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Fitness consequences of ovicide in a parasitoid wasp

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Abstract

Ovicide, superparasitism and host rejection are alternative reproductive tactics facing female parasitoid wasps encountering an already-parasitized host. Superparasitism is simply the addition of an egg or a clutch of eggs by the secondary parasitoid, but under ovicide the primary clutch is removed or destroyed. Host rejection occurs if the wasp leaves without laying a clutch.

The ectoparasitoid *Laelius pedatus* (Say) (Hymenoptera: Bethylidae) performs ovicide in this situation. Clutch manipulation experiments show that secondary clutches suffer high mortality in competition with primary clutches, which increases with increasing time delay between clutches. Primary clutches however suffer little in competition with secondary clutches, even if there is minimal time delay between clutches. These data suggest that the offspring of ovicidal females are substantially fitter than the offspring of superparasitizing females.

Handling time and clutch size do not differ significantly between first (sole) parasitoids and second (ovicidal) parasitoids. The same is true for offspring survival and development time. However, offspring of second females are slightly smaller. This suggests that parasitized and unparasitized hosts are resources of similar quality when ovicide is performed.

These data strongly support the predictions of evolutionary models of ovicide. They may also give some insight into the taxonomic distribution of ovicide in parasitoids.

Introduction

Natural selection theory predicts that organisms are more commonly selected to maximize their own individual fitness or the fitness of the genes they carry, rather than the fitness of some larger unit such as the group or species (e.g., Fisher, 1930; Dawkins, 1976; Maynard-Smith, 1976; Williams, 1992). Some striking evidence for this comes from the behaviour of insect parasitoids which kill conspecifics (Salt, 1961; Godfray, 1987). Such behaviour is clearly not for the good of the species, but can be attributed to individual or gene selection.

Here I describe behaviour by females of a parasitoid wasp, *Laelius pedatus*, which kill conspecific eggs on encountering a parasitized host. In most parasitoid species, the second female to arrive at a host can either reject the host or perform superparasitism, laying her own clutch in addition to the first (van Alphen & Visser, 1990). Host rejection can be favourable because the wasp can invest the time or eggs in better quality hosts elsewhere (Charnov & Skinner, 1984). Superparasitism can be favourable if the secondary clutch is not at a great competitive disadvantage from the first clutch, or if better quality hosts are rare and host rejection does not pay. A third tactic is possible if the wasp can remove the competition for host resources embodied in the first clutch. She can then make the host a higher quality resource for her own offspring. Such behaviour is known as ovicide. Ovicide is rarely reported but is known from the Pteromalidae, Aphelinidae, Ichneumonidae, Braconidae, and Bethylidae (review in Godfray, 1994). It appears to be most widespread in the Bethylidae, being reported from *Goniozus trian-*

gulifer Kieffer (Legaspi *et al.*, 1987), *G. nephantidis* (Muesebeck) (Hardy & Blackburn, 1991), *G. platynotae* (=*floridanus*) Ashmead (Goertzen & Doutt, 1975), *G. marasmi* Kurian (Venkatraman & Chacko, 1961) and *Sclerodermus macrogaster* (Ashmead) (Wheeler, 1928). Within the Bethylidae, superparasitism also occurs in the absence of ovicide in *G. indicus* Ashmead (Cherian & Israel, 1942) and *G. platynotae* (Goertzen & Doutt 1975), and both superparasitism and ovicide occur in *G. triangulifer* (Legaspi *et al.*, 1987), and *G. platynotae* (Goertzen & Doutt, 1975), where the first clutch is incompletely removed prior to oviposition. In the Bethylidae ovicide occurs through female wasps eating eggs, but in other families it seems to mainly occur by females stinging eggs (Godfray, 1994). It is not known at present if the apparent rarity of ovicide is primarily due to lack of reporting or because it is genuinely absent in the majority of parasitoid species.

The conditions under which adaptive ovicide might evolve in parasitoids have been modelled by Strand & Godfray (1989) using a game theoretical approach (Maynard-Smith, 1982). Whether ovicide evolves depends on the relative pay-offs of ovicide, superparasitism and host rejection. The model assumes that the benefits of ovicide result from increased offspring survival and quality relative to superparasitism, and that a cost is imposed by the time taken for a female to perform ovicide (if she is time limited).

Strand & Godfray's model predicts that ovicide is more likely to evolve when the competitive advantage of the first clutch under superparasitism is large. This increases the relative pay-off of ovicide. The model also predicts that ovicide is more likely when unparasitized hosts are rare. This makes host rejection a relatively unfavourable strategy. Finally, ovicide is more likely when the time taken to perform ovicide is small. This reduces the costs of ovicide.

To the author's knowledge the only explicit test of these predictions is on the wasp *Bracon hebetor* Say (Hymenoptera: Braconidae) (Strand & Godfray, 1989), an ectoparasitoid of phycitiine moths (Lepidoptera: Pyralidae). It was found that the competitive advantage of the first over the second clutch increased with the time between ovipositions, conditions which favour the evolution of ovicide over superparasitism. Also, as predicted by theory, wasps performed ovicide more often with a decrease in the host encounter rate, and with an increase in the proportion of parasitized hosts encountered; conditions which make host-rejection less favourable.

Some of the assumptions of the Strand & Godfray model may not hold for all parasitoids. Importantly, a parasitized host may not always be a lower quality resource than an unparasitized host, and handling time is not the only factor which may affect this (Takasu & Hirose, 1988, 1991). In addition Strand & Godfray (1989) made the implicit assumption that wasps will never remove their own eggs. Although some wasps avoid self-superparasitism (van Dijken *et al.*, 1992), this is not universal. For example the bethylid *G. platynotae* sometimes eats its own eggs (Goertzen & Doutt 1975). In a model of ovicide in granivorous weevils, Smith & Lessells (1985) incorporated the likelihood of removing one's own eggs. Not surprisingly as this likelihood increased ovicide was less likely to evolve.

