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Source: *The Journal of Animal Ecology*, Vol. 63, No. 4 (Oct., 1994), pp. 963-978
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/5273
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Journal of Animal Ecology 1994,
63, 963–978

The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae)

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Summary

1. The relationship between the size of a female parasitoid and its fitness is a major element of models of optimal clutch size, of host species selection, of the evolution of siblicide in parasitoids and of some sex allocation models.

2. In estimating this relationship, usually only size-dependent longevity and/or fecundity is considered, neglecting differences in searching efficiency for hosts, although this is an important component of fitness. The relationship between a number of constraints and female size was studied in the parasitoid *Aphaereta minuta*. Larger females were found to have more eggs available, have larger eggs, live longer and have a higher searching efficiency within patches than small females, but searching efficiency for patches and travel speed were found to be independent of size.

3. The size-dependent constraints were combined into one fitness measure. To this end, the characteristics of a natural habitat were measured and, together with the relationships between female size and these constraints, incorporated into a dynamic programming model in order to calculate the fitness of females of different sizes. Fitness was found to increase linearly with female size.

4. Even from very accurate measures of the size-fitness relationship made under laboratory conditions it remains doubtful whether the relationship holds under field conditions. Three experiments to estimate the relationship between female size and fitness in the field were carried out, all showing an increase in fitness with female size.

5. Comparing the results from the field and the laboratory experiments indicates that fitness increases much more rapidly with increasing female size in the laboratory than under field conditions.

Key-words: dynamic programming, fitness, parasitoid size.

Journal of Animal Ecology (1994) **63**, 963–978

General introduction

Perhaps the outstanding experimental challenge in parasitoid behavioural ecology is to understand the relationship between the size of a female and her fitness (Godfray 1994). An understanding of this relationship is crucial in order to be able to make quantitative predictions in a number of areas. In optimal clutch size models, there is a trade-off between the number and the size of the offspring. The size of the offspring needs to be related to their fitness before the fitness curve (the relationship between per capita fitness and clutch size) can be calculated, which is important in determining the optimal clutch size (Godfray 1987; Ives 1989; Lessells 1991; Godfray, Partridge & Harvey 1991). In solitary parasitoids, often the size of the offspring is influenced by the host species from which it emerged. The fitness of parasitoids of different sizes needs to be known when calculating the value of a host of a particular species to a foraging female parasitoid, which is important in modelling host-species selection (Charnov & Stephens 1988). Furthermore, the relationship between size and fitness is also relevant to models of the evolution of siblicide in parasitoids (Godfray 1987; Rosenheim 1993). It should be taken into account when modelling sex ratio, both when there is an interaction between sex ratio and clutch size (Godfray 1986), and when host quality varies. In models of the latter it is assumed

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that female fitness increases more rapidly with size than male fitness (Charnov 1979; King 1987). The relationship between female size and fitness is also of interest when evaluating rearing methods when there is either a trade-off between number produced and parasitoid size, or where females reared from different hosts differ in size (Bigler, Meyer & Bosshart 1987).

Despite its importance, many studies have used very crude measurements to estimate the relationship between parasitoid size and fitness. This estimation is usually based on egg load at emergence, lifetime reproductive success when given unlimited hosts or longevity, either with or without access to hosts or food (see Table 1). There are a number of problems with these kinds of estimates of the relationship between female size and fitness. First, females of different sizes are likely to differ in more constraints than longevity and number of eggs available. The ability to find hosts might especially depend on size. Only very few studies take this into account (see Table 1). Secondly, when there is more than one size-dependent constraint, the relationship between female size and fitness need to be estimated incorporating all these constraints. No framework to do so is available. Thirdly, the estimation of the relationship between female size and fitness based on laboratory experiments might differ strongly from that based on field data. This last point has been made several times in the past few years (Lessells 1991; Hardy, Griffiths & Godfray 1992; Godfray 1994), but has received only minor attention from experimentalists (see Bigler, Meyer & Bosshart 1987 and Kazmer & Luck 1992 for exceptions).

In this paper I try to meet these criticisms. Controlled laboratory and field experiments are carried out on the differences in constraints for different-sized females of the gregarious parasitoid *Aphaereta minuta*. Not only fecundity and longevity are studied, but also the host-finding abilities in relation to female size (Part 1). Next, the fitness of females of different sizes is calculated using the size-dependent constraints. Fitness will not only depend on a parasitoid's constraints but also on the characteristics of the habitat in which it searches for hosts. Therefore, the constraints and the characteristics of a natural environment are combined in a dynamic programming model that calculates the fitness of different-sized females (Part 2). Finally, in Part 3 the results of three field experiments on the relationship between female size and fitness are presented, and the accuracy and the limitations of these methods are discussed.

Part 1: differences in constraints for different size females

INTRODUCTION

In general, the fitness of a female parasitoid will depend on her constraints, her decisions and on the environment. The constraints of a parasitoid are its fecundity, longevity and host-finding ability. Decisions that need to be taken by gregarious parasitoids searching for hosts with a patchy distribution (like *A. minuta*) concern clutch size, the sex ratio of the eggs and patch time allocation. The main characteristics of the habitat are the distance between patches and the distribution of hosts over these patches. In this part of the paper I will present data on the differences in constraints for parasitoids of different sizes. Together with the decisions and the habitat characteristics these constraints will be incorporated in a dynamic programming model that is explained in Part 2.

All three types of constraints (longevity, fecundity and host-finding abilities) may depend on female size. Most studies have, however, focused on longevity and on the number of eggs available (Table 1). Sometimes these two constraints are combined by measuring lifetime number of eggs laid/offspring produced with *ad libitum* hosts. The exceptions are the work of Klomp & Teerink (1967) on egg length in relation to female size in *Trichogramma embryophagum*, of Bigler *et al.* (1987) on walking speed in *Trichogramma maidis* and of van den Assem, van Iersel & Los-den Hartogh (1989) who studied lifetime number of progeny of large and small female *Lariophagus distinguendus* that were in direct competition for hosts (see Table 1). The relationship between size and longevity or fecundity is usually found to be positive and linear. Exceptions are the relationship between longevity and size in *Pteromalus puparum*, which has a domed shape (Takagi 1985), and the absence of a relationship between size against longevity and lifetime number of progeny for *Spalangia cemeroni* (King 1988).

Here, I will not only study fecundity and longevity but also the size of eggs and a number of estimates of host-finding ability (searching efficiency on a patch, searching efficiency for patches and travel speed) in relation to size of female *A. minuta*.

METHODS

The parasitoid and host

Aphaereta minuta (Nees) (Hymenoptera: Braconidae) is a gregarious, polyphagous endoparasitoid of larvae of Diptera that live in decaying plant and animal material (Evans 1933). The host larva continues to grow after being parasitized and the parasitoids emerge from the host pupae. The female parasitoid searches for hosts by vibrotaxis, detecting vibrations produced by the host.

