Clutch size in a larval–pupal endoparasitoid: consequences for fitness

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Summary

1. *Aphaereta minuta* (Hymenoptera: Braconidae) is a gregarious larval–pupal endoparasitoid of many Diptera species. Several larval instars can be parasitized and the size differences between host species can be considerable. After parasitization, however, the host larva continues to grow and the parasitoid's eggs hatch after the host pupates. We question whether this delay between the moment of oviposition and that of resource availability for offspring development hampered the ovipositing female in making optimal clutch size decisions.

2. Using an optimality approach we analysed the relationship between clutch size (number of eggs) and fitness in different instars of the host *Delia antiqua* in the laboratory.

3. Clutch size was artificially manipulated, and the relationship between clutch size and fitness was quantified using the following parameters: offspring egg to adult survival, sex ratio of emerging adults and size of emerging daughters (since size and number of eggs are positively correlated, size is a measure of fecundity).

4. Survival to adult stage was slightly positively correlated with clutch size in first instar host larvae and negatively correlated with clutch size in second instar host larvae. Sex ratio (proportion daughters) increased with increasing clutch size. The size of both males and females on emergence was negatively related to clutch size, and more strongly to the number of emerging adults.

5. The calculated Lack clutch size (whereby fitness is maximized per clutch) increased with larval host stage, as did the observed clutch size.

6. For each instar the observed clutch size was lower than the calculated Lack clutch size. We argue that under natural conditions females are selected to lay a clutch lower than the Lack clutch size.

Key-words: *Aphaereta minuta*, Braconidae, clutch size, Hymenoptera, parasitoid, reproductive strategy.

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Introduction

In recent years there has been a significant increase in the interest in clutch size in invertebrates, with particular emphasis on the gregarious parasitic wasps which lay more than one egg in each insect host (e.g. reviewed by Godfray 1987). Using the adaptionist approach, optimality models have been developed to explain the evolution of clutch sizes and predict variability in this life-history parameter under various conditions, for instance limited resource (i.e. host) availability, or limitation of time or eggs available to the

foraging female wasps (Iwasa, Suzuki & Matsuda, 1984; Parker & Courtney 1984; Charnov & Skinner 1984, 1985; Waage & Godfray 1985).

Although there are quantitative data on clutch size for several parasitoid species (Waage 1986; Godfray 1987; le Masurier 1987), rigorous experimental testing of the expanding body of theory has lagged behind. To test quantitatively the predictions of the models on optimality of clutch size decisions, experimental studies are needed in which clutch size can be manipulated (e.g. Waage & Ng 1984; Takagi 1985; Dijkstra 1986; Taylor 1988; Hardy, Griffiths & Godfray

1992). In all cases where the relationship between clutch size and fitness was quantified, observed clutch sizes were found to be lower than the calculated 'Lack clutch size' [defined as 'the clutch size that maximizes the gain in fitness from each host' (Godfray, Partridge & Harvey 1991)]. The Lack clutch size is only expected when animals lay a single clutch in their lifetime or when opportunities to lay additional clutches are very rare. When smaller clutches are observed this may indicate that factors other than the opportunity to find a host are limiting. When egg supply is limited, females are selected to maximize their fitness gain per egg and so lay clutches of a single egg, assuming there is no Allee effect (Parker & Courtney 1984; Iwasa *et al.* 1984; Waage & Godfray 1985). When time available for oviposition is limited, the animal is expected to maximize its overall rate of gain of fitness (Charnov & Skinner 1984, 1985; Iwasa *et al.* 1984; Parker & Courtney 1984) and clutch size will depend on the 'travel time' between ovipositions, approaching the Lack clutch size only when travel time is long.

Manipulation of clutch size is relatively easy in the case of ectoparasitoids that lay their eggs on the exterior of the host's body (e.g. Dijkstra 1986; Taylor 1988; Hardy *et al.* 1992), but more difficult with endoparasitoids that lay their eggs internally. We know of only two studies with endoparasitoids where, to a certain extent, clutch size was experimentally manipulated. Waage & Ng (1984) studied parasitoids that attack lepidopteran eggs and Takagi (1985) reported on clutch size in a pupal parasitoid.

