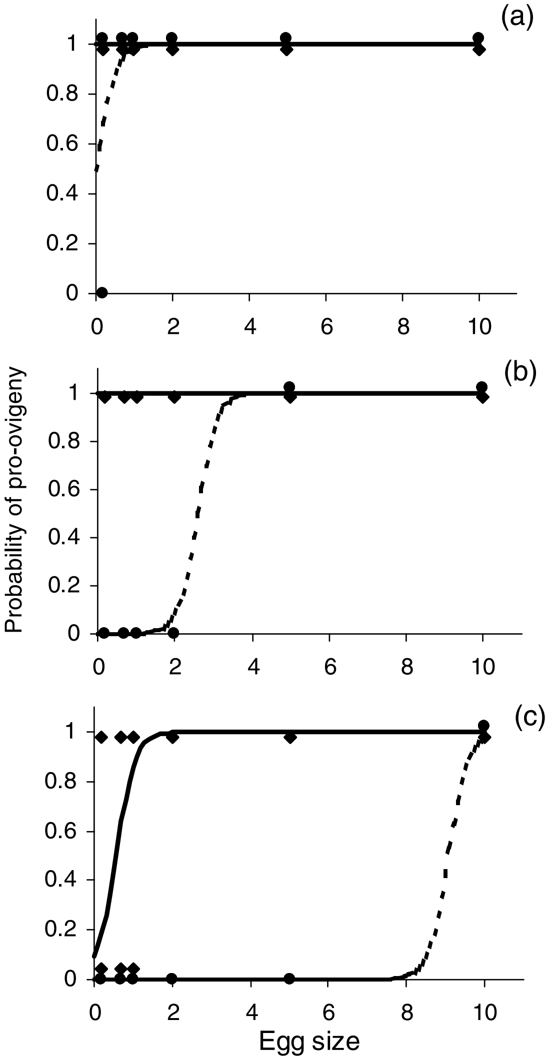

**Fig. 1.** The estimated probability of strict pro-ovigeny as a function of egg size (amount of resources per egg) for (a) small ($Q = 15$), (b) medium ($Q = 25$) and (c) normal ($Q = 50$) body size, for uniform (◆, ——) and random (●, - - -) patch distributions.

**Table 2.** Logistic regression of egg production strategy (strict pro-ovigeny = 1, otherwise 0)

| | *B*-coefficient | Standard error of *B* | *P* |
|---|---|---|---|
| Constant | 54.23 | 14.9 | <0.001 |
| Body size | −1.05 | 0.29 | <0.001 |
| Egg size | 4.07 | 1.08 | <0.001 |
| Patch distribution | −3.85 | 1.07 | <0.001 |

such a case is to allocate to capital energy reserves only those resources needed to find a single patch and convert all the remaining resources into eggs (initial egg load). Obviously, this is a strictly pro-ovigenic strategy, resulting from the small body size of females relative to the cost of travel.

As a second example, note that small to medium-sized females with very large egg size ($a = 5$ or 10) very likely will be unable to produce sufficient eggs to parasitize all hosts present in one patch: $Q$ is lower in these females, and egg size would need to be increased at the expense of initial egg load (see, for example, Parker and Begon, 1986). Therefore, females do not gain fitness by postponing any egg maturation to the next patch visit. Rather, their optimal strategy is to visit one patch and lay their entire egg complement. As in the previous example, this is a strictly pro-ovigenic strategy.

The conditions making strict pro-ovigeny the optimal strategy are thus predicted to be: (1) small body size relative to the cost of finding host patches, rather than body size *per se*; (2) large egg size relative to the total amount of allocatable resources, rather than egg size *per se*; and (3) low stochasticity in patch encounters that is a consequence of uniformity in host spatial distribution. We now proceed to examine the empirical evidence for this hypothesis.

Our prediction that strict pro-ovigeny should evolve in relation to small body size is supported empirically, although the observed size ranges (forewing wing length) of species showing strict pro-ovigeny and those showing synovigeny (OI < 1) overlap to a high degree: 0.55–3.54 and 0.46–7.95 mm, respectively (Jervis *et al.*, 2003). That is, strict-pro-ovigeny is by no means confined to small-bodied parasitoid wasps. This is to be expected, given that the ovigeny index is determined by the size of $Q$ relative to travel costs (see above). Indeed, the available evidence is that the largest of the strictly pro-ovigenic species for which body size data are available, *Trybliographa rapae* (Eucoilidae) (forewing length 3.54 mm and approaching medium size for a parasitoid), has to forage for widely dispersed host patches in nature (T.H. Jones, personal communication). Between-patch travel costs may be particularly high in relation to $Q$ in the case of some of the smallest species. Mymarids are among the tiniest of parasitoid wasps and, at least in those parasitizing leafhoppers and planthoppers, the hosts (eggs) typically occur as widely separated patches, relative to the body size of the individual wasp (Bakkendorf, 1934, 1943; Waloff and Jervis, 1987).