The *A. minuta* females used in the experiments were from a culture originated from parasitoids bred from parasitized hosts collected on tomatoes in October, 1991 near Modanio (Chalkidiki, Greece). In total 190 (129 females and 61 males) parasitoids emerged from the original collection. From the same tomatoes *Drosophila hydei* (Sturtevant) (Diptera: Drosophilidae)

Table 1. An overview of the relationship between size and fitness as used in a number of studies [see King's (1987) Table 6 for 12 more references]

Species	Measured	Relation	Reference	Comment
Trichogramma embryophagum (Trichogrammatidae)	Longevity (with hosts)	Positive, $P = ?$	Klomp & Teerink (1967)	
	Longevity (without hosts)	Positive, $P = ?$	Klomp & Teerink (1967)	
	No. eggs laid in lifetime	Positive, $P = ?$	Klomp & Teerink (1967)	
	Length eggs	Positive, $P = ?$	Klomp & Teerink (1967)	
Nasonia vitripennis (Pteromalidae)	Oocyte number	Positive, $P = ?$	O'Neill & Skinner (in Charnov & Skinner, 1984)	
Trichogramma evanescens (Trichogrammatidae)	Longevity (without hosts)	Positive, $P < 0{\cdot}001$	Waage & Ng (1984)	
	No. eggs in ovarioles when 2 days old	Positive, $P < 0{\cdot}001$	Waage & Ng (1984)	
	No. hosts parasitized in lifetime	Positive, $P < 0{\cdot}001$	Waage & Ng (1984)	
Pteromalus puparum (Pteromalidae)	Longevity (without hosts)	Domed	Takagi (1985)	1
	No. eggs laid in lifetime	Positive, $P < 0{\cdot}01$	Takagi (1985)	
Trichogramma maidis (Trichogrammatidae)	No. progeny in lifetime	Large ♀♀ = small ♀♀	Bigler *et al.* (1987)	2
	Longevity (with hosts)	Large ♀♀ = small ♀♀	Bigler *et al.* (1987)	2
	Walking speed	Large ♀♀ = small ♀♀	Bigler *et al.* (1987)	2
	% Parasitism in field insectary (release exp.)	Large ♀♀ = small ♀♀	Bigler *et al.* (1987)	2
	% Parasitism in maize field (release exp.)	Large ♀♀ = small ♀♀	Bigler *et al.* (1987)	2
Spalangia cameroni (Pteromalidae)	No. progeny in lifetime	No relationship, $P = 0{\cdot}47$	King (1988)	
	Longevity (with hosts)	No relationship, $P = 0{\cdot}41$	King (1988)	
Lariophagus distinguendus (Pteromalidae)	Longevity (with hosts)	Positive, $P < 0{\cdot}001$	van den Assem *et al.* (1989)	
	No. progeny in lifetime	Positive, $P < 0{\cdot}001$	van den Assem *et al.* (1989)	3
	No. progeny in lifetime (competition)	Large ♀♀ > small ♀♀	van den Assem *et al.* (1989)	3
Diglyphus begini (Pteromalidae)	No. progeny in 3 days	Positive, $P < 0{\cdot}001$	Heinz (1991)	4
Goniozus nephantidis (Bethylidae)	Longevity (with hosts)	Positive, $P < 0{\cdot}01$	Hardy *et al.* (1992)	
	Longevity (without hosts)	Negative, $P < 0{\cdot}01$	Hardy *et al.* (1992)	
	No. progeny in lifetime	Positive, $P < 0{\cdot}01$	Hardy *et al.* (1992)	
Aprostocetus hagenowii (Eulophidae)	Initial no. eggs in ovarioles	Positive, $P < 0{\cdot}001$	Heitmans, Haccou & van Alphen (1992)	
Trichogramma pretiosum (Trichogrammatidae)	Comparing size, distr. emerging vs. searching ♀♀	♀♀ Search larger ♀♀ emerging	Kazmer & Luck (1992)	
	Ratio released vs. ratio offspring recaptured (field)	Large ♀♀ > small ♀♀	Kazmer & Luck (1992)	5

1, the peak of the domed curve is at two-thirds of the range of the female sizes.

2, females reared from different host species are compared, the females from one species being smaller than that of the other species (but there might also be other differences between the two types of females).

3, the experimental set-up was explicitly chosen in such a way that potential differences in searching efficiency (larger females have longer ovipositors) did not play a role.

4, although the females were only presented with hosts on days 2–4, this is the period in which the majority of ovipositions occur.

5, females reared from different host species are compared (thereby differing in size), and a genetic marker is used to be able to distinguish between the offspring of the two types of females.

emerged, which were used to initiate a host culture. Six-day-old larvae were used as hosts in the experiments.

Experiment A: number of eggs, egg size and longevity

In the laboratory, parasitized *D. hydei* larvae were collected and individually reared on an artificial medium (tomato juice, dry yeast and agar). Emerging parasitoids were stored individually at 20°C in jars containing an agar layer without food. After death, the head width and the tibia length were measured and the females were dissected to determine the number and size of the eggs in their ovarioles (mean of 10 eggs). The data on longevity were used to fit a Weibull distribution with one of the parameters being a linear combination of the explanatory variables head width and sex.

Experiment B: searching efficiency within patches

A single female *A. minuta* was introduced onto a tomato, cut in two, on which 50 *D. hydei* larvae had been introduced 24 h earlier. The females were free to leave the patch; when the patch was left for more than 10 min the experiment was ended. Parasitoids still present after 480 min were removed from the patch. A few females (five) had short patch times and very high values for their searching efficiency. Therefore, only experiments with patch times longer than 150 min were included in the analysis. The hosts were kept at 20°C and dissected after 5 days to count the number of parasitoid eggs. This period of 5 days is necessary because the eggs cannot be found in the host until just before the parasitoid larvae hatch (probably because the eggs are imbedded in the host tissue). From the total time spent searching (T) and the proportion of the hosts that remained unparasitized (α_0) the searching efficiency on the patch, s', can be calculated using the equation (Free, Beddington & Lawton 1977; Visser & Driessen 1991):

$$s' = 1/T \cdot \ln 1/\alpha_0.$$

Experiment C: searching efficiency for patches

In a large field cage (7·2 × 7·2 × 2·5 m) at Silwood Park (Ascot, UK) 32 patches (a Petri dish of 14 cm diameter in which two rotten tomatoes were placed on a layer of vermiculite) containing larvae of *D. hydei* were laid down in three concentric circles around the point of release of the parasitoids. The hosts in a patch were either 4, 6, 8 or 10 days old (age in days since eggs were laid). Every 2 days, the eight patches with the oldest larvae were replaced by patches containing hosts of 4 days old (starting off with hosts of different ages prevented the need to replace all patches on the same day). On day 1, 197 *A. minuta* females were released. All females had been measured and marked with a colour (Driessen & Hemerik 1992) to indicate to which of six size classes they belonged; thus, the initial size distribution was known.