In these manipulation studies, hosts were used which practically ceased to develop after being parasitized. Such hosts constitute a fixed quantity of resource. This facilitates the production of clutch sizes attuned to differences in host size and therefore quality. For some species of parasitoids, however, hosts continue to develop and grow following oviposition. These parasitoids are termed koinobionts. A larval-pupal parasitoid for instance, oviposits into larvae which develop into a pupa before the parasitoid's eggs hatch, only then is the host killed and the available resources are shared by the developing parasitoid larvae. Due to this delay between oviposition and the cessation of host development, estimating the resource which will be eventually available to offspring is a potentially complex problem for such a parasitoid. This estimation problem is interesting from a proximate point of view (the process by which parasitoids estimate eventual pupal size), but especially intriguing in the light of optimization. Do ovipositing parasitoids make 'correct' clutch size decisions, i.e. do females vary their clutch sizes in a way that benefits their fitness?

Aphaereta minuta (Nees) (Hym.: Braconidae) is a polyphagous larval-pupal endoparasitoid of many differently sized Diptera species which develop in ephemeral substrates such as decaying plant and ani-

mal material. First and second instar larvae are preferred for oviposition (Evans 1933). *Aphaereta minuta* is pro-ovigenic, females have their full egg supply available for oviposition on emergence. In a previous paper (Vet *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. (i) 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. (ii) 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 this paper we examine the clutch size decisions of *A. minuta* in a quantitative way. We manipulate clutch size and analyse how this affects parasitoid fitness when developing in *Delia antiqua* (Meigen) (Diptera: Anthomyiidae). Unlike other studies in which fitness calculations were restricted to a single host developmental stage, we analysed and compared fitness consequences of clutch size in host larvae of two different ages. In these host stages a considerable range of clutch sizes can be achieved. Fitness curves based on clutch size, survival to adult stage and fecundity of daughters are calculated. Fitness is calculated through female function only, we therefore included the sex ratio of the offspring.

Materials and methods

PARASITIDS

The culture of *A. minuta* originated from females that emerged from onion baits, containing *D. antiqua* larvae, collected near Wageningen, the Netherlands. A laboratory culture of *A. minuta* was maintained on first and second instar larvae of the onion fly *D. antiqua* at 23°C, 70% RH. Adult parasitoids were maintained under a 16 L: 8 D photocycle regime at 12°C and fed on a sugar solution.

HOSTS

First and second instar *D. antiqua* larvae were used as hosts, larvae were reared on decaying onions under a 16 L: 8 D photocycle regime at 23°C, 70% RH.

EXPERIMENTS

Seven-day-old mated *A. minuta* females were individually offered first instar *D. antiqua* larvae (4 days after fly oviposition) or second instar larvae (6 days after fly oviposition) at a density of 20 larvae per Petri dish (5.5 cm in diameter). To estimate clutch size, the number of quiverings of the last abdominal segments and the ovipositor sheath was counted, which corresponds with clutch size (Vet *et al.* 1993). To obtain hosts with a reduced number of parasitoid eggs, parasitizations were interrupted. To obtain hosts with an increased number of parasitoid eggs, parasitized larvae were allowed to be superparasitized or females were offered hosts infrequently.

Parasitized larvae were incubated individually in small (30-ml) plastic cups containing a surplus of *D. antiqua*-rearing medium, consisting mainly of water, carrot powder and yeast (at 25°C, 50–70% RH, 16 L: 8 D photocycle regime). The number of adult parasitoids that emerged from each host was counted. Adults were sexed on emergence and their size (tibia length) measured. To determine potential fitness of females of different sizes, a number of emerged females of different sizes were dissected to count the number of eggs they contained.

STATISTICAL ANALYSIS

To estimate the relation of variables with each other we first tried several non-linear regression models (e.g. exponential models) to describe the data, but linear models gave the best fit. Regression coefficients were compared by comparison of regression lines as described in Sokal & Rohlf (1981).