L. pedatus is another bethylid species which removes conspecific eggs from hosts (Mayhew, 1996). Here, simple laboratory experiments attempt to determine the effects of ovicide on the fitness of the mothers and offspring. Two major questions are addressed that affect the decisions of females arriving at a parasitized host: Firstly, how is the fitness of offspring affected by ovicidal versus superparasitism strategies? Secondly, given that wasps are ovicidal, is a parasitized host a lower or higher quality resource than an unparasitized host (if it is lower, host rejection will become more favourable)? Because ovicide is common in this species, it is predicted that offspring should be fitter under ovicide than superparasitism, and/or that parasitized hosts should be resources of equal or higher quality than unparasitized hosts.

Materials and methods

Biology of L. pedatus

L. pedatus is an idiobiont ectoparasitoid of the larvae of dermestid beetles (Coleoptera: Dermestidae) (Mertins, 1980). Females paralyze hosts with repeated stings and prepare them for oviposition by removing setae from an area of the ventral thorax and abdomen. Handling time may be several hours and for much of this time females are inactive near the host. It is likely that this time is used to mature the sizeable eggs prior to oviposition. 1–6 eggs are laid on the depilated region of the ventrum. After oviposition the female immediately abandons the host: there is no evidence of brood guarding, which is known from bethylids in the genera *Goniozus* (e.g., Hardy & Blackburn, 1991), *Prosierola*

(Doutt, 1973), *Sclerodermus* (Kühne & Becker, 1974) and *Pristocera* (Baker, 1976). The eggs hatch 3–4 days after oviposition, the larvae grow quickly and pupate about ten days after oviposition.

Cultures

The host used in this study was *Anthrenus flavipes* (Leconte) (Coleoptera: Dermestidae). Both wasps and hosts were obtained from D. J. W. Morgan (Silwood Park, UK) who had maintained wasps on *Anthrenus* spp. for several generations, but the hosts originally came from the Central Science Laboratory, Slough, U.K., and the wasps from the USDA, Hoboken, New Jersey. Hosts were reared on a diet of fish-meal, yeast and cholesterol. Both culturing and experiments took place at 27 °C and 70% r.h. under a L14: D10 photoperiod. Hosts weighing 1.5–5 mg were used during the experiments.

Experiments

Two experiments were performed, each with treatments and controls. For clarity each treatment is identified by a letter (Table 1). In the first experiment, the fitness of wasp offspring is compared in the presence and absence of another clutch of eggs to assess what the offspring gain when mothers remove the first clutch. The second experiment assesses the resource quality of a parasitized versus an unparasitized host by comparing fitness-related variables in the mothers and their offspring.

Offspring fitness under superparasitism versus ovicide. In this set of treatments, single weighed hosts were placed in 3 cm petri dishes lined with filter paper, and one or two clutches of eggs added by either a wasp, or by the experimenter using a mounted needle. They were checked each day until pupation and the number of offspring recorded. On emergence the date, and the number, sex, and size (thorax length) of offspring was recorded.

The treatments differed in the number of eggs on each host, their age, and in how they came to be placed on the host; by the wasp or by the experimenter. Treatment A ($n = 48$) simulated superparasitism by a second female but with no difference in the age of the clutches. The first clutch of 3 eggs was laid by a wasp in the normal way, whilst the second clutch was of variable size (1–5 eggs) and was transferred to the host with a mounted needle by the author. Because superparasitism was never observed naturally in these experiments, it was not known precisely where a superparasite would oviposit on the host. However, females were observed laying large clutches of five or six eggs, with each egg being placed in progressively more posterior positions on the host around the shaved ventral region. Therefore, the second clutch was placed on the shaved area of the host ventrum posterior to the first clutch (Figure 1), making, in effect, an artificially enlarged single clutch. Treatment B ($n = 54$) was the same as treatment A except that the transferred eggs were two days younger than the first clutch. Comparing the above two treatments thus measures the effect of time delay between the laying of the first and second clutches under superparasitism. Treatment C ($n = 82$) comprised hosts on which a clutch of 3 eggs had been laid by a wasp, removed and then a clutch of 1–5 eggs transferred to it. Comparing this treatment with treatment A measures the effect of the first clutch on the second clutch whilst controlling for the transferral of eggs by the experimenter. Treatment D ($n = 50$) comprised a host on which a clutch of 3 eggs had been laid, removed, replaced in the same position, and a second clutch of 1–5 eggs laid on the same day added. This treatment is a repetition of treatment A, except that both clutches have been transferred by the experimenter, therefore any differences in clutch fitness must be due to order of oviposition. Comparisons made in the analysis are summarized in Table 2.

Where more than one clutch was on a host, offspring could be individually identified until pupation on the basis of spatial position, recorded daily by drawings. Since wasp larvae pierce the host cuticle immediately after eclosion and feed only from this single puncture (Mertins, 1980), their relative spatial positions remain constant during feeding. In these treatments only 8 offspring died between pupation and emergence and in every case the clutch to which the dead individuals belonged could be identified, either because only one clutch survived to pupation, or because every individual on the host died. Thus differential mortality between clutches was recorded with complete certainty. However, upon emergence it was impossible to distinguish individuals from different clutches. Thus for *L. pedatus* measures of offspring quality are combined for all offspring on a host.