All patches were inspected every hour (the first 2 days: 13 rounds per day: first 08·00, last 20·00 h), once every 2 h (days 3–7: 7 rounds per day: first 08·00, last 20·00 h) or 3 times a day (days 8–12: first 08·00, last 20·00 hours), and the number and sizes of the searching females recorded. After 12 days no more parasitoids were seen on the patches. From these data, the mean number of hours spent on a patch in the lifetime of a parasitoid of a specific size class can be calculated by dividing the total number of hours spent on patches by parasitoids of a size class by the total number of parasitoids released belonging to that size class.

In the cage a number of other insect species were present: about 25 Asilidae (Diptera), grasshoppers, some *Drosophila busckii* and many spiders of the genus *Xysticus*.

Experiment D: travel speed

In a similar field cage to the one in the previous experiment, eight pairs of patches (two Petri dishes of 14 cm diameter, the first containing two rotten tomatoes with larvae of *D. hydei* and in the other a rotten onion containing *Delia antiqua* (Meigen) (Diptera: Anthomyiidae) larvae, placed on a layer of vermiculite) were distributed in a circle around the point of release of the parasitoids. The distance from this point to the patches was 2·25 m. In total 116 parasitoids were released. The parasitoids were given access to patches for 2 h on the day before the experiments. These patches consisted either of two rotten tomatoes containing larvae of *D. hydei* (37 parasitoids), a rotten onion containing *Delia antiqua* larvae (39 parasitoids) or only a layer of vermiculite (40 parasitoids). All parasitoids were marked to indicate their previous experience. After the release of the parasitoids (at 08·40 h), parasitoids were recaptured during 11 rounds on the day of release (until 17·40 h, no recaptures during the last two rounds) and on four rounds on the next day (from 10·30 to 12·00 h).

The recaptured parasitoids were measured (head width and tibia length). From the time from release until recapture, and the distance travelled (2·25 m), the travel speed could be calculated.

Statistics

Most of the results were analysed using generalized linear modelling techniques (Aitkin *et al.* 1989), using GLIM (version 3·77; Numerical Algorithms Group, Oxford, 1985). Using this technique, a full model is initially fitted to the data, after which each factor is removed from the model in turn. Whether the removal of a factor causes a significant increase in deviance is tested with an *F*-test. In the case of the longevity data, the data were fitted to a Weibull distribution of which the rate parameter is a linear combination of explanatory variables. In this case, a chi-square approximation is used in deciding whether the removal of one of these variables significantly increased the deviance (see Aitkin *et al.* 1989).

RESULTS

Experiment A: egg load, egg size and longevity vs. parasitoid size

The number of eggs in the ovarioles increased with female size, both when measured as head width [$F_{(1,59)} = 228$, $P < 0{\cdot}001$; Fig. 1] and as tibia length [$F_{(1,59)} = 168$, $P < 0{\cdot}001$). The size of the eggs also increased with head width [$F_{(1,60)} = 193$, $P < 0{\cdot}001$; Fig. 2] and with tibia length [$F_{(1,60)} = 162$, $P < 0{\cdot}001$).

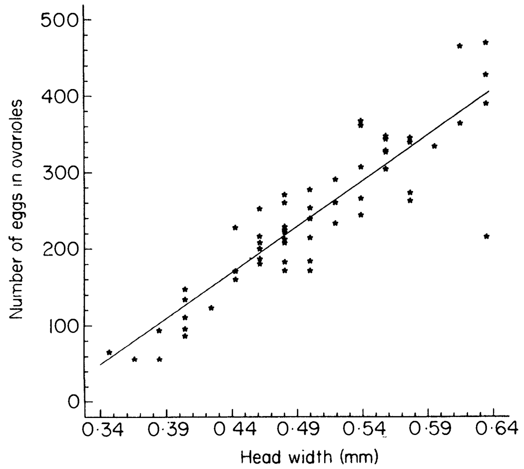

Fig. 1. The number of eggs present in the ovarioles of parasitoids of different size (head width) when kept until dead without food and hosts [number of eggs = −360+1197 head width (mm), $n = 61$].

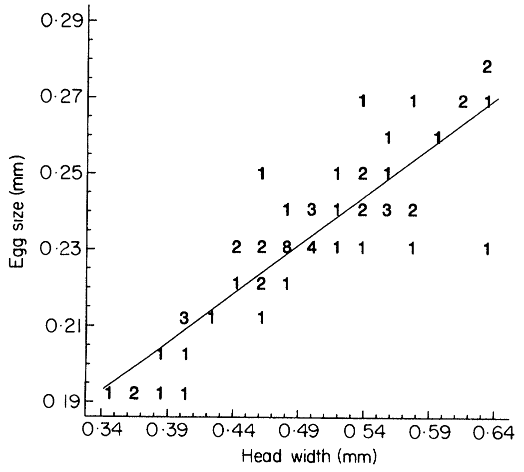

Fig. 2. The size of eggs (mean of 10 eggs) present in the ovarioles of parasitoids of different size (head width) when kept until dead without food and hosts [egg size (mm) = 0·106+0·256 head width (mm), $n = 62$]. Numbers indicate overlapping data points.

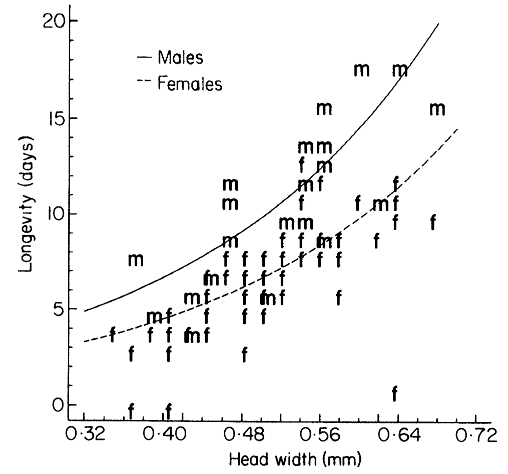

Fig. 3. The longevity of parasitoids of different size (head width) when kept until dead without food and hosts; observed data and means from the fitted Weibull distribution (n♂ = 22, n♀ = 66).

A Weibull distribution was fitted to the longevity data. The fit of the distribution improved both by incorporating size ($\chi^2 \approx 36{\cdot}65$, $P < 0{\cdot}005$) and sex ($\chi^2 \approx 60{\cdot}33$, $P < 0{\cdot}005$). The shape parameter α and the rate parameter λ of the best fitted Weibull are:

$$\alpha = 4{\cdot}0$$

$$\lambda\text{♀} = e^{-0{\cdot}17-15{\cdot}63\,\mathrm{hw(mm)}}$$

$$\lambda\text{♂} = e^{-1{\cdot}74-15{\cdot}63\,\mathrm{hw(mm)}}.$$

In Fig. 3 both the observed longevity data and the mean of the Weibull distribution is plotted against head width (for males and females). The mean of the Weibull distribution is given by $\Gamma(1+1/\alpha)/\lambda^{1/\alpha}$ [Aitkin *et al.* 1989; with the value of the gamma function $\Gamma(1+1/\alpha) = 0{\cdot}9064$ (for $\alpha = 4$)]. Clearly, longevity increases with size, both for males and for females. Also males live longer than females of the same size.