Results

SURVIVAL TO ADULT STAGE

Figure 1 shows survival to adult stage for first and second instar larvae as a function of clutch size. In the

Fig. 1. Relationship between survival to adult stage and clutch size for first (○) and second (●) instar larvae. Regression lines are based on all data, over the range shown by the regression line, but points are shown when $n > 4$. All parasitizations that resulted in the emergence of at least one individual were used.

analysis all parasitizations with at least one individual emerging were used. When we included unsuccessful parasitizations (no individuals emerging) in the analysis, we found the same regression coefficients. Beside a simple linear regression model several non-linear models were fitted to the data, but the linear model gave the best results. Survival to adult stage was slightly positively correlated with clutch size in first instar larvae (survival = $0.794 + 0.018$ clutch size, $n = 116$, $r^2 = 0.05$, $P < 0.05$) and negatively correlated with clutch size in second instar larvae (survival = $0.951 - 0.008$ clutch size, $n = 270$, $r^2 = 0.05$, $P < 0.001$). However, the regression coefficients of the relation between clutch size and survival to adult stage were not significantly different between first and second instar larvae ($P > 0.05$).

For construction of the fitness curve over the wider range of clutches, we chose to extrapolate the regression equations. Survival was set at one whenever extrapolation of the regression equations yielded a survival greater than one (first larval instar, clutch size > 11).

SEX RATIO

Figure 2 shows the relationship between clutch size and sex ratio (proportion daughters) for normal ovipositions (so no interrupted or superparasitizations). Most broods yielded one or two sons. The regression coefficients of the relation between sex ratio and clutch size were different for both instars ($P < 0.01$). Sex ratio was less affected by clutch size in second instar larvae (first instar; proportion daughters = $0.557 + 0.032 \times$ clutch size, $n = 94$, $r^2 = 0.07$, $P < 0.01$, second instar; proportion daughters = $0.738 + 0.007 \times$ clutch size, $n = 178$, $r^2 = 0.04$, $P < 0.01$). Although sex ratio's of interrupted and superparasitizations were not included in the regression analysis of Fig. 2 they were measured. Interrupted parasitizations yielded offspring with a somewhat higher proportion of daughters (0.90) than

Fig. 2. Relationship between sex ratio (proportion daughters) and clutch size for first (○) and second (●) instar larvae. Regression lines are based on all data of normal parasitizations only (no interrupted or superparasitizations). Points are shown when $n > 4$. All parasitizations that resulted in the emergence of at least one individual were used.

normal (0.82) and superparasitizations (0.79). These differences were significant ($P < 0.001$, multiple comparison test, based on Kruskal-Wallis rank sums).

For construction of the fitness curve over the wider range of clutches, we chose to extrapolate the regression equations of the normal parasitizations (see Fig. 2 for the range of clutches). The proportion of daughters was set at one whenever extrapolation of the regression equations yielded a proportion of daughters greater than one (first larval instar, clutch size > 14).

SIZE OF THE EMERGING DAUGHTERS

Figures 3a and 4a show the relationship between the size of the emerging daughters and clutch size, for first

and second instar host larvae, respectively. The size of the emerging daughters was strongly inversely related to clutch size, for both instars (first instar; tibia length = $4.995 - 0.138 \times \text{clutch size}$, $n = 83$, $r^2 = 0.42$, $P < 0.001$, second instar; tibia length = $4.926 - 0.089 \times \text{clutch size}$, $n = 221$, $r^2 = 0.62$, $P < 0.001$). This effect was stronger for larvae parasitized in the first instar ($P < 0.01$). All parasitizations resulting in some offspring were included in this analysis (normal, interrupted and superparasitization). Figures 5a and 6a show the relationship between tibia length of the daughters and the number of emerging adults ($\delta + \text{♀}$). Tibia length was strongly inversely related to the number of emerging adults (first instar; tibia length = $4.920 - 0.134 \times \text{number of emerging adults}$, $n = 83$, $r^2 = 0.43$, $P < 0.001$, second

Fig. 3. Relationship between offspring size and clutch size in first instar larvae. All parasitizations that resulted in the emergence of at least one individual were used.

Fig. 4. Relationship between offspring size and clutch size in second instar larvae. All parasitizations that resulted in the emergence of at least one individual were used.