Quality of parasitized versus unparasitized hosts. Two treatments were performed in which wasps and hosts were observed in detail up to oviposition, and then the development of offspring was observed at

Table 1. The differences between experimental treatments

Treatment	Summary	Number of clutches per host	Number of clutches allowed to develop per host	Size of first clutch (eggs)	Size of second clutch (eggs)	1st clutch laid by wasp or experimenter	2nd clutch laid by wasp or experimenter	Age difference between clutches (days)
A	Simulated instantaneous superparasitism	2	2	3	1–5	Wasp (d)*	Experimenter (d)	0
B	Simulated delayed superparasitism	2	2	3	1–5	Wasp (d)	Experimenter (d)	2
C	Simulated instantaneous ovicide	2	1	3	1–5	Wasp (r)	Experimenter (d)	0
D	Simulated instantaneous superparasitism	2	2	3	1-5	Experimenter (d)	Experimenter (d)	0
E	Natural single clutch	1	1	3	–	Wasp (d)	–	–
F	Natural ovicide	2	1	3	2-5	Wasp (r)	Wasp (d)	1

* d, allowed to develop; r, removed.

Table 2. Statistical comparisons made and points addressed

Treatments compared	Variables compared	Point addressed by comparison
E, F	Clutch size, handling time, offspring survival, size and development time	Quality of parasitized host versus unparasitized host
A, C	Survival of 2nd clutch	Effect of 1st clutch on 2nd clutch survival
A, E	Survival of 1st clutch	Effect of 2nd clutch on 1st clutch survival
A, B	Survival of both clutches	Effect of clutch age difference on relative survival of clutches
D	Survival of 1st clutch versus 2nd clutch	Effect of oviposition priority on survival independent of placement method

daily intervals. Single weighed hosts were placed in 3 cm petri dishes lined with filter paper. A single female wasp, 0–1 day old, mated, and naive to hosts was introduced to the dish at 11.30 h (BST) on the day of observations. Every 30 min the number of eggs on the host and behaviour of the wasp was recorded. Behaviour of the wasp was categorized in the following way: stinging the host; resting away from the host; biting the host; resting on the host; shaving the host; crawling around the dish; cleaning itself; antennating host; removing eggs; ovipositing. Once the wasp had oviposited it was removed and the eggs left to develop. They were checked each day until pupation, and the number of offspring recorded. On emergence the date, and the number, sex, and size (thorax length) of offspring was recorded. In treatment E ($n = 26$) the host was unparalyzed. In treatment F ($n = 43$) the host bore a clutch of 3 eggs (0–1 d old) laid by a wasp (Table 1). Comparing the fitness-related variables in treatments E and F thus tests whether parasitized and unparasitized hosts are similar quality resources given that wasps will perform ovicide. Comparing the offspring survival in

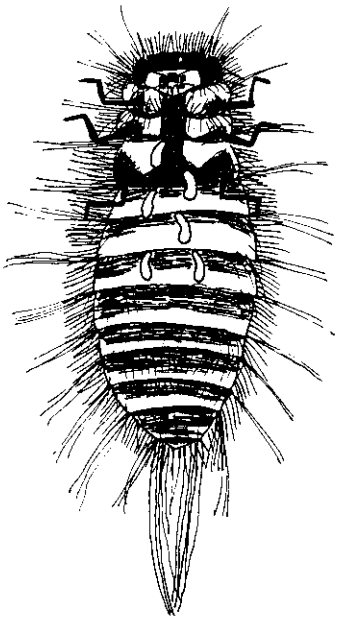


Figure 1. A paralyzed host (length 5 mm) with eggs. The anterior three eggs were laid by a wasp but the posterior three eggs were added by the author to simulate superparasitism by another wasp.

treatment E with that of the first clutch in treatment A tests for the effect of the second clutch on the first clutch, whilst controlling for the fact that in both cases clutches were laid by a wasp rather than transferred to the host by the experimenter (Table 2).

Analysis

Data were analyzed using general linear modelling in the GLIM statistical package. Poisson errors were assumed for count data and binomial errors for proportion data. The appropriateness of these errors was assessed by a heterogeneity factor (HF) calculated by dividing the residual deviance by the residual degrees of freedom. When HF>1.2, indicating overdispersion, the model was rescaled using the value of (Pearson's X^2/df) as a scaling factor. The % scaled deviance (%dev.) is used as an informal measure of explanatory power. Models were minimally adequate, meaning that they consisted only of those terms whose removal caused a significant loss in explanatory power. Because the size of hosts used was quite variable, host weight was always investigated as an independent variable, and therefore controlled for statistically where necessary.

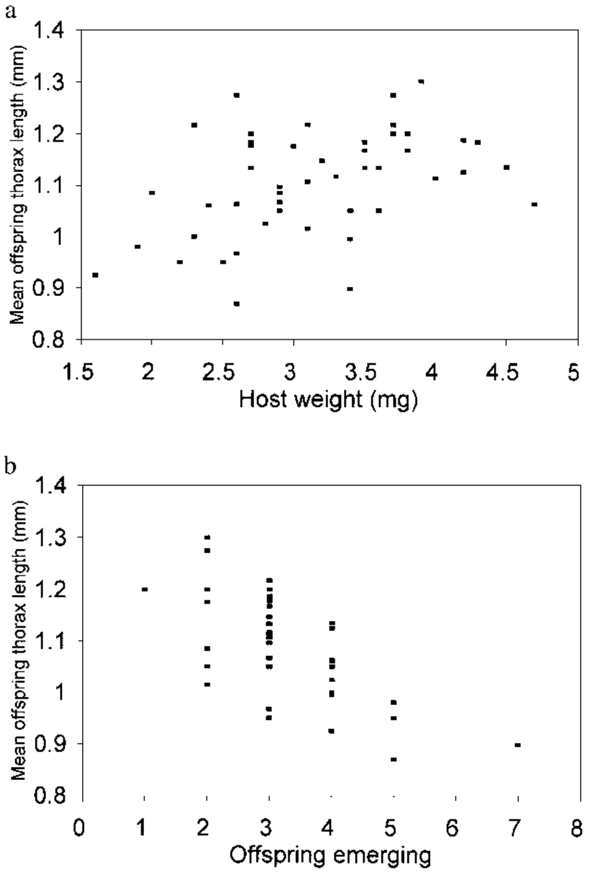
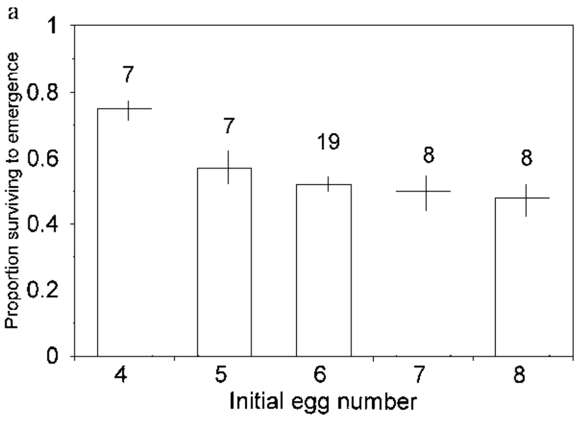