Experiment B: searching efficiency on patches vs. female size

The searching efficiency, s', expressed as proportion tomato searched per min, increases with female head width [$F_{(1,16)} = 22{\cdot}65$, $P < 0{\cdot}001$; Fig. 4).

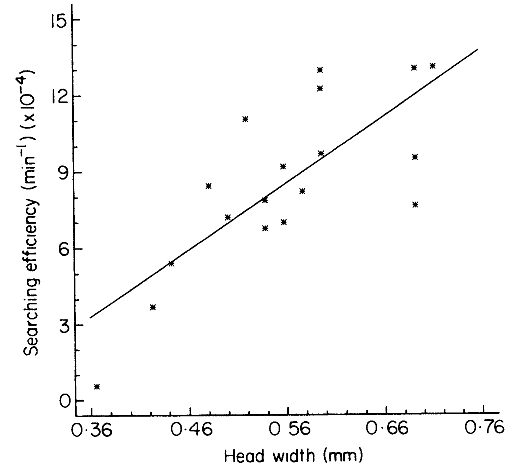

Fig. 4. The searching efficiency within a patch (calculated as $s' = 1/T$. ln $1/\alpha_0$; see text) of parasitoids of different size [$s' = -6{\cdot}1\ 10^{-4}+26{\cdot}1\ 10^{-4}$ head width (mm), $n = 18$].

Experiment C: searching efficiency for patches vs. female size

During the 12 days the experiment in the field cage lasted, a total of 66 rounds was made in which a parasitoid was seen searching on the patches 2013 times. To calculate the total time spent on a patch in a female's lifetime all observations of a female of a certain size class were multiplied with a correction factor, then summed and divided by the number of females released in that size class. This correction factor is needed because the number of rounds made per day differed (see Methods). No correction was made to observations made on days on which a round was made every hour (13 rounds per day), observations made on days on which seven rounds were made were multiplied by 1·86 (13/7) and observations on three-round days by 4·33 (13/3). The total time spent on a patch in a female's lifetime for the six size classes is shown in one of the lines of Fig. 5.

In general, smaller females spent less time on patches in their lifetime than larger females did. Females in the largest size class were, however, observed less often than females from the largest but one size class, but note that there were only 12 females in the largest size class.

Experiment D: travel speed vs. female size

Of the 116 females released in the field cage, 99 were recaptured. The travel speed (m h^{-1}) was calculated by dividing 2·25 m (the distance between the release point and the patches) by the number of hours in between release and recapture. When head width (mm) was included as an explanatory variable, this did not result in a significantly better fit [$F_{(1,95)} = 1\cdot90$, $P > 0\cdot10$]. Thus, size does not appear to be important in determining travel speed. Surprisingly, including the substrate on which the females were experienced on the day before release (tomato, onion or only vermiculite) did significantly increase the fit of the model [$F_{(1,96)} = 11\cdot01$, $P < 0\cdot005$), females experienced on tomato travelled faster than the ones experienced on onion or on only vermiculite ($n_{\mathrm{tomato}} = 34$, $n_{\mathrm{onion}} = 32$ and $n_{\mathrm{inexp.}} = 33$).

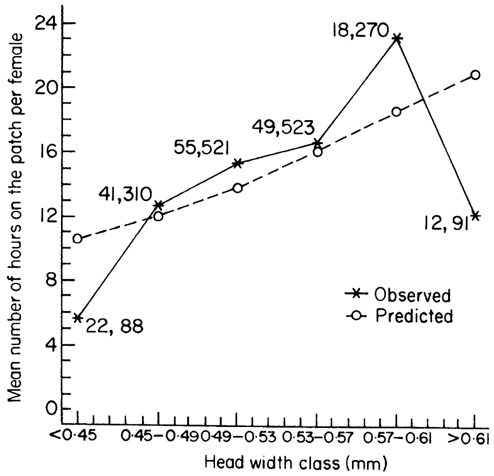

Fig. 5. The mean number of hours spent searching on a patch in a large field cage experiment by parasitoids of different size (head width). The first number given for each data point is the number released, the second number is the total number of times females belonging to that size class have been seen on a tomato during the 12 days of the experiment. Predicted points are calculated assuming that different sized females only differ in their longevity (see text).

DISCUSSION

The number of eggs in the ovarioles, egg size and longevity depend on the size of the parasitoid. Larger females also have higher searching efficiencies on patches than smaller individuals. Travel speed is not influenced by female size. The searching efficiency for patches, measured as the total time spent on patches in a female's lifetime, initially increases with female size, although it decreases for the largest size class. However, does this difference in time spent on patches indicate a real difference in searching efficiency for patches or is it simply caused by differences in longevity?

A number of factors influence the total time spent on patches in a female's lifetime: the longevity of the female, the ability to locate patches, the travel speed between patches and decisions on patch time allocation (including whether to land on a patch). All these factors might depend on the size of the parasitoid. In order to evaluate whether the searching efficiency for patches depends on female size, the hypothesis is tested that only the longevity is influenced by parasitoid size, and that the ability to locate patches, travel speed and patch time allocation is independent of female size. In order to do this, the total number of parasitoids expected to be alive on each round was calculated, using a Weibull distribution with parameters $\alpha = 4\cdot0$ and $\lambda = e^{-0\cdot17-15\cdot63\ \mathrm{hw\ (mm)}}$ (parameters from the longevity experiment, see Experiment A results). In order to get a predicted value for the total time spent on patches in a female's lifetime, these 'observations', were first corrected in the same way as the real data (see Experiment C results), then summed and divided by the number of parasitoids 'released' in the size class. This gives a value for the mean number of 'hours alive in the cage' for females of different size classes. Before these results can be compared with the real data a correction is needed. Obviously, it is not expected that all parasitoids that are still alive in the field cage will be seen on a patch. Therefore, the predicted values were multiplied by 0·18 (total time spent on patches summed for all size classes as predicted, divided by the total time spent on patches summed for all size classes for the females actually observed; note that this correction is independent of female size). In other words, we assume that a female that is alive somewhere in the cage is actually observed on a patch with a probability of 0·18. This corrected predicted value for the total time spent on a patch in a female's lifetime for each of the six size classes is shown in Fig. 5, in which also the line for the observed females is plotted.

Under the hypothesis tested, the slope of both lines should be the same. If larger females are much better at finding patches than small ones, the slope of the observed line is expected to be more steep than the predicted one. Although the observed line is not monotonically increasing, the differences between the predicted and observed value are not large and it is therefore concluded that the observed differences are mainly due to differences in longevity.

