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# The dynamics of egg production, oviposition and resorption in a parasitoid wasp

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## Summary

1. The extent to which parasitoid wasps are limited by their egg supply is very important in understanding their reproductive strategies. Egg reserves are dynamic, with most wasps maturing new eggs throughout their life (synovigeny) and many species resorbing eggs that are not used in oviposition. We investigated the extent to which a parasitoid modulates its egg reserves in the light of its experience in finding hosts.
2. The egg dynamics of the Encyrtid Wasp *Leptomastix dactylopii*, a solitary parasitoid of mealybugs, were studied in the laboratory. This species is synovigenic and practises egg resorption.
3. We allowed newly emerged wasps to experience one of four environments of increasing value in terms of reproductive opportunities. We proposed that wasps that experienced good quality environments would maintain more mature eggs ready for oviposition. Dissection of wasps subject to different periods of host deprivation after the experimental treatment failed to confirm the hypothesis: egg load was independent of experience.
4. We also proposed that any adjustment of egg supply to make up for eggs oviposited would be effected through a reduction in egg resorption. Instead, we found that the wasp quickly made up for eggs oviposited by increased egg production.

*Key-words:* Egg dynamics, encyrtid, oviposition, parasitoid, resorption

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## Introduction

Parasitoid wasps have proved themselves to be very valuable experimental models for investigating many problems in the evolution of reproductive strategies. Parasitoids lay their eggs in, or on, the bodies of other insects, their larvae developing on a single host from which they must obtain all the resources they need to achieve maturity. Because of the importance of the host to the immature parasitoid, the reproductive decisions made by the ovipositing female – when to leave a patch of hosts, whether to attack a particular host, how many eggs to lay, whether the eggs are male or female – have a very clear and direct link to Darwinian fitness. Over the past 15 years there have been numerous behavioural ecological studies of host selection, clutch size and sex ratio in parasitoids; studies that have both improved our understanding of parasitoid biology, and shown the degree to which we can comprehend the evolution of reproductive strate-

gies using an optimality approach (reviewed by Godfray 1994).

Models designed to predict parasitoid reproductive behaviour differ in the assumptions made about the proximate quantity maximized by natural selection. One class assumes parasitoid reproductive success is limited by time and seeks to predict the strategy that maximizes the insect's rate of gain of fitness. A second class of models allows parasitoids to be partially limited by egg supply. These models are typically more complicated because instead of the simple, time-invariant strategy that is normally predicted by models assuming rate maximization, the optimal strategy with egg limitation is usually state dependent, typically a function of egg supply. Allowing reproductive strategy to be influenced by egg load raises a series of new problems concerned with understanding the dynamics of egg production. The simplest approach is to assume that the female insect achieves maturity with a fixed complement of eggs which it uses up over its lifetime. Such parasitoids are termed pro-ovigenic. However, the more common pattern is for parasitoids to mature eggs throughout their lifetime, typically after bouts of feeding. A common source of food for

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these synovigenic parasitoids is the hosts themselves and females of many species face a choice when encountering a host of either using them as an oviposition site or indulging in what is called non-concurrent host feeding (Jervis & Kidd 1986) which destroys the host. The relationship between egg supply, oviposition and host feeding has been closely studied in recent years, both experimentally and theoretically (Antolin & Williams 1989; Kidd & Jervis 1991; Minkenberg, Tatar & Rosenheim 1992; Rosenheim & Rosen 1992; Chan & Godfray 1993; Collier, Murdoch & Nisbet 1994; Collier 1995; Heimpel & Rosenheim 1995). Apart from its intrinsic interest to parasitoid biologists, the relatively simple link between behaviour, state and fitness makes this a good model system of state-dependent behaviour.

Our aim here is to investigate another aspect of egg supply that will influence parasitoid oviposition strategies: egg resorption and the balance between egg resorption and egg production. It has long been known that many synovigenic parasitoids (and many other types of insects, Bell & Bohm 1975) resorb eggs, although the precise role of egg resorption is unclear. Most frequently, egg resorption is assumed to be a means of recycling eggs that have reached maturity but have not been required for oviposition; or a means of obtaining nutrients at times of stress. We study whether the parasitoid adjusts the number of mature eggs it carries and its rate of egg resorption in environments of different quality where it can expect to encounter different numbers of hosts.