Figure 2. Effect of host weight (a) and the number of offspring emerging (b) on the size of offspring in a brood. Data are from treatment A.

Results

Offspring fitness under superparasitism and ovicide

When superparasitism was imposed artificially by adding eggs (treatment A), the mean size of offspring emerging was positively correlated with host weight ($r^2 = 0.174$, $F_{(1,47)} = 8.16$, $P < 0.01$) (Figure 2a), negatively correlated with the number of offspring emerging ($r^2 = 0.378$, $F_{(1,46)} = 21.02$, $\mathrm{P} < 0.001$) (Figure 2b), and the number pupating ($r^2 = 0.387$, $F_{(1,46)} = 21.54$, $\mathrm{P} < 0.001$), but not correlated with the number of larvae ($r^2 = 0.043$, $F_{(1,46)} = 2.37$, $\mathrm{P} > 0.1$) or eggs ($r^2 = 0.001$, $F_{(1,46)} = 0.044$, $\mathrm{P} > 0.1$) on the host (4–8). The probability of survival to emergence was negatively correlated with the initial number of eggs (%dev= 12.4, $X_1^2 = 4.52$, $\mathrm{P} < 0.05$) (Figure 3a), but the total number surviving did not depend significantly on the initial number



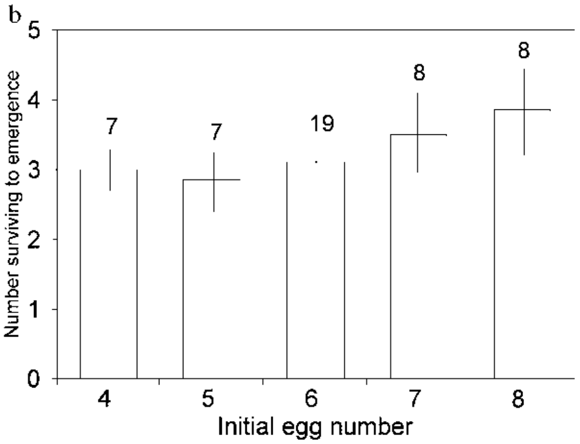


Figure 3. Survival (mean ± SE, figures indicate number of replicates) of offspring when eggs were added to an original clutch of three (treatment A), as a function of the total number of eggs on the host. Survival is shown both as the proportion surviving (a) and as the number surviving (b).

of eggs (%dev= 8.47, $X_1^2 = 1.23$, $P > 0.1$) (Figure 3b). Thus mortality approximately compensated for any increase in the total number of eggs. The probability of survival was not correlated with host weight (%dev= 0.2, $X_1^2 = 0.068$, $P > 0.7$). The survival of the first clutch was not correlated with the size (%dev= 0.4, $X_1^2 = 0.24$, $P > 0.6$) or survival of the second clutch (%dev= 3.6, $X_1^2 = 2.15$, $P > 0.1$). The survival of the second clutch was not correlated with the survival of the first clutch (%dev= 3.3, $X_1^2 = 1.96$, $P > 0.1$).

The probability of survival of the second clutch was significantly lower when the first clutch was present (treatments A & C) (%dev= 21.4, $X_1^2 = 43.21$, $P < 0.001$), and survival of the first clutch was significantly lower when the second clutch was present (treatments A & E) (%dev= 7.3, $X_1^2 = 6.81$, $P < 0.01$). However, the effect of competition was much greater on the second clutch than the first clutch (Figure 4). Two hypotheses could account for this asymmetry. Firstly, it could be an artefact resulting from whether the second clutch was positioned on the host by the experimenter or the wasp. Alternatively, the second clutch could be at a disadvantage because the first clutch of eggs has a superior position on the host: a true advantage of oviposition priority. To attempt to discriminate between these hypotheses, survival of clutches in treatment D was compared. Here both clutches received the same handling treatment so any differences must be due to oviposition priority. Survival (mean ± SE) of the first clutch here was 0.727 ± 0.048 and survival of the second clutch was 0.360 ± 0.052 (Figure 4). Because first and second clutches on the same host are not truly independent, the difference in survival was analyzed by a pair-wise nonparametric test (Wilcoxon signed ranks test: $n = 50$, P (two-tailed) < 0.005). This strongly suggests that oviposition priority is the major reason for first clutch advantage. Since clutches were of the same age, egg position is likely to have been important in determining the outcome of competition between broods.