Large female *A. minuta* are found to have larger eggs than small females. Both the fitness consequences and the costs of having larger eggs are unclear. It might simply be an allometric effect, with no costs or benefits involved, or there may be a trade-off between number and size of eggs. This needs more study, although in the data presented here there does not seem to be support for a trade-off. Egg size increases, not decreases, with number of eggs when fitted into a linear model of egg size and female size [$F_{(1,58)} = 13{\cdot}11$, $P < 0{\cdot}001$; egg size $= 0{\cdot}145 + 0{\cdot}129$ head width (mm) $+ 0{\cdot}0001$ number of eggs).

The next question to be answered is how these differences in constraints between different-sized females translate into differences in fitness.

Part 2: a dynamic programming model of size and fitness

INTRODUCTION

It is obvious that the question of how the size-related constraints translate into fitness differences cannot be answered without taking the environment into account. The fitness of a short-lived parasitoid with many eggs may be higher than that of a long-lived one with a low fecundity, but in a different environment this might be the opposite. One important characteristic of the environment is the abundance of hosts.

Two simple situations can be distinguished (see also Wilson & Lessells 1994). The first is when a pro-ovigenic female (with *e* eggs in her ovarioles) never encounters more than e/lc hosts, where lc is the clutch size which maximizes the fitness per host (the Lack clutch size; Lack 1947). In this case, all females will die with eggs in their ovarioles and are, therefore, strictly time limited (if they had more time they would have produced more offspring). The fitness of a female will thus be directly related to her longevity and her searching efficiency. Increasing either of these will result in more offspring. The second simple situation is when females always encounter more than *e* hosts. In that case all females will still be alive after they laid their last egg and are thus strictly egg limited (if they had more eggs they would have realized more offspring). Their fitness will then be directly related to their fecundity.

For solitary, monophagous parasitoids this dichotomy of egg- vs. time-limitation is useful (see Driessen & Hemerik 1992). For gregarious parasitoids, like *A. minuta*, however it does not hold. When encountering more than e/lc, but less than *e* hosts in a lifetime, both an increase in fecundity and an increase in longevity lead to an increase in fitness. In other words, for a range of encounter rates with hosts, gregarious parasitoids are both egg- and time-limited. This is because for that range of encounter rates the optimal clutch size is below the lc and above 1. So, if the parasitoids have a higher fecundity they will lay larger clutches and gain more fitness, but if they are longer-lived, they would parasitize more hosts, laying smaller clutch sizes (see also Mangel 1987; Wilson & Lessells 1994).

Studies using fecundity or longevity as a fitness measure implicitly assume parasitoids to be either egg- or time-limited. When combining constraints on fecundity and longevity, a model in which parasitoids can be both egg- and time-limited is needed. Therefore, in order to calculate the relationship between size and fitness, I used a dynamic programming model (Mangel & Clark 1988; Houston *et al.* 1988). However, first the question why a model is needed to calculate this relationship must be answered. With the constraints and the environment known, the problem lies in how foraging decisions of parasitoids might depend on their size (or size-related fecundity and longevity). Suppose that the clutch size decisions are known for females of different sizes, then fitness could be calculated using a Monte Carlo simulation model, as for instance Driessen & Hemerik (1992) did for the solitary parasitoid *Leptopilina clavipes*. In gregarious parasitoids there is, however, an important problem. Clutch size decisions will depend on egg load and age, and therefore data should be available for parasitoids of different ages, and with different egg loads, and all combinations of these, for an experimental situation that resembles the natural environment. In general, these data will not be available. It is then that a dynamic programming model can be used to calculate the optimal clutch size decisions, depending on egg load and the age of the parasitoid.

In the model, first the optimal clutch size decisions for the different sized females are calculated, given their constraints and the characteristics of the environment. This results in a so-called optimal decisions table in which, for each combination of egg load and age, the optimal clutch size is stored. Next, the model can be used to calculate the fitness of females of different sizes using a Monte Carlo simulation. In such a simulation, parasitoids have a certain probability of encountering a host within a time step and a certain probability of dying between time steps. When a host is encountered, the size of the clutch laid depends on the age of the parasitoid and on the egg load, and can be found in the optimal decisions table. After the parasitoid has died its lifetime fitness is calculated by adding up the fitness returns from all parasitized hosts.

To run the model, data on the size-dependent constraints (longevity, fecundity and searching efficiency) and the characteristics of the environment (the distribution of hosts) are necessary.

METHODS

Characteristics of the environment

In a tomato field near Modanio, Greece (the same site where the strain of *A. minuta* was collected the year before) a plot of 2 × 2 m was randomly selected. From all tomatoes on the ground the coordinates were measured and all hosts present per tomato counted (Fig. 6). Almost all hosts were either *Drosophila* sp. or *Muscina* sp. (Diptera: Muscidae) larvae.

The distance between tomatoes was small. Within the plot, the mean distance to the nearest neighbour was 18·6 cm and the average distance between tomatoes within the plot 96·3 cm. These figures are overestimates because tomatoes on the border of the plot might have been closer to tomatoes outside than to ones inside the plot. The mean number of hosts per infested tomato (excluding four unripe tomatoes), was 142/26 = 5·5 *Muscina* and 15/26 = 0·6 *Drosophila* larvae.

Size-dependent constraints

The longevity of a female is assumed to depend on her size: the probability of dying is a function of age, described with a Weibull distribution with parameters $\lambda = e^{-0{\cdot}17-15{\cdot}63\ \mathrm{hw\ (mm)}}$ and $\alpha = 4{\cdot}0$ (taken from longevity experiment, see Experiment A results). The fecundity of a female is also assumed to depend on her size (number of eggs at emergence = $-360+1197$ head width; taken from fecundity experiment, see Experiment A results).

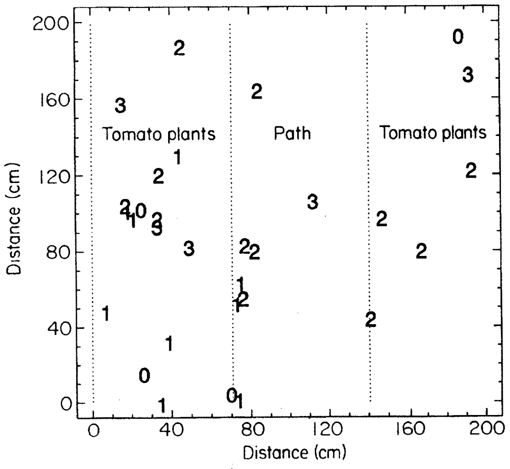

Fig. 6. A map of a 2 × 2 m plot in a tomato field in Modanio (Greece). The numbers indicate the positions of each of the tomatoes in the plot: 0 = no host larvae present, 1 = 1–3 hosts present, 2 = 4–10 hosts present and 3 = more than 10 hosts present in that tomato.