One barrier to the study of egg dynamics is the difficulty of measuring the actual number of eggs resorbed. We chose to work with the wasp *Leptomastix dactylopii* which, together with most other members of the family Encyrtidae, have an egg structure that facilitates the study of resorption. The egg in the ovariole is double bodied, consisting of two bulbous structures connected by a neck with chitinized patches (sometimes called 'bands' or 'aeroscopic plates'; Zinna 1959; Lloyd 1966). After resorption, the chitinized neck is still visible as a remnant in the ovariole, allowing the number of resorbed eggs to be counted after dissection.

In the absence of hosts, female *L. dactylopii* begin to resorb eggs after about 96 h (Lloyd 1966). We gave 1-day-old mated females experience of (i) the host's food plant in the absence of hosts or host remnants; (ii) the host's food plant with host remains but no hosts; (iii) a low density of hosts; and (iv) a high density of hosts. The four treatments represented successively more profitable environments for the wasp. After exposure to the different treatments, the wasps were maintained without further hosts and fixed numbers dissected after 2, 4, 6, 8 and 10 days. The experiment was designed to test the following hypotheses:

1. Wasps exposed to more profitable conditions will maintain a larger reserve of mature eggs (in expectation of greater oviposition opportunities). On dis-

section, we predicted an increasing number of eggs in the ovarioles of wasps in treatments (i) through (iv).

2. Larger egg reserves (including replenishment of eggs laid in hosts) will be achieved by a reduction in the rate of egg resorption.

## Materials and methods

Parasitoids for the experiments were obtained from cultures kept at Wye College, University of London, and reared on *Plannococcus citri* feeding on sprouted potatoes (*Solanum tuberosum*) kept in plastic boxes (28 x 16 x 9 cm<sup>3</sup>). Two 6-cm holes were cut in the sides of the box and covered with fine mesh to provide air flow and avoid excess humidity. The cultures were maintained, and the experiments conducted, at 25 ± 2.5 °C, 70 ± 5% r.h. under a 16:8 L:D photoperiod.

All experiments were performed with standardized females obtained as follows. Mealybug mummies were collected from culture and placed individually in small glass tubes (length 5 cm, diameter 1 cm). A drop of honey solution was provided as food for the parasitoid when it emerged. On the day of emergence (Day 1), females were placed with two males in a small Petri dish (5-cm diameter) containing a drop of honey solution and left for 48 h to ensure mating. On Day 3, females were allocated randomly to the different treatments.

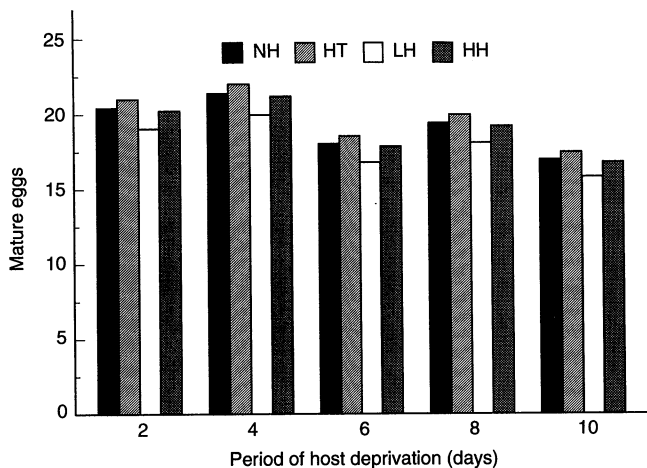
In the four treatments, standardized female parasitoids were exposed for 24 h (from 0800 on Day 3) to leaf discs cut from one of the mealybugs' foodplant (bean, *Phaseolus vulgaris*). The leaf discs (2.5-cm diameter) were placed in a plastic Petri dish (10.5-cm diameter), underside facing upwards, on a layer of agar to maintain humidity. In those treatments involving mealybugs, insects of uniform size (2.39, SE: 0.05 mm) were selected from the rearing boxes and placed on the leaf disc 24 h before the start of the experiment. The four treatments were as follows.

1. No hosts (NH): a leaf disc with no host or host remains.
2. Host traces (HT): one leaf disc on which 10 mealybugs had fed for 24 h, but which had been removed immediately before the experiment.
3. Low host density (LH): one leaf disc with 10 mealybugs.
4. High host density (HH): three consecutive leaf discs with 15 hosts each. The parasitoids were released onto the first leaf disc at 0800, onto the second at 1300, and onto the third at 1800. The females thus spent ≈ 5 h of the light period on each patch. In order to keep the time of exposure to the hosts constant across treatments (24 h), females were left on the third patch for the remaining 8 h of the dark period.