When a time delay of two days between the clutches was imposed (treatment B), survival of the second clutch reduced to zero (%dev= 52.7, $X_1^2 = 67.14$, $P < 0.001$), whereas survival of the first clutch was

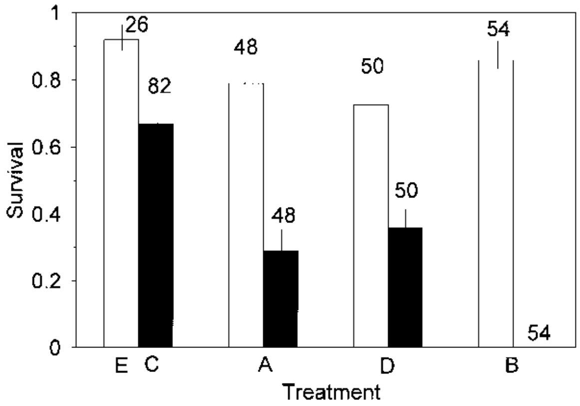


Figure 4. Survival (mean ± SE, n) of first (white bars) and second (filled bars) clutches when developing alone (treatments E and C), under instantaneous superparasitism (treatments A and D) and under delayed superparasitism (treatment B). In treatment D both clutches were laid by the experimenter; in all others the first clutch was laid by a wasp and the second clutch by the experimenter. Figures indicate number of replicates.

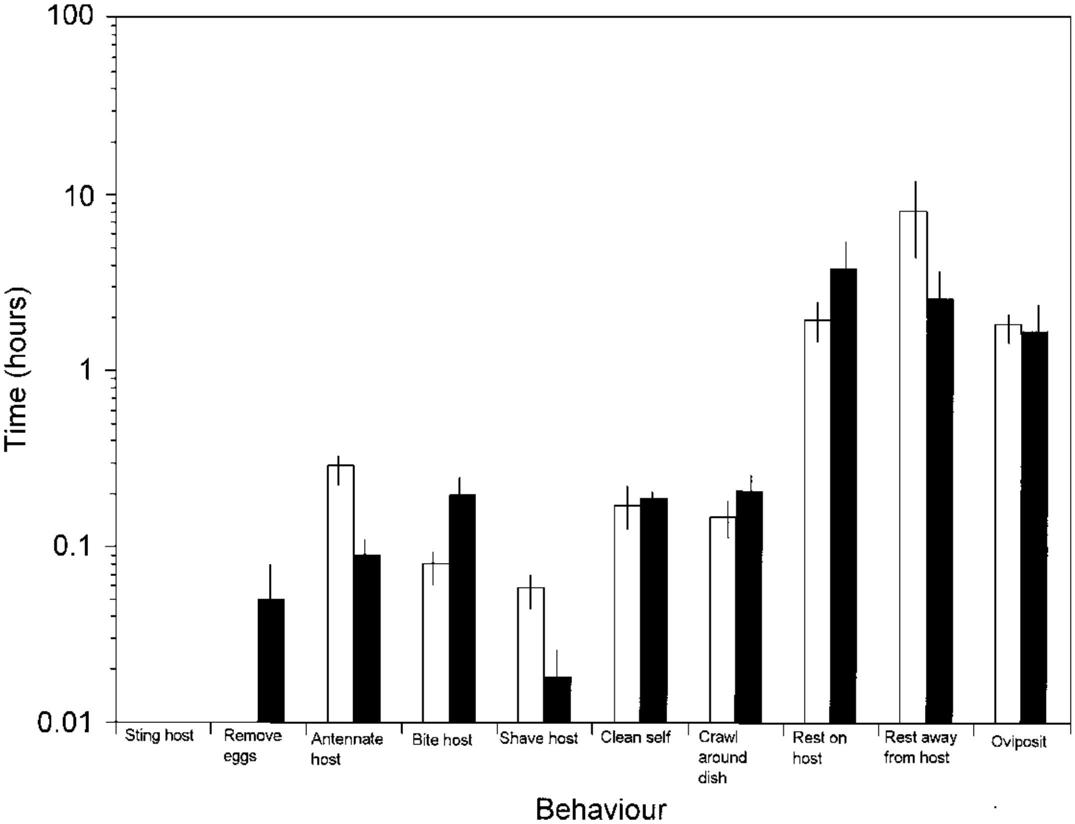


Figure 5. The time (mean ± SE) spent in different components of host handling from first encounter to leaving, ordered approximately in temporal sequence from left to right, for first (white bars) and second (filled bars) females laying three eggs (n = 26, 28). Note the logarithmic scale.

not significantly affected (%dev= 1.7, $X_1^2 = 2.6$, $P > 0.1$) (Figure 4).

Quality of parasitized versus unparasitized hosts

When first females were placed in a petri dish with a host they normally spent only a few seconds searching before contacting it and stinging it. Once the host was quiescent they spent several minutes by the host antennating it (mean 0.29 h ± SE 0.06 h)and biting the legs or antennae (0.08 ± 0.04 h) (Figure 5). After this inspection behaviour, the host was prepared by removing the setae from the ventral thorax and abdomen (0.058 ± 0.032 h). Throughout this period the wasp would often leave the host and crawl activity around the dish (0.15 ± 0.05 h), or clean its body of the host setae which had attached themselves to it (0.17 ± 0.07 h). The majority of the handling time was spent resting motionless either on (1.96 ± 0.19 h) or by the host (8.23 ± 3.89 h) following host preparation. Finally the wasp oviposited on the host, lasting 1.88 h (± 0.21).