Large eggs relative to the total amount of allocatable resources also favour the evolution of strict pro-ovigeny in our model. An advantage of larger eggs has recently been demonstrated for a parasitoid wasp species in which egg size declines with female age: neonate larvae arising from such eggs are more likely to survive starvation compared to those from small eggs (Giron and Casas, 2003). However, not only is there a well-established positive correlation between body size and egg size within parasitoid species generally (Jervis *et al.*, 2004), but also the relationship is isometric. That is, smaller females lay absolutely smaller eggs, and these are no larger in proportion to body size (based on O'Neill and Skinner, 1990; Visser, 1994). Exceptions to the aforementioned pattern are known, but with these egg size is uncorrelated with body size (see, for example, Fitt, 1990). This suggests the existence of an underlying constraint upon increasing egg size in small females, and as a result strict pro-ovigeny is unlikely to evolve via larger resource investment per egg in smaller females.

The third condition predicted to be related to the evolution of an ovigeny index equal to 1 is a uniform distribution of host patches, and the concurrent reduction of the stochasticity in the number of host patches encountered. Not only are systems with spatially uniform distributions of host patches probably rare (e.g. Taylor *et al.*, 1978), but also the strictly pro-ovigenic species for which there is habitat information exploit aggregated hosts (see above). We therefore consider that the prevalence of host patchiness in nature has been important in constraining the evolution of strict pro-ovigeny among the world's parasitoid wasp fauna.

It is important to note that we only aim to predict the optimal ovigeny index given certain biological parameters, *not* the evolution of the parameters themselves. Conceivably, small-bodied species with widely dispersed hosts may be under selection for increased body size because larger females are better dispersers (Ellers *et al.*, 1998) and, consequently, the optimal ovigeny index would also change. Other species may have to cope with phylogenetic or physiological constraints on body size, so that small body size and the associated ovigeny index equal to 1 are maintained.

Perhaps other factors, not included in the model, are involved in the evolution of strict pro-ovigeny. For example, maintaining the reproductive apparatus to produce eggs could be costly. Conversely, it may be costly to maintain a large egg load. Furthermore, while the model includes an ecological cost (egg-limitation), it omits other ecological costs such as:

1. *Competition between parasitoids for hosts*: progeny mortality associated with superparasitism may drive initial egg loads up far beyond the actual host availability, and so potentially lead to strict pro-ovigeny.
2. *A higher mortality rate in older females*: this could drive parasitoids towards adopting strict pro-ovigeny (for a discussion, see Jervis *et al.*, 2001, 2003).

Extreme values for the number of hosts per patch or stochasticity in the number of hosts per patch did not lead to strict pro-ovigeny, although we previously found the ovigeny index to be positively correlated with those parameters when using a different parameter range (Ellers and Jervis, 2003). This shows that the relationship between ecological parameters and optimal strategies is not necessarily linear, and caution should be exercised when extrapolating findings to unexplored parameter space.

Model predictions aside, the *empirical* finding that strict pro-ovigeny is a rare reproductive strategy (Jervis *et al.*, 2001) has important consequences for theoretical studies of key aspects of parasitoid ecology, such as optimal foraging, clutch size allocation and host–parasitoid population interactions. For example, strict pro-ovigeny has been used to estimate the incidence of time-limitation, which has been the paradigm of optimal foraging theory (Driessen and Hemerik, 1992; Rosenheim, 1996; Sevenster *et al.*, 1998; Van Baalen, 2000; but see Ellers *et al.*, 2000b). Also, the extent to which egg-limitation can stabilize host–parasitoid dynamics has been modelled under the assumption of strict pro-ovigeny (Getz and Mills, 1996; Van Baalen, 2000; but see Shea *et al.*, 1996). Clearly, modellers should consider that: (1) egg load can increase as well as decrease – in synovigenic parasitoids, it fluctuates within often narrow limits, whereas in strictly pro-ovigenic parasitoids it declines monotonically (Heimpel and Rosenheim, 1998); and (2) it can evolve to match ecological conditions.

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