At 0800 on Day 4, all females were removed from the leaf discs and placed in a glass tube (length 5 cm,

diameter 1 cm) with a small drop of honey solution which was renewed every second day. The females had no access to hosts. A fifth of the females from each treatment were dissected after five different periods of host deprivation: 2, 4, 6, 8 and 10 days. The numbers of mature and resorbed eggs in the oviducts were counted, and the length of the hind tibia was measured to obtain an index of body size. Fifteen replicates were obtained for each of the four treatment by five host deprivation combinations. The few females that escaped or that died stuck to the honey solution were not included in the analysis. The mealybugs in the high- and low-density treatments (HH, LH) were dissected and the number of parasitoid eggs they contained counted.

Data were analysed using generalized linear modelling techniques implemented on the GLIM statistical package (McCullagh & Nelder 1989). Because the data consisted of counts, we assumed Poisson errors (with a logarithmic link function). We checked the appropriateness of these assumptions by examining the distribution of the residuals from the full model, and checking that the residual deviance and the residual degrees of freedom were approximately equal. In analysing the results, we always controlled for adult wasp size which is known to have an important influence on egg load. We included the period of deprivation in the model before testing for the effects of treatment. Because our sample size is relatively high, not all statistically significant effects are biologically significant. Statistical significance is determined using  $\chi^2$ -tests although with a Poisson error distribution this is only justified asymptotically. To judge biological significance, we give the percentage deviance around the mean attributable to each factor, an informal measure equivalent to the sum of squares ( $r^2$ ) in traditional ANOVA.



**Fig. 1.** The numbers of mature eggs carried by wasps from the four different experience regimes and which had been dissected after different periods of host deprivation. Size influences egg load and the histograms represent the expected number of eggs carried by a wasp of average size. The treatments are (see also text): NH, no hosts; HT, host traces; LH, low host density; HH, high host density.

## Results

Female wasps in the low-density treatment laid 5.66 (SE: 0.69) eggs while wasps in the high-density treatment laid 10.12 (SE: 0.32) eggs. The difference was statistically significant ( $\chi^2 = 31.45$ ,  $df = 1$ ,  $P < 0.001$ ) although less than the threefold difference in the numbers of hosts presented. Larger wasps tended to lay more eggs (controlling for treatment, female size was highly significant:  $\chi^2 = 53.95$ ,  $df = 1$ ,  $P < 0.001$ ). Unfortunately, although wasps were allocated at random to treatments, those in the high-density treatment were significantly ( $F = 9.45$ ,  $df = 3$ ,  $202$ ,  $P < 0.001$ ) larger (hind tibia length 1.30 mm, standard error 0.5) than in the other three treatments (1.19 mm, standard error 0.5) ( $F = 9.45$ ,  $df = 3$ ,  $202$ ,  $P < 0.001$ ). However, controlling for treatment, the difference between the number of eggs laid in the high- and low-density treatments was still significant ( $\chi^2 = 20.19$ ,  $df = 1$ ,  $P < 0.001$ ). In drawing histograms of egg load and resorption, we control for wasp size and present egg numbers for wasps of approximately average size (hind tibia length 1.2 mm).

We expected females that had experienced a high-quality environment to maintain a larger number of eggs ready for oviposition (Hypothesis 1). The data did not support this hypothesis (Fig. 1). The full model for the data contains the terms wasp size ( $\chi^2 = 228.1$ ,  $df = 1$ ,  $P < 0.001$ ), period of deprivation ( $\chi^2 = 28.33$ ,  $df = 4$ ,  $P < 0.001$ ) and the interaction between treatment and size ( $\chi^2 = 7.855$ ,  $df = 3$ ,  $P < 0.049$ ). The main effect of treatment was not significant ( $\chi^2 = 7.209$ ,  $df = 3$ ,  $P = 0.066$ ). The interaction between size and treatment was only just significant and biologically rather unimportant, explaining just 1.9% of the deviance of the data. The significant interaction was caused by larger wasps in the low host density treatment having comparatively fewer mature eggs. The period of deprivation explained 7% of the deviance, although the number of mature eggs did not vary linearly with the period of deprivation. By far the most important variable predicting egg load was body size which accounted for 56.7% of the deviance.