Fig. 5. Relationship between adult size and the number of emerging adults for first instar larvae. All parasitizations that resulted in the emergence of at least one individual were used.

Fig. 6. Relationship between adult size and the number of emerging adults for second instar larvae. All parasitizations that resulted in the emergence of at least one individual were used.

instar; tibia length = $5.041 - 0.117 \times \text{number of emerging adults}$, $n = 229$, $r^2 = 0.73$, $P < 0.001$). This relationship was much stronger than the relationship between the size of the emerging daughters and clutch size, suggesting that mortality occurs early in the development of the parasitoids. The regression coefficients were not different for the two instars.

SIZE OF THE EMERGING SONS

The size of male offspring was not different from the size of female offspring (in cases where parasitizations

yielded both male and female offspring with known sizes, Mann-Whitney U -test, $P = 0.95$, $n = 274$) and was also inversely related to clutch size (first instar; tibia length = $5.020 - 0.138 \times \text{clutch size}$, $n = 63$, $r^2 = 0.49$, $P < 0.001$, second instar; tibia length = $4.763 - 0.080 \times \text{clutch size}$, $n = 174$, $r^2 = 0.49$, $P < 0.001$) and to the number of emerging adults (first instar; tibia length = $4.968 - 0.137 \times \text{number of emerging adults}$, $n = 63$, $r^2 = 0.50$, $P < 0.001$, second instar; tibia length = $4.851 - 0.101 \times \text{number of emerging adults}$, $n = 181$, $r^2 = 0.58$, $P < 0.001$) as shown in Figures 3b, 4b, 5b and 6b. Similar to the

results for emerging daughters, the relationship between tibia length of the sons and the number of emerging adults was stronger than the relation between tibia length of the sons and clutch size. For parasitized larvae in the first instar, the regression coefficients for sons and daughters were not different. Male size and female size were equally affected by clutch size and the number of emerging adults. For parasitized larvae in the second instar, the regression coefficients were smaller for sons than for daughters (only significantly when considering the number of emerging adults) so the size of the sons was less affected by clutch size and number of emerging adults than the size of daughters. The size of sons emerging from larvae parasitized in the first instar was more strongly affected by clutch size and the number of emerging adults than the size of sons emerging from larvae parasitized in the second instar ($P < 0.05$).

FECUNDITY

The relationship between fecundity and female size is shown in Fig. 7. Fecundity (number of eggs in the abdomen) positively correlated with female size (tibia length) (fecundity = $-220.68 + 111.91 \times \text{size}$, $n = 64$, $r^2 = 0.68$, $P < 0.001$).

CLUTCH SIZE AND FITNESS

A fundamental problem with constructing fitness curves is the choice of the parameters to measure fitness. It is generally assumed that fitness of the mother increases with the fecundity and longevity of her daughters (Charnov & Skinner 1984; Waage & Ng 1984; Takagi 1985; Hardy *et al.* 1992). However, it is still not clear how these two parameters influence fitness under natural conditions. The fitness measure employed here (and in other papers) is a measure for

Fig. 7. Relationship between female fecundity and size.

the maximum obtainable fitness because it measures the potential number of grandchildren.

For the fitness calculation we used clutch size, survival to adult stage, sex ratio of offspring and fecundity of daughters:

$$F = c \cdot s \cdot sr \cdot f,$$

where F = fitness, c = clutch size, s = survival to adult stage, sr = sex ratio (proportion daughters) and f = fecundity of daughters. Survival to adult stage and sex ratio are expressed as a function of clutch size. To determine fecundity we used the relationship between the number of emerging adults and their size. The different regression equations can be found in the result sections leading to the figures concerned (1, 2, 5, 6 and 7). Figure 8 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. For the sex ratio, extrapolation started at clutch size >9 for the first larval instar and at clutch size >17 for the second instar, but for the other parameters the regression is calculated over the wider ranges of manipulated clutches, ranging from clutch 1 to 11 for the first instar and 1 to 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

Fig. 8. Fitness curves for parasitization of first (○) and second (●) instar *D. antiqua* larvae. Observed values (*) give the mean clutch size of unmanipulated parasitizations. See text for range of clutches over which the fitness curve is an estimation beyond the range of manipulated clutches.

parasitizations [5.25 ± 1.99 ($n = 180$) and 8.50 ± 2.04 ($n = 545$), respectively].