The third size-dependent constraint, the encounter rate with hosts, is not so straightforward, as it depends on the searching efficiency within patches, the searching efficiency for patches, the distance between patches and the number of hosts per patch. In the dynamic programming model the environment is assumed to be homogeneous with a constant host density. There are two reasons why this simplification is justified: (i) the distances between patches (tomatoes) in the field are very small indicating very short travel times between patches, and (ii) the results presented in Part 1 of this paper indicate that there is no difference in searching efficiency for patches between different-sized females. The overall searching efficiency of the parasitoids in the model is therefore assumed to be the same as that within a patch, and to depend on size ($s' = -6{\cdot}1\ 10^{-4}+26{\cdot}1\ 10^{-4}$ head width, taken from the searching efficiency experiment, see Experiment B results).

The density of hosts is taken to be 5, similar to the number of *Muscina* larvae per tomato in the field.

Fitness curve

To calculate the optimal clutch size decisions it is also necessary that the per capita fitness return to the female for each egg laid in a clutch of a certain size (the fitness curve), is known. Of the four relationships that need to be known to calculate the fitness curve, three are taken from a study of Vet *et al.* (1994) on clutch size decisions in *A. minuta*, using *Delia antiqua* as a host species. The second instar larvae of this species are similar in size to the larvae of *Muscina* that are attacked in the field in Greece. The three relationships with clutch size (c) used are:

Probability of egg survival

$$(surv) \quad = 0{\cdot}951-0{\cdot}008.\,c$$

Sex ratio (proportion ♂♂)

$$(sr) \quad = 0{\cdot}262-0{\cdot}007.\,c$$

Head width female offspring (mm)

$$(hw\,♀) \quad = 0{\cdot}744-0{\cdot}013.\,c.$$

The fourth relationship needed to calculate the fitness curve is that between size of a daughter and her fitness [*fitness* ♀ (*hw* ♀)]. This is actually the relationship that is being calculated using the dynamic programming model. This problem is solved by starting with an arbitrary relationship, calculating the fitness of different sized females and thereby finding a new relationship between size and fitness. This relationship is then used to calculate a new fitness curve, the dynamic programming model is run again, etc., until convergence. With these four relationships the fitness curve is calculated:

fitness clutch = *c. surv.* (1-*sr*)*.fitness* ♀ (*hw* ♀).

THE MODEL

The model is based on a clutch size model by Mangel & Clark (1988, pp. 131–141). First, a number of size-dependent parameters is calculated: the encounter rate with hosts, L, the number of eggs in the ovarioles, e, at emergence (the initial egg load) and the two parameters of the survival function, determining the probability of surviving from t to $t+1$, $s(t)$. With these parameters of the survival function, the time horizon, T, is calculated: the probability of being alive at time $= T$ is smaller than 0·001. The fitness function at time $= T$ is set to zero and the optimal clutch size when a host is encountered at time $= T-1$ is calculated, depending on the egg load of the parasitoid. For this, the following dynamic programming equation is used (with t = time, c = clutch size, $w(c)$ = the fitness curve and $F(e, t, T)$ = the parasitoid's fitness when it has e eggs at time t with end time T, given that it will take optimal decisions from t to T):

$$F(e,t,T) = (1-L).\,s(t).\,F(e,t+1,T) + L.\max_{1\leqslant c\leqslant e}\,[w(c)+s(t).\,F(e-c,t+1,T)].$$

By going backwards in time until $t = 1$ a matrix of size 'initial egg load' by 'T' is filled with the optimal decisions on the clutch size, c.

The Monte Carlo model also starts with the calculation of L, e and $s(t)$, depending on the parasitoid's size. The simulation starts at $t = 1$ and calculates whether a host is encountered. If so, the optimal clutch size $c(e, t)$ is laid. Next, it is calculated whether the parasitoids survives until $t = 2$. This is repeated until the parasitoid dies or has laid all its eggs, after which the simulation ends. The absolute fitness of the parasitoid is then calculated by adding up the fitness returns from the clutches laid [using the fitness curve w(c)]. For each parasitoid size, 25 simulations are run. Lastly, the fitness for the different sized females is expressed as relative fitness to that of a female with a head width of 1 mm.

From this, the regression of female size vs. fitness is calculated. If this relationship is different from the one used to calculate the fitness curve, the whole process is repeated, using a new fitness curve (calculated with the new relationship between size and fitness). In Fig. 7 the relationship between size and female fitness to which the model converges is shown, together with those when only longevity or only fecundity is taken into account.

CONCLUSION AND DISCUSSION

The fitness of a female strongly increases with female size. The relationship calculated from the dynamic programming model falls in between those for strictly egg-limited and strictly time-limited animals (Fig. 7). The exact position of the dynamic programming relationship will depend strongly on the encounter rate with hosts, and therefore on the characteristics of the habitat. The fact that the dynamic programming line is close to that for egg-limited animals might be due to the high density of infested tomatoes, and therefore high encounter rates with hosts, in the tomato field in Modanio. A much lower encounter rate will lead to larger clutches being laid, but never more than the *lc*. Therefore, longevity will become increasingly important with decreasing encounter rates. The dynamic programming line will then lie much closer to that for time limited animals and, more important, the slope of that line might be different. This stresses the importance of the knowledge of the natural environment.

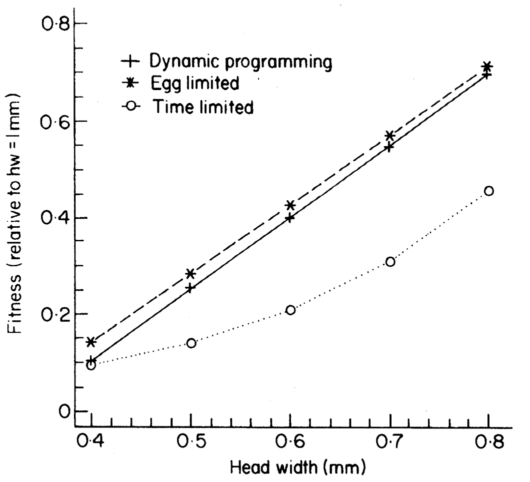

Fig. 7. The fitness (relative to that of a female with a head width of 1 mm) of parasitoids of different size (head width) as calculated (a) with a dynamic programming model taking all size dependent constraints into account, (b) when only the number of available eggs is considered, and (c) when only longevity is considered.

Part 3: estimating the size–fitness relationship in the field

INTRODUCTION

No matter how accurately the relationship between female size and fitness is estimated under laboratory conditions, it remains doubtful whether that relationship resembles the one that exists in a natural environment. In this part of the paper, I will describe three methods of estimating the relationship between size and fitness in the field. Next, I will present data from these three methods and discuss their accuracy and limitations.

METHODS

Method A: estimating the number of eggs laid in a lifetime under field conditions

The rationale for this method is that the number of eggs laid in a female's lifetime under field conditions is a very good measure of fitness. By measuring the rate at which eggs are laid by different sized females under field conditions and multiplying this by their longevity, the number of eggs laid in a lifetime can be calculated. The rate of egg laying can be estimated by collecting females that have been in the field for a known period of time, by doing a release–recapture experiment, and measuring their egg load and size. Initial egg load is closely correlated with size, and, if the parasitoids do not develop new eggs, the number of eggs laid is simply the number at emergence (as estimated from their size) minus the number found at dissection.

In a tomato field near Modanio (Greece), in September 1992, 287 marked females were released (see Driessen & Hemerik 1992 for marking method). During a period of 9 days, part of the field was searched by two persons for 1 h 30 min, twice a day. During this time about 1150 female *A. minuta* were observed on the tomatoes or on the tomato plants. Any marked individuals encountered were collected. Of these animals, head width and tibia length were measured and the number of eggs in their ovarioles counted after dissection.

Method B: comparing the size distribution of emerging females and females found searching on patches in the field

The aim of this method is to determine whether the size distribution of females actually searching on a patch is the same as the size distribution of emerging females (see also Kazmer & Luck 1992). The difference between these distributions is an indication of the degree of selection on size. An assumption of the method is that the time spent searching for hosts is the limiting resource (time-limited animals), and that the searching efficiency is independent of female size. In other words, that the time spent on patches is a good fitness measure. A problem is that the method is only meaningful when the population sampled at emergence and the one sampled searching on patches are the same. Thus, the method is unreliable when only one substrate is sampled to estimate the distribution of searching females when more substrates are used by the population. Another problem occurs when the size distribution of emerging females changes over the season, and therefore emerging females and searching females, collected at the same time, cannot be compared.

In the same tomato field near Modanio (Greece), 25 tomatoes, on which female *A. minuta* were seen foraging on previous days, were collected. After 10 days at 20°C, all pupae were washed from the tomato remains and the 51 pupae found were stored individually in a vial with an agar base. These pupae were checked daily for emergence of parasitoids and flies. From 18 pupae flies emerged (all *Muscina*), and from 30 pupae (also all *Muscina*) in total 230 female and 128 male parasitoids emerged, all *A. minuta*. In the same tomato field 226 female *A. minuta* that were searching on tomatoes were caught. They were killed and their head width and tibia length measured.

Method C: estimating the number of eggs laid by wild caught females

In this method the number of eggs laid by females of different sizes from the time they emerged until captured is compared. An obvious problem is that the age of the parasitoid is not known. Comparing the number of eggs laid by females of different sizes is only valid when assuming a stable age distribution (no relationship between the size of a female and its age at catching).

The method is simple, and involves catching a number of females in the field, measuring their size and counting the number of eggs in the ovarioles. Because of the strong relationship between size and number of eggs at emergence, the number of eggs laid from emergence until capture is known. Although *A. minuta* emerges with a large number of mature eggs, and can therefore be considered pro-ovigenic, it is important to know whether they do develop new eggs. To study this, the parasitoids that emerged from the pupae from the sampled tomatoes for Method B were killed on day of emergence (treatment 1); given a tomato (without hosts) for 3 days and then killed (treatment 2); or were kept in a small cage and given two tomato halves every day until they died (treatment 3). Of all females head width, tibia length, number of eggs in their ovarioles and egg size (mean of five eggs) was measured.

RESULTS

Method A: estimating the number of eggs laid in a lifetime under field conditions

Of the 287 insects released only nine were recaptured (Table 2). Analysing these data showed that both the size of the female and the time in the field had a significant effect on the number of eggs laid in the field [$F_{(1,7)} = 8{\cdot}25$, $P < 0{\cdot}05$ and $F_{(1,7)} = 54{\cdot}80$, $P < 0{\cdot}005$, respectively]. Surprisingly, female size had a negative effect on the number of eggs laid: smaller females laid more eggs per hour spent in the field than the larger females.

In order to estimate the total number of eggs laid in a lifetime, the average longevity (taken from the longevity experiment, see Experiment A results, p. 967) was used as the value for the number of hours spent in the field. This gives the following expression for the number of eggs laid in a lifetime:

$$\text{number of eggs laid per lifetime} = 217 + 2{\cdot}5\,(24 \times 0{\cdot}9064\,/(e^{-0{\cdot}17 - 15{\cdot}63\,\text{head width}})^{1/4}) - 441{\cdot}4\ \text{head width}.$$

This relationship is plotted in Fig. 8. The number of

Table 2. Results from a release–recapture experiment in the field near Modanio (Greece). The size of recaptured females was measured (head width and tibia length) and from that the number of eggs at emergence calculated. The total number of eggs laid while in the field is calculated by subtracting the number of eggs found at recapture from the number of egg at emergence. Division by the time spent in the field gives the number of eggs laid per hour. In total, nine animals were recaptured. The data were fitted to the model: number of eggs laid = 217+2·5 time (h)−441·4 head width (mm)

Head width (mm)	Tibia length (mm)	No. eggs at emergence*	Time in field (h)	No. eggs at recapture	No. eggs laid in field
0·52	0·65	250	18	188	62
0·42	0·50	133	24	54	79
0·46	0·60	193	17·5	123	70
0·54	0·67	269	17·5	271	0
0·62	0·79	359	47·5	315	44
0·56	0·65	273	95·25	52	221
0·56	0·65	273	17	233	40
0·48	0·64	219	17	189	30
0·48	0·60	204	41	95	109

*Mean as calculated from (number of eggs = −360+1197 head width) and (number of eggs = −268+774 tibia length), taken from the fecundity experiment (see Experiment A results, p. 967).

eggs laid in a lifetime increases monotonically with female size (for females with a head width of 0·4 mm and larger).

Method B: comparing the size distribution of emerging females and females found searching on patches in the field

The size distributions of head width and of tibia length are available for both the parasitoids caught searching on tomatoes and for parasitoids emerging from the collected pupae (Fig. 9). For both measures of size the females emerging were smaller than the ones found searching in the field (distributions differ significantly, Kolmogorov-Smirnov two-sample test, $P < 0{\cdot}001$). Although the difference in female size is significant, the difference in the average sizes is small (0·604 vs. 0·588 mm for head width and 0·761 vs. 0·749 mm for tibia length).

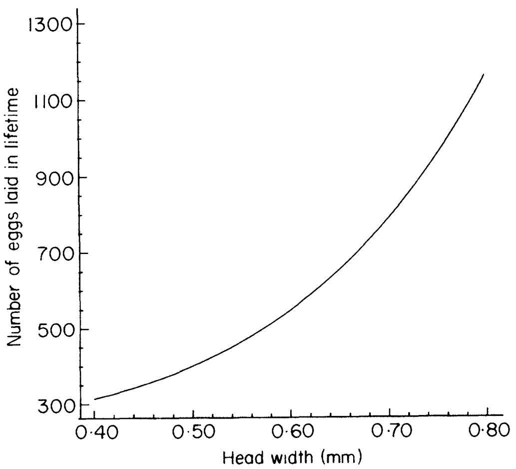

Fig. 8. The number of eggs laid in a lifetime by parasitoids of different size (head width) as calculated by combining from a release–recapture experiment in the field (see Table 2) and longevity data from the laboratory.