Second females performed much the same kinds of behaviour on encountering a host (Figure 5). However, there were several qualitative differences. Second females did not sting the host (it was already paralyzed) and on encountering it began by removing any previous clutch of eggs. They initially inspected the host by antennating in the ventral thoracic and abdominal region where the eggs are laid. On finding a clutch of eggs, the female took one in her mandibles and lifted it away from the host (Figure 6). She then attempted to drop the egg but this appeared difficult because the eggs were large and sticky, and the forelegs were often used to help deposit it on the ground. Because the first instar larvae of the wasp are immobile, removal of the egg from the host is tantamount to killing it. Females were never observed to eat an egg or its contents, as seen in all other ovicidal bethylids, though eggs were often damaged during removal and probably did not

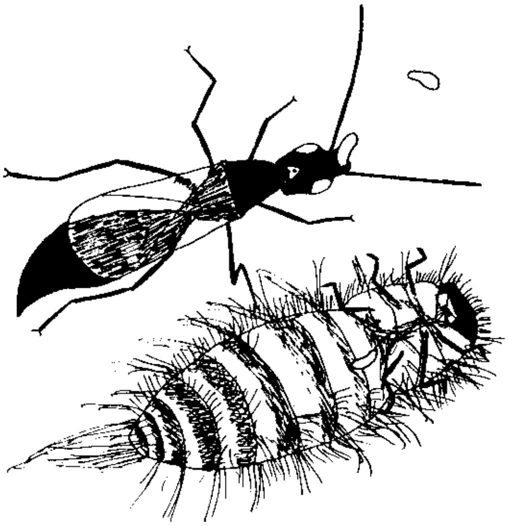


Figure 6. A female *L. pedatus* (length 4 mm) removing an egg from a parasitized host prior to oviposition. One egg remains on the host, and one has already been removed and lies away from the host.

eclose successfully. Following egg removal a female often cleaned herself with her legs or rested before returning to remove another egg. The previous clutch was always completely removed ($n = 43$), on average 0.95 h (± 0.25) after introducing the wasp into the petri dish but the actual egg removal took little time (0.05 ± 0.03 h); most of the time during the egg-removal period was spent inspecting the host, cleaning, or resting motionless. Only once did I observe a second female shaving the host after egg removal; this had already been done by the first female. The majority of the handling time was taken up after egg removal by resting motionless followed by oviposition, just as in first females (Figure 5).

The mean size of clutches laid by first and second females on average did not differ significantly (treatment F) though they were not always the same in a given case (means ± SE): 1st clutch $= 3.00$ (± 0.00), 2nd clutch$=$ 3.19 (± 0.10), $n = 43$, $X_1^2 = 0.24$, $P > 0.6$) (Figure 7a). The weight of the host did not significantly affect the size of the second clutch ($X_1^2 = 1.24$, $P > 0.2$). In comparing the fitness-related characteristics of first and second females and their offspring (treatments E and F) only clutches of 3 eggs were compared to control for effects of clutch size ($n = 26$ and 28).

Because host handling times were skewed towards longer times the natural logarithm of handling time was analyzed. Ln(handling time) was not significantly affected by host weight ($F_{(1,53)} = 1.03$, $P > 0.1$) or treatment ($F_{(1,53)} = 1.51$, $P > 0.1$) (Figure 7b). Because the various components of handling time were not always observed in a given wasp and were also heavily skewed in duration, comparisons were made by a non-parametric test (Mann-Whitney U-test, two-tailed). None of the three major components of handling time differed in duration for first and second females (resting on host: $P = 0.531$, resting away from host: $P = 0.179$, oviposition: $P = 0.202$) (Figure 5). Of the other smaller behavioural components the only significant difference was in time spent antennating the host, which was longer in first females ($P = 0.035$), although the power of these tests is very low for rarely observed types of behaviour. For example, there is no significant difference in time spent removing eggs ($P = 0.089$), even though no first females could have done this and all second females did it, because it took so little time that it was rarely observed during sampling.

Neither survival of offspring ($X_1^2 = 1.76$, $P > 0.1$) nor egg-adult development time ($F_{(1,53)} = 1.06$, $P > 0.1$) differed significantly between the two treatments (Figures 7c,d). However, the mean size (thorax length) of offspring emerging from a host was negatively correlated with the sex ratio (proportion males) of emerging offspring ($r^2 = 0.135$, $F_{(1,52)} = 7.02$, $P < 0.025$), positively correlated with host weight ($r^2 = 0.151$, $F_{(1,52)} = 7.86$, $P < 0.01$), and was significantly smaller in treatment F than E (mean difference$=$ 0.053 mm, SE$=$ 0.016 mm, $r^2 = 0.132$, $F_{(1,52)} = 6.84$, $P < 0.025$), though it was not affected by (host weight ÷ offspring emerging) ($F_{(1,52)} = 2.05$, $P > 0.1$), nor was the interaction between treatment and host weight significant ($F_{(1,52)} = 0.11$, $P > 0.1$) (Table 3).

Discussion

Ovicide in parasitoid wasps is an alternative tactic to superparasitism or host rejection in which conspecific eggs are removed or destroyed in addition to oviposition. Evolutionary models of ovicide predict that such behaviour will evolve: (1) when the competitive advantage of the first clutch under superparasitism is great; (2) when unparasitized hosts are rare; (3) when ovicide takes little time; and (4) when there is little risk of removing one's own eggs. This paper has confirmed that conditions 1 and 3 are satisfied for *Laelius pedatus*. First, under superparasitism the second clutch is

