The relation between clutch size and fitness in a larval-pupal endoparasitoid

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The larval-pupal endoparasitoid \textit{Aphaereta minuta} attacks larvae of Diptera species of different sizes. Females oviposit in young larval stages but the eventual size of the host pupa determines host food availability for competing offspring. We studied clutch size decisions by this parasitoid. Previous work showed that females vary their clutch considerably and lay larger clutches in larvae of host species that produce larger pupae. Here we present evidence that females also lay larger clutches in larger larvae than in smaller larvae of the same host species. We measured the consequences of clutch size variation for fitness in different instars of the host \textit{Delia antiqua}. Clutch size was manipulated and the relation between clutch size and fitness was quantified. The calculated Lack clutch size increased with larval host stage. When host encounter rate is low, clutch size approaches the Lack value.

Keywords: \textit{Aphaereta minuta}; Braconidae; clutch size; Hymenoptera; reproductive strategy.

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INTRODUCTION

For an insect parasitoid, the size of the host determines the amount of food available for its offspring. The capacity to allocate different numbers of offspring to hosts of different sizes, and so of different quality, potentially enables polyphagous gregarious parasitoids to optimally exploit host resources. Indeed, as predicted by optimality models (Godfray 1987), literature reports on a positive correlation between clutch size and host size (e.g. Takagi 1986). Koinobiont parasitoids that attack on-growing hosts have a difficult task to make optimal decisions on the allocation of the number of eggs to hosts, as the eventual size of the host has not yet been reached at the moment of oviposition. The parasitoid \textit{Aphaereta minuta} (Nees) (Hymenoptera: Braconidae) is a polyphagous larval-pupal endoparasitoid of many fly species, the larvae of which feed on ephemeral food sources. Young larvae are preferred for oviposition and the parasitoid eggs hatch during or just after the pupation of the host (Evans 1933). Hence, at the moment of oviposition the female is faced with a problem of how to
estimate the amount of resource that, after pupation of the host, is going to be available for its offspring. The foraging female parasitoid can encounter and parasitize larvae that greatly differ in age and size and potential to grow further. How does she deal with such variation in resources and how is she to optimize the allocation of her offspring?

Optimality models have been developed to explain the evolution of clutch sizes and predict variability in this life-history parameter under various conditions such as limited resource (i.e. host) availability or limitation of time or eggs available in the foraging female wasps (Charnov & Skinner 1984, 1985, Iwasa et al. 1984). Overall, when the relation between clutch size and fitness was quantified, observed clutch sizes were found to be lower than the calculated «Lack clutch size» (being the clutch size that leads to the greatest gain in parental fitness when maximizing the fitness gain per clutch is equivalent to maximizing lifetime fitness (Godfray et al. 1991)). The Lack clutch is only expected when animals lay a single clutch in their life or when opportunities to lay additional clutches are very rare. When eggs are limited, for example, females are selected to maximize their fitness gain per egg and so lay clutches of a single egg (under the assumption there is no Allee effect). When time available for oviposition is limited the animal is expected to maximize its overall rate of gain of fitness and clutch size will depend on the time between ovipositions, approaching the Lack clutch size only under long travel time conditions.

In a previous paper (Yet et al. 1993) it was shown that ovipositing females indeed considerably vary their clutch size in response to both inter- and intraspecific variation in host size. (1.) Female A. minuta lay more eggs in larvae of host species that will produce larger pupae, even when the larvae of the different species are the same size at the moment of oviposition, (2.) females lay more eggs in older/larger larvae when compared to younger/smaller larvae of the same host species. When parasitized at an older stage, host larvae developed into larger pupae than when parasitized at a younger stage. An explanation for this strategy of laying smaller clutches in younger host larvae is that young dipteran larvae have a lower chance of survival to the pupal stage than older larvae. This can be due to the short period of substrate availability, the strong scramble type competition between the fly larvae and the longer period of being exposed to other natural enemies. In the present study we investigate whether clutch size is influenced by the size (or instar) of the host larva at the moment of oviposition. We manipulate clutch size and analyze how it affects parasitoid fitness in D. antiqua larvae of two different ages. Fitness curves are based on clutch size, survival to adult stage, sex ratio and fecundity of offspring. We also study the effect of host-encounter rate on clutch size decisions.

MATERIALS AND METHODS

Parasitoids
The culture of A. minuta originated from females that emerged from onion baits containing D. antiqua larvae collected near Wageningen, The Netherlands. A. minuta was maintained on first and second instar larvae of the onion fly D. antiqua.