Discussion

Aphaereta minuta varies her clutch size in response to variation in host size, as shown by the present and previously reported results (Vet *et al.* 1993): females lay larger clutches in larvae that grow into larger pupae. However, while differences in pupal size are very clear when comparing different host species, these differences are much less obvious when comparing between larval instars of one host species (Vet *et al.* 1993).

We argued previously that the observed smaller clutches in younger larvae seems adaptive: smaller larvae are expected to have a much lower probability of survival than older larvae under natural conditions (see Introduction). The findings of the present paper give an additional functional explanation. The calculated Lack clutch size differs between larval stages. It is lower in younger larvae than in older larvae, and in these calculations host larvae were not competing for food or subject to predation as they generally are in the field. Younger larvae are, indeed, poorer quality hosts, and *A. minuta* has apparently developed a mechanism to recognize this variation and adaptively respond to it.

Different components are shown to affect parasitoid fitness. Our data show that survival from egg stage to emerging parasitoid for larvae parasitized in the second instar decreased with clutch size. This decreasing survival is not due to a total loss of large clutches. Even very large clutches give rise to some offspring, suggesting that mortality occurs early in the development of the parasitoids. Clutch size and survival in first instar larvae show a positive correlation, although a relatively weak one. We have no clear explanation for this phenomenon.

Like most hymenopterous parasitoids, *A. minuta* is a haplodiploid species which means that fertilized eggs develop into daughters and unfertilized eggs develop into male progeny. The mating structure of *A. minuta* under field conditions is still unknown. If there is a high degree of sibmating, the sexual composition of the brood at emergence thus influences the mating opportunities of brood members and can have important fitness consequences (Hamilton 1967). The observed sex ratio of the offspring in this study concerns the secondary sex ratio which may be different from the sex ratio at oviposition (primary sex ratio), caused by differential mortality between sexes. Hardy's (1992) review showed that many hymenopteran species have precise control of sex ratio, and it seems that primary sex ratio should be adjusted according to the distribution of mortality within broods and to sexually differential mortality. When females were interrupted during oviposition, their progeny still consisted of both daughters and sons, suggesting that

fertilization occurs at a certain rate during each oviposition. The higher proportion of daughters of the interrupted clutches indicates that the first eggs in the oviposition sequence are often fertilized, giving rise to female offspring.

The size of the offspring was strongly influenced by clutch size but, not surprisingly, even more strongly by the number of emerging parasitoids; a better determinant of the severity of competition within the host. This decreasing effect of number of competitors on the size of the offspring will be due to scramble-type sibling competition for a limited resource and has been found in many studies (Waage & Ng 1984; Ikawa & Okabe 1985; Takagi 1985; Dijkstra 1986; Taylor 1988; Hardy *et al.* 1992). If *A. minuta* larvae stimulate host growth (Vet *et al.* 1993), these results show that there is a limit to the extent of this stimulation.

The effect of clutch size on male size was weaker than on female size (as was found in *Goniozus nephantidis* by Hardy *et al.* 1992), perhaps due to the fact that males of gregarious parasitoids generally emerge earlier and so compete less. An alternative explanation, using a selection argument, could be that under strong local mate competition circumstances, the one or few males are under strong selection to be sufficiently able to inseminate all sisters. It has been suggested, however, that males suffer less severe fitness penalties than do females for the same reduction in body size (e.g. Charnov *et al.* 1981). There are only few data on the relation between male size and longevity, copulatory success and sperm complement (Grant *et al.* 1980; Waage & Ng 1984).

A problem in studying the fitness consequences of clutch size decisions in endoparasitoids is the difficulty of obtaining large clutches from a single mother. It is expected that the largest clutches produced will not exceed the Lack size, but for proving that the fitness of the largest natural clutches is really the Lack solution, larger clutches than the Lack should be included in the analysis. The only way to obtain larger clutches is by forcing females to superparasitize, but superparasitism may produce aberrant sex ratios (Werren 1980; Suzuki, Tsuji & Sasakawa 1984; Orzak & Parker 1986). In this paper we therefore chose to estimate the sex ratios in super-normal clutches by extrapolating the regression of sex ratio versus clutch size from the data of normal clutches.