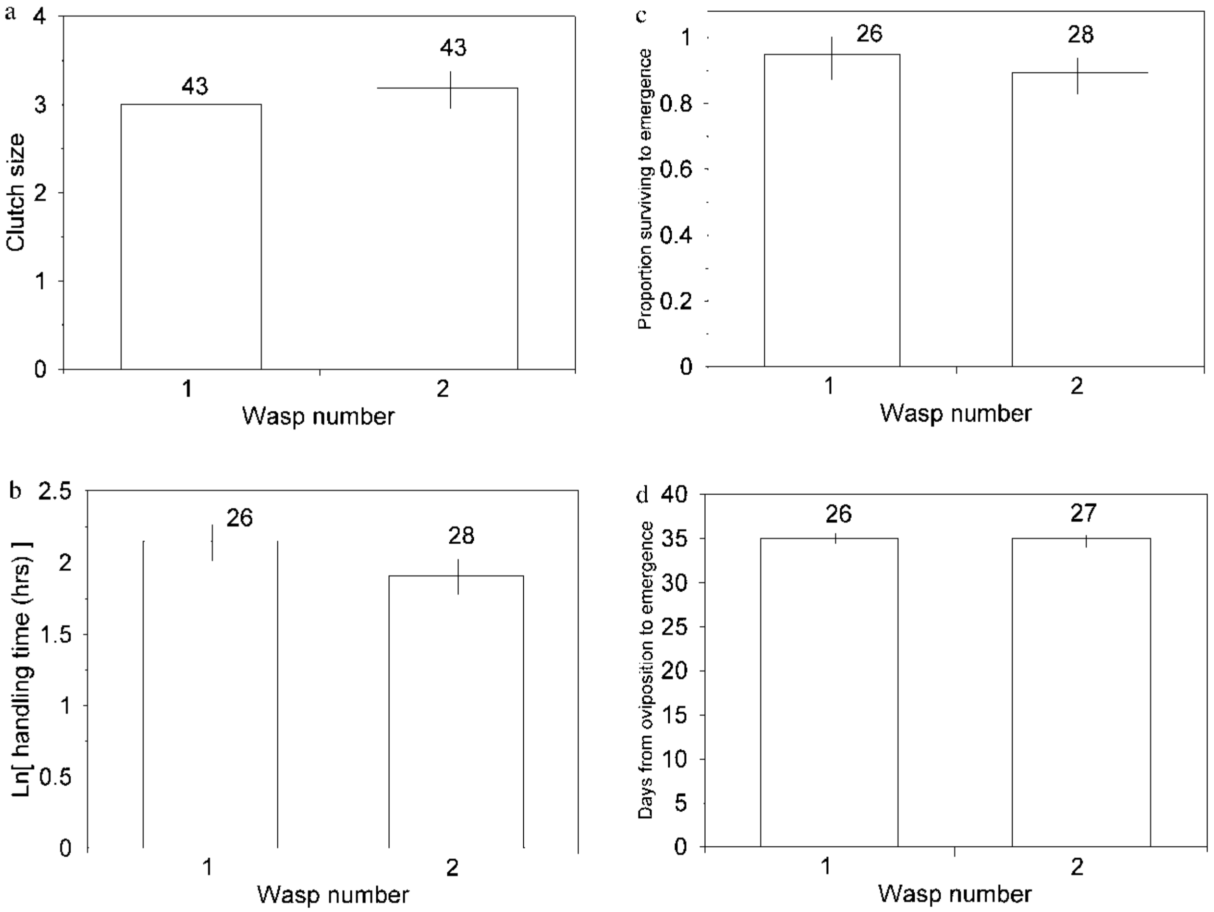


Figure 7. Fitness-related variables (mean ± SE, figure, indicate number of replicates) in wasps which are first or second to encounter a host: a) Clutch size b) Ln(handling time) c) Offspring survival d) Offspring development time.

Table 3. Multiple regression model of the size of the offspring (mean thorax length per brood) of first (E) and second (F) females. Terms are assessed by subtraction from the full model

Term	r^2	Effect (mm)	F	df	P
Brood sex ratio (proportion males)	0.135	−0.120.sr	7.02	1,52	< 0.025
Host weight (mg)	0.151	+0.019.wt	7.86	1,52	< 0.01
Treatment	0.132	F = E − 0.053	6.84	1,52	< 0.025
Error	0.582				

at a competitive disadvantage relative to the first clutch which increases with increasing time delay between ovipositions. Next, second females do not take longer to handle the host than first females, and the offspring of second (ovicidal) females are only slightly less fit than those of first (sole) females.

A strong competitive advantage to the first clutch under superparasitism was found in another ovicidal wasp, *Bracon hebetor* (Strand & Godfray, 1989), and has been observed in other, non-ovicidal parasitoid wasps where there is some time delay between laying the first and second clutches (van Alphen & Visser, 1990). However, in *L. pedatus*, the first clutch has a competitive advantage even when the first and second clutches are the same age. Thus, competition between the two clutches is asymmetric. These conditions should considerably increase the adaptive value of ovicide. The reason for competitive asymmetry is at present unclear but a possibility is that egg position on the host is important to the subsequent nutrition of the immobile larvae. Many bethylid species position eggs in very exact positions on the host (e.g., Peter & David, 1991). This may also be the reason why ovicide occurs through egg eating or egg removal in bethylids whereas in other families it occurs by stinging the eggs without removing them; perhaps it is important to free the optimal positions on the host for the second clutch of eggs.

Unfortunately in the absence of genetic markers in *L. pedatus*, it is difficult to distinguish between offspring of different clutches at emergence. Thus the only fitness variable under superparasitism for which there is reliable data is survival. The size of offspring decreased as the number emerging increased, and because smaller parasitoid wasps are generally less fit than larger ones (e.g., van den Assem *et al.*, 1989; Visser, 1994; Kazmer & Luck, 1995; West *et al.*, 1996), this might suggest that superparasitism produces adverse qualitative effects on offspring fitness. However, because the number of wasps emerging did not significantly increase when the number of eggs on the host increased, the effect of size is in fact unimportant. Competition between offspring of gregarious parasitoids is often assumed to be scramble (e.g., Visser, 1996), with survival being unaffected by density except at very high densities, and with strong density-dependent effects on offspring quality. However, in *L. pedatus* larval competition is perhaps better characterized as contest, even though no fighting occurs between larvae.