Thus the number of mature eggs in the wasps' ovarioles depends only weakly on the period of host deprivation, and is uninfluenced by past experience. Wasps in treatments where oviposition occurred must thus resorb fewer eggs or produce more eggs. Logically, it is less wasteful of resources to reduce resorption and hence we predicted fewer resorbed eggs in wasps that had experienced good patches (Hypothesis 2). Again, the data do not support the hypothesis (Fig. 2). The full model describing the number of resorbed eggs now contains wasp size ( $\chi^2 = 124.58$ ,  $df = 1$ ,  $P < 0.001$ ), the period of deprivation ( $\chi^2 = 773.5$ ,  $df = 4$ ,  $P < 0.001$ ) and the interaction between treatment and deprivation ( $\chi^2 = 30.23$ ,  $df = 12$ ,  $P = 0.0026$ ). The treatment main effect was not significant

( $\chi^2 = 5.44$ ,  $df = 3$ ,  $P = 0.14$ ). However, as before, while the interaction term is statistically significant, it explains only 2.8% of the deviance and is thus of minor significance biologically. The interaction is caused by relatively high numbers of resorbed eggs in the host traces treatment after two days of host deprivation. Inspection of Fig. 2 shows no clear pattern underlying this interaction. Adult wasp size accounts for 11.5% of the deviance while the period of deprivation accounts for 71.4% of the deviance.

If reduced resorption cannot explain how wasps that have laid eggs in hosts achieve equal egg loads to wasps that have laid eggs, then increased egg production must be responsible. Total egg production was calculated by summing for each wasp the numbers of eggs laid (if any), the numbers of eggs resorbed and the number of mature eggs in the oviducts at dissection. Below we present a statistical analysis of egg production (Fig. 3), although as we have already

analysed the components of egg production this is not an independent analysis. The full model contains wasp size ( $\chi^2 = 493.70$ ,  $df = 1$ ,  $P < 0.001$ ), the period of deprivation ( $\chi^2 = 100.32$ ,  $df = 3$ ,  $P < 0.001$ ) and treatment ( $\chi^2 = 85.01$ ,  $df = 3$ ,  $P < 0.001$ ), and also the interaction between size and treatment ( $\chi^2 = 13.74$ ,  $df = 3$ ,  $P = 0.0033$ ) and the three-way interaction ( $\chi^2 = 30.04$ ,  $df = 12$ ,  $P = 0.0028$ ). The two interaction terms, while statistically significant, are of only low biological significance, explaining 1.6% and 3.1% of the deviance, respectively. Wasp size is of major importance, explaining 55.8% of the deviance in egg production. Total egg production increases cumulatively with time, the period of deprivation explaining 11.3% of the deviance. Wasps that have attacked hosts produce more eggs, treatment explaining 9.6% of the deviance.

### Discussion

In our experiments, wasps maintained a constant egg load irrespective of their recent experience and how many eggs they had laid. They achieved this constant egg load not by reducing the number of eggs they resorbed, but by increasing the rate of egg production after oviposition. We thus refuted both the hypotheses we aimed to test.

By an unfortunate accident, the size of wasps in one treatment (high density) was significantly larger than in the other three treatments. Wasp size can only be measured accurately after death (anaesthetization potentially changes behaviour) and hence we had to allocate wasps to treatments blindly. Wasp size is an important correlate of egg load and production and thus in all analyses we included wasp size in the analysis before examining the two treatments. The statistical models we fitted to egg load, production and resorption included interaction terms that were statistically significant but that explained a very small amount of the deviance and so were of low biological significance. We explored whether these interactions might have resulted from the unequal distribution of wasp sizes across treatments by repeating the analysis but omitting the high-density treatment. In all cases, qualitatively identical results were found. The interaction terms are caused by a shallower than expected relationship between mature egg load and size in the low host density treatment, and a tendency for wasps in the host traces treatment to have resorbed fewer than expected eggs when dissected after two days of host deprivation. These patterns were not expected and we have no *a posteriori* explanation for them.