Many studies have revealed that longevity and fecundity are related to body size in parasitoids (e.g. Waage 1986). Our observation that the number of eggs in the abdomen increases with size is in accordance with these studies. It seems important that longevity also increases with size. When an increase in number of eggs is not accompanied by an increase in longevity, there is a maximum to the number of eggs used. If not, a further increase in the egg complement does not contribute to an increase in fitness. We calculated the Lack clutch size using mean survival, sex ratio and size-related fecundity and assumed

longevity, and other factors, such as 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. Searching ability of females seems to be related to their size (M.E. Visser, personal communication). When we assume that larger females have a higher searching ability compared to smaller females, the fitness benefit for producing larger daughters is greater. In such a case, smaller clutches will be favoured and the calculated Lack clutch will be lower. Considering searching ability as a monotonically increasing function of female size, for example, a fivefold increase in searching ability for the largest females compared to the smallest females lowered the calculated Lack clutch size to half of its original value (for second instar larvae). Field experiments to test the hypothetical relation between size and searching ability are in progress (Visser 1994).

The data presented here show that the observed clutch sizes lie below the calculated Lack clutch sizes. This is in accordance with earlier studies of parasitoids (Waage & Ng 1984; Takagi 1985; Dijkstra 1986; Taylor 1988; Hardy 1992) and this may be due to an overestimation of the Lack clutch size (Hardy *et al.* 1992). However, perhaps it is more likely that fitness maximization per clutch (the Lack solution) is, in fact, not functional. 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. Driessen & Hemerik (1992) simulated the foraging life of a solitary pro-ovigenic parasitoid of *Drosophila* larvae, using a model based on field-measured parameters. They concluded that, although time-limitation is most likely for parasitoids of *Drosophila*, egg-limitation will become important when foraging in a favourable environment. This could also apply to *A. minuta*. We expect that, under field conditions, the initial localization of host-infested substrates is a limiting factor. However, once such a substrate is located, a female may find a surplus of hosts due to the clustered host distribution (scramble type competing dipteran larvae on ephemeral substrates) which will increase the probability of laying her full egg supply and becoming egg-limited. (There will obviously be strong selection on microhabitat searching ability in such species!) Under such conditions females are selected to lay a clutch between that which maximizes fitness per egg and that which maximizes fitness per clutch (Godfray 1987). Hence, the clutch size will be lower than the Lack clutch size, as we found for each of the host instars under laboratory conditions. Interestingly, the observed clutches are at similar distances from the Lack in the first and second instar. The prevalence of egg- and time-limited conditions will determine how close the observed clutch is to the Lack value. An

increase in time between ovipositions is expected to push the observed clutch towards the Lack value (Charnov & Skinner 1984, 1985), which we indeed found to be the case for *A. minuta* (A. Datema & L.E.M. Vet, manuscript submitted for publication).