Hosts
Larvae of different ages of Delia antiqua (Meigen)(Diptera: Anthomyiidae), were
used as hosts (first, second and third instar larvae). *D. antiqua* was reared on decaying onions at 23 °C, 70 % RH.

**Experiments**
Mated females were offered hosts in Petri dishes containing an agar layer with host rearing medium. Parasitoids were observed during oviposition and the number of quiverings of the last abdominal segments and the ovipositor sheath was counted (a direct determiner of clutch size, see Vet et al. 1993). Larvae were incubated individually in a plastic cup (30 ml) containing a surplus of rearing medium. The number, sex ratio and size of their offspring was investigated. Clutch size was manipulated by interruption, superparasitization or low host-encounter rates (inter-oviposition time of 24 or 48 hours).

**RESULTS**

**Clutch size and fitness**
For the fitness calculation we used clutch size, survival to adult stage, sex ratio of offspring and fecundity of daughters; \( F = c.s.srf \), where \( F = \) fitness, \( c = \) clutch size, \( s = \) survival to adult stage, \( sr = \) sex ratio (proportion daughters) and \( f = \) fecundity of

![Figure 1](https://example.com/figure1.png)

*Figure 1.* Fitness curves for parasitization of first and second instar *D. antiqua* larvae. Observed values give the mean clutch size of unmanipulated parasitizations.
daughters. Survival to adult stage and sex ratio are expressed as a function of clutch size. To determine fecundity we used the relation between the number of emerging adults and their size. Figure 1 shows the fitness curves for parasitization of first and second instar larvae. Part of the curve is calculated with extrapolated regression lines and so is only an estimation (>11 for the first instar and >20 for the second larval instar). The calculated Lack clutch size for parasitization of first and second instar larvae was 12.88 and 17.27 respectively, being larger than the observed clutch size of unmanipulated parasitizations ($5.25 \pm 1.99 \ (n = 180)$ and $8.50 \pm 2.04 \ (n = 545)$ respectively).

**Effect of host-encounter rate**

Clutch size in second instar *D. antiqua* larvae increased with inter-oviposition time and approached the calculated Lack clutch when inter-oviposition times were 48 h (Figure 2).

![Graph showing clutch size](image_url)

*Fig. 2.* Clutch size for successive ovipositions of *A. minuta* in second instar *D. antiqua* larvae for different inter-oviposition times. Mean (bars) and SE (lines).
DISCUSSION

Clutch size optimality models commonly predict that larger clutches should be placed on better-quality hosts (Godfray et al. 1991). For parasitoids this quality will be determined by host size. For several parasitoid species there is evidence of a positive relationship between clutch size and the size or instar of the host species (e.g. Hardy et al. 1992).

Within second instar *D. antiqua* larvae, clutch size also increased with host size (data not shown), so host instar is not the only factor that determines clutch size.

*A. minuta* generally oviposits into young larvae. As the host larva is only at the beginning of its growth, the parasitoid has to estimate the expected pupal size because host size at parasitization is not a direct determiner of the amount of food available to the developing parasitoids. In addition she has to consider several factors that may reduce clutch survival. When parasitizing young larvae she has to account for a relatively high mortality of the host larvae. This relatively high mortality was found in the laboratory under optimal conditions (surplus of food, no predators etc.) and is expected to be much more intense under field conditions. Diptera host larvae feed on ephemeral substrates and food competition can be very intense due to the high number of fly eggs laid and the scramble type competition. Many young larvae never make it to the pupal stage. Furthermore, the longer period of exposure to natural enemies imposes an extra mortality risk for younger larvae.

The calculated Lack clutch size differs between larval stages. It is lower in younger larvae than in older larvae. We calculated the Lack clutch size using survival, sex ratio and size-related fecundity. In our calculations we considered longevity and other factors like behavioural characteristics to be constant. Behavioural characteristics, such as host selection, host discrimination and searching ability will also determine the reproductive success of a female under field conditions. The data presented here show that the observed clutch sizes lay below the calculated Lack clutch sizes. This is in accordance with earlier studies with parasitoids (e.g Waage & Ng 1984, Hardy et al. 1992). This may be due to an overestimation of the Lack clutch size (Hardy et al. 1992). The correct calculation of the Lack clutch size depends on the knowledge of the relationship between adult size and realized fitness. However, perhaps it is more likely that fitness maximization per clutch (Lack) is, in fact, not adaptive. This will be the case when reproductive success is not limited by the opportunity to produce more than one clutch, but by other factors such as time or eggs. Whether *A. minuta* is time- or egg-limited remains unclear without field data. As expected, an increase in time between ovipositions is pushes the observed clutch towards the Lack value (Charnov & Skinner 1984, 1985).
REFERENCES