The first hypothesis we tested was that wasps that had experienced good conditions early in life should maintain a larger supply of mature eggs in their oviducts ready for oviposition. This is an adaptive hypothesis and its failure may be explained by other adaptive considerations or by constraints on the wasp. It is possible that in the environment in which the

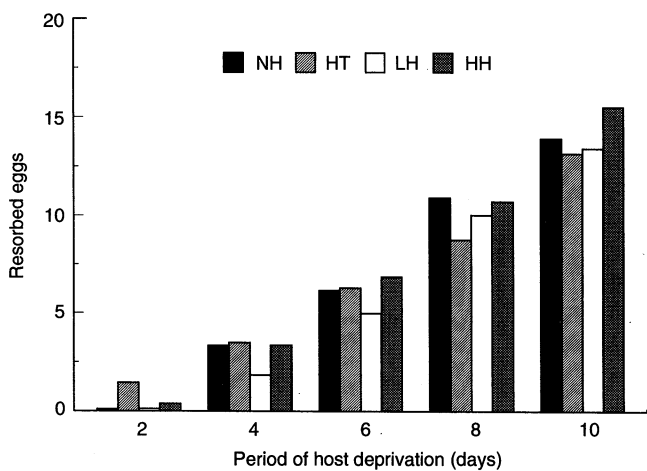


Fig. 2. As Fig. 1 but the histograms represent the number of resorbed eggs counted on dissection.

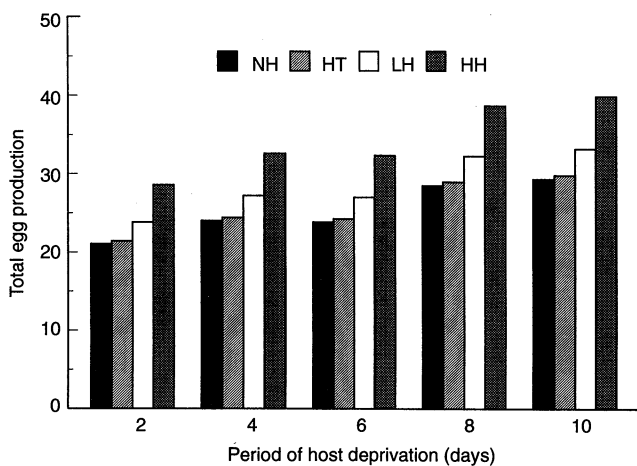


Fig. 3. As Fig. 1 but now the total number of eggs produced by a wasp of average size is plotted. The total is made up of the mature eggs, resorbed eggs and (in LH and HH treatments) eggs laid in hosts.

wasp evolved there is no, or only a weak, correlation between conditions experienced by the insect on one day and on subsequent days. Alternatively, the wasp may be selected to maintain the maximum possible number of mature eggs in its oviducts so that the egg load is determined by a structural or physiological constraint (which, one could argue, in its turn is determined by wider trade-offs in the animal's life history). Similarly, the correlation between parasitoid size and egg load may have an adaptive explanation: large females tend to live longer and thus require more eggs. Alternatively, the correlation may be due to an allometric constraint.

We expected adjustments of egg load in response to treatment to be affected by a reduction in resorption, rather than an increase in egg production (Hypothesis 2). In fact, we found the reverse. One explanation for this result is that egg supplies were replenished very quickly: by the first dissection, two days into the period of host deprivation, there was no statistical difference in the number of eggs carried by wasps in the four treatments. Quickly replenishing oviposited eggs allows the wasp to utilize local, and perhaps temporary, areas of high host abundance. It would be interesting to repeat this experiment with older wasps that had already begun to resorb eggs to see whether they compensated for the eggs they had oviposited in the same manner.

Wasps at the end of the experiment, approximately 2-weeks old, carrying 15–20 eggs, had already resorbed 10–15 eggs, and, depending on the treatment, had oviposited between 0 and 15 eggs. Wasps over about 96-h old, resorb eggs at a steady rate of about 1–1.5 eggs per day (Fig. 2). Resorption is associated with only a weak decline in egg load which suggests that the main purpose of resorption observed here is not to provide nutrients at a time of stress (wasps were regularly fed throughout the experiment which also makes nutrient stress an unlikely explanation). It thus seems more likely that resorption is a means of maintaining a constant supply of newly mature eggs. Designing an experiment to demonstrate that mature eggs decline in quality with time is, unfortunately, difficult. It would be interesting to know the costs associated with resorption, something that may be measurable using physiological techniques.

*Leptomastix dactylopii* does not host feed, although it is not known whether it obtains resources from feeding on honeydew or other host remains. We found no difference in the egg dynamics of wasps that had not oviposited but that had been exposed to host plant with or without honeydew (replacing the NH and HT treatments with a single composite treatment led to no reduction in the explanatory power of any of the statistical models). This does not exclude honeydew as of importance to the wasp, but suggests that at least

for well-fed wasps it is not a significant factor influencing egg load and resorption.

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