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References

- Charnov, E.L., Los-den Hartog, R.L., Jones, W.T. & van den Assem, J. (1981) Sex ratio evolution in a variable environment. *Nature*, **289**, 27–33.
- Charnov, E.L. & Skinner, S.W. (1984) Evolution of host selection and clutch size in parasitoid wasps. *Florida Entomologist*, **67**, 5–21.
- Charnov, E.L. & Skinner, S.W. (1985) Complementary approaches to the understanding of parasitoid oviposition decisions. *Environmental Entomology*, **14**, 383–391.
- Dijkstra, L.J. (1986) Optimal selection and exploitation of hosts in the parasitic wasp *Colpoclypeus florus* (Hym.: Eulophidae). *Netherlands Journal of Zoology*, **36**, 177–301.
- Driessen, G.J.J. & Hemerik, A. (1992) The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. *Ecological Entomology*, **17**, 17–27.
- Evans, A.C. (1933) Comparative observations on the morphology and biology of some hymenopterous parasites of carrion-infesting Diptera. *Bulletin of Entomological Research*, **24**, 385–405.
- Godfray, H.C.J. (1987) The evolution of clutch size in invertebrates. *Oxford Surveys in Evolutionary Biology* (eds P.H. Harvey & L. Partridge), Vol. 4, pp. 117–154. Oxford University Press, Oxford.
- Godfray, H.C.J., Partridge, L. & Harvey, P.H. (1991) Clutch size. *Annual Review of Ecology & Systematics*, **22**, 409–429.
- Grant, B., Burton, S., Contoreggi, C. & Rothstein, M. (1980) Outbreeding via frequency-dependent selection in the parasitoid wasp, *Nasonia* (= *Mormoniella*) *vitripennis* Walker. *Evolution*, **34**, 983–992.
- Hamilton, W.D. (1967) Extraordinary sex ratios. *Science*, **156**, 477–488.
- Hardy, I.C.W. (1992) Non-binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. *Oikos*, **65**, 143–158.
- Hardy, I.C.W., Griffiths, N.T. & Godfray, H.C.J. (1992) Clutch size in a parasitoid wasp: a manipulation experiment. *Journal of Animal Ecology*, **61**, 121–129.
- Ikawa, T. & Okabe, H. (1985) Regulation of egg number per host to maximize the reproductive success in the gregarious parasitoid, *Apanteles glomeratus* L. (Hymenoptera: Braconidae). *Applied Entomology & Zoology*, **20**, 331–339.
- Iwasa, Y., Suzuki, Y. & Matsuda, H. (1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theoretical Population Biology*, **26**, 205–227.
- le Masurier, A.D. (1987) A comparative study of the relationship between host size and brood size in *Apanteles* spp. (Hymenoptera: Braconidae). *Ecological Entomology*, **12**, 383–393.
- Orzak, S.H. & Parker, E.D. (1986) Sex-ratio control in a parasitic wasp, *Nasonia vitripennis*. I. Genetic variation in facultative sex-ratio adjustment. *Evolution*, **40**, 331–340.

- Parker, G.A. & Courtney, S.P. (1984) Models of clutch size in insect oviposition. *Theoretical Population Biology*, **26**, 27–48.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman and Company, San Francisco.
- Suzuki, Y., Tsuji, H. & Sasakawa, M. (1984) Sex allocation and effects of superparasitism on secondary sex ratios in the gregarious parasitoid, *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). *Animal Behaviour*, **32**, 478–484.
- Takagi, M. (1985) The reproductive strategy of the gregarious parasitoid, *Pteromalus puparum* (Hymenoptera: Pteromalidae) I. Optimal number of eggs in a single host. *Oecologia*, **70**, 321–325.
- Taylor, A.D. (1988) Host effects on larval competition in the gregarious parasitoid *Bracon hebetor*. *Journal of Animal Ecology*, **57**, 163–172.
- Vet, L.E.M., Datema, A., Welzen, K. van & Snellen, H. (1993) Clutch size in a larval-pupal endoparasitoid: I. Variation across and within host species. *Oecologia*, **95**, 410–415.
- Visser, M.E. (1994) The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). *Journal of Animal Ecology*, **63**, 963–978.
- Waage, J.K. (1986) Family planning in parasitoids: adaptive patterns of progeny and sex allocation. *Insect Parasitoids: 13th Symposium of the Royal Entomological Society of London* (eds J.K. Waage & D.J. Greathead), pp. 63–96. Academic Press, London.
- Waage, J.K. & Godfray, H.C.J. (1985) Reproductive strategies and population ecology of insect parasitoids. *Behavioural Ecology* (eds R.M. Sibly & R.H. Smith), pp. 449–470. Blackwell Scientific Publications, Oxford.
- Waage, J.K. & Ng, S.M. (1984) The reproductive strategy of a parasitic wasp. I. Optimal progeny allocation in *Trichogramma evanescens*. *Journal of Animal Ecology*, **53**, 401–415.
- Werren, J.H. (1980) Sex ratio adaptations to local mate competition in a parasitic wasp. *Science*, **108**, 1157–1159.

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