Method C: estimating the number of eggs laid by wild caught females

The females caught searching in the field were dissected and measured. From these data the number of eggs laid until capture can be calculated, when the relationship between size and number of eggs at emergence is known, as well as whether or not *A. minuta* develops new eggs over its lifetime. To this end, a statistical analysis was carried out on the number of eggs in the ovarioles with size and treatment (i.e. killed at emergence, killed after 3 days or kept until dead) as variables. In the analysis the interaction term between size (both as head width and as tibia length) and treatment was significant [$F_{(1,203)} = 25{\cdot}5$, $P < 0{\cdot}001$ and $F_{(1,203)} = 49{\cdot}6$, $P < 0{\cdot}001$, respectively], thus both factors had an effect on egg load (Fig. 10). Although for treatments 2 and 3, the relationships between the number of eggs and tibia length are quite similar, lumping them in the model significantly increases the deviance [$F_{(2,203)} = 3{\cdot}71$, $P < 0{\cdot}05$].

A similar analysis of egg size showed that the interaction term between head width and treatment was significant [$F_{(1,203)} = 6{\cdot}28$, $P < 0{\cdot}005$], thus both factors had an effect on egg load (Fig. 11). When size was taken as tibia length the interaction term was not significant, but both main effects, size and treatment, were significant [$F_{(1,205)} = 495{\cdot}74$, $P < 0{\cdot}005$ and $F_{(1,205)} = 4{\cdot}37$, $P < 0{\cdot}025$ respectively].

Interestingly, egg load was generally higher in the group that was not killed directly, while egg size was smaller in that group. This suggests a trade-off between number and size of eggs. In conclusion, both egg load and egg size depend on female size, and also

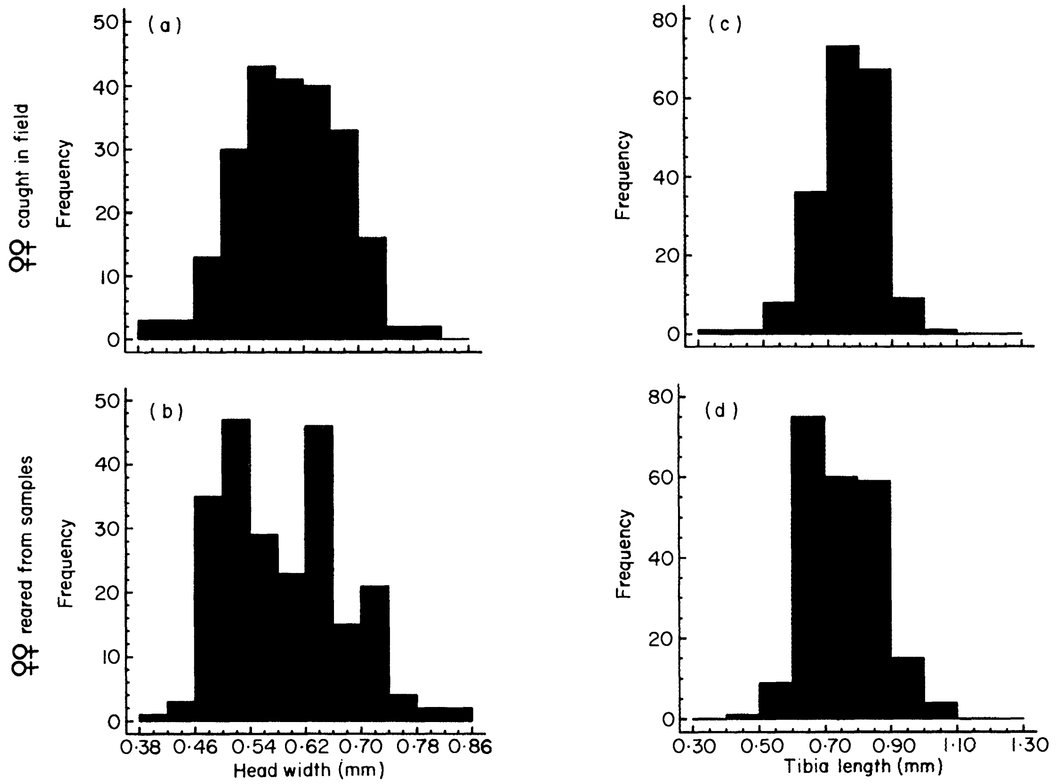

Fig. 9. Frequency histograms of the size of parasitoids that were caught while searching for hosts in the field (a = head width; c = tibia length) and of the size of parasitoids reared from hosts collected in the field (b = head width; d = tibia length).

age and/or food has an influence on these characteristics.

Using the equation for the number of eggs in the ovarioles when unlimited access to tomatoes (as observed in the field), the number of eggs laid by the females caught in the field was calculated (Fig. 12). The number of eggs laid until capture increases with increasing female size ($r = 0{\cdot}34$, $n = 100$, $P < 0{\cdot}005$).

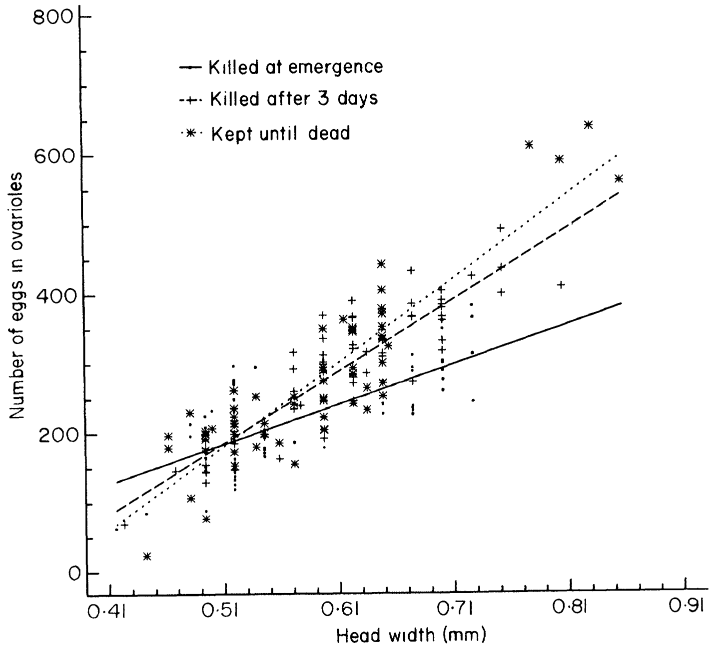

Fig. 10. The number of eggs present in the ovarioles of parasitoids of different size (head width) when (a) killed on day of emergence [number of eggs = −105+567 head width (mm), $n = 79$], (b) killed after 3 days [number of eggs = −336+1023 head width (mm), $n = 66$] and (c) kept until dead [number of eggs = −428+1195 head width (mm), $n = 64$] with food, but without hosts.