The fitness of offspring and parents of second females when ovicide is performed is critical to the evolution of ovicide, since this determines whether parasitised hosts will be accepted or rejected in favour of unparasitized hosts. Depending on the detailed natural history a parasitized host could be a much worse resource than an unparasitized host, if ovicide takes time or the host deteriorates (Strand & Godfray, 1989). Alternatively, since the host has already been overcome and prepared, a parasitized host could be a better resource than an unparasitized host (e.g., Takasu & Hirose, 1988, 1991). In *L. pedatus* experiments suggest that a parasitized host with eggs is a slightly worse resource than an unparasitized host. Handling time, clutch size, offspring survival and development time are not significantly different if the female is first or second to arrive. Interestingly, experienced *G. triangulifer* produce smaller clutches on parasitized hosts than on unparasitized hosts (Legaspi *et al.*, 1987), though this may be because they do not always completely remove the first clutch. In *L. pedatus* the offspring of second females are slightly smaller than those of first females on average. This may be due to host deterioration over the time delay between ovipositions (1 day in treatment F). Mayhew (1996) showed that larger wasps live longer if kept unfed in the laboratory; a reduction of 0.05 mm in thorax length will reduce lifetime by 2–3 d (from a maximum of 23 d) in females and by 1–2 d (from a maximum of 13 d) in males. Relative to superparasitism, however, the second clutch is probably still much fitter. In biological terms, this means that we expect a female foraging for hosts to accept a parasitized host with eggs in much the same way as an unparasitized host.

There is one other consideration which is likely to increase the probability of acceptance of parasitized hosts. In these experiments there was no opportunity for hosts to escape parasitism because they were confined in a petri dish with the wasp. However, hosts do often escape initial encounters with wasps in dishes (pers. obs.). I speculate that in nature parasitized hosts are a less risky use of time and energy than unparasitized hosts which may escape initial encounters, and that this may make acceptance of parasitized hosts more likely still; in effect the searching and handling efficiency for parasitized hosts may be greater.

These experiments have not touched on two important factors predicted to influence ovicide: the frequency of parasitized hosts and the probability of removing one's own eggs. They are briefly considered now. Since there was little variation in the probability of ovicide in *L. pedatus* (it was always 1), experiments on the effect of host experience were not feasible as they were for *B. hebetor* (Strand & Godfray, 1989). However, given the prediction that unparasitized and parasitized hosts should be accepted with almost equal probability by *L. pedatus*, it is also predicted that host experience will not affect relative behaviour towards these: wasps should accept hosts more on the basis of size than on whether or not they are parasitized.

Some observations suggest that *L. pedatus* is unlikely to remove its own eggs. Firstly, on a given host, ovicide is completed before oviposition starts (pers. obs., $n = 43$) (c.f. *B. hebetor*, Antolin *et al.*, 1995). This means that wasps will not mistake their own and conspecific eggs on the same host. Secondly, females leave the host immediately on completion of oviposition. Since eggs hatch after three days on average, only if wasps return to the same host in this period can they remove their own eggs. It is unknown how commonly this occurs in nature. In *G. platynotae* females have been observed to eat their own eggs (Goertzen & Doutt, 1975) which suggests that recognition of their own eggs is imperfect. However, *G. triangulifer* is less likely to commit ovicide if it has already laid a clutch of eggs (Legaspi *et al.*, 1987). This may be a mechanism to prevent self-ovicide.

This study has only considered behaviour towards eggs on hosts which have been abandonned by the first female to lay. Because *L. pedatus* does not brood guard after oviposition, in common with other members of its genus but not all bethylid species, there are no costs associated with fighting to defend a clutch in this species. However, many more bethylid species defend the host prior to oviposition, so it is possible that there might be fighting costs associated with unparasitized hosts. Although I did not specifically investigate this, I never saw females react aggressively towards each other in the presence of a host, and they seemed rather to avoid one another. A bethylid species which behaves similarly is *G. packmanus* (Gordh & Medved, 1986). Mertins (1980) estimated that an average female *L. pedatus* might lay 71 eggs in her lifetime, so a single clutch does not represent a large fraction of the total offspring a female might produce, and may not be a resource worth defending.

Behaviour towards conspecific larvae would also be worth investigating. First instar larvae pierce the host exoskeleton and begin feeding soon after hatching, completing development in 3–4 days. Therefore, the condition of host as a resource for second females probably deteriorates rapidly after eclosion. Although I have no data on this, I expect females to reject hosts containing larvae frequently on the basis of the models considered above. *G. nephantidis* do not attack larvae, but this is not universal amongst the Bethylidae (Hardy & Blackburn, 1991). Similarly if ovicide occurs repeatedly on the same host, the host is expected to deteriorate over time and is more likely to be rejected.

Finally, I consider in more general terms the reasons why ovicide is observed in *L. pedatus*. I have shown that egg removal carries few costs in this species. The eggs are large and occur in a single clutch, and take little time to remove. For many other wasps, notably endoparasitoids, eggs may be much more difficult and costly to locate and destroy. Secondly, larval competition in *L. pedatus* is strongly asymmetric. This is probably because there are a few locations on the host which are optimal for piercing the host cuticle and feeding effectively. Under superparasitism, the first female thus gains a considerable advantage over the second. The same situation is likely to hold for other bethylids, many of which position the eggs very precisely on the host. This may also explain why bethylid species remove eggs from the host whereas other ovicidal wasps do not. For species where egg position is not so critical, superparasitism may not be so disadvantageous. Thus the combination of a precise oviposition position and few large, externally-laid eggs may have made *L. pedatus*, and other bethylids, particularly prone to evolve ovicidal tactics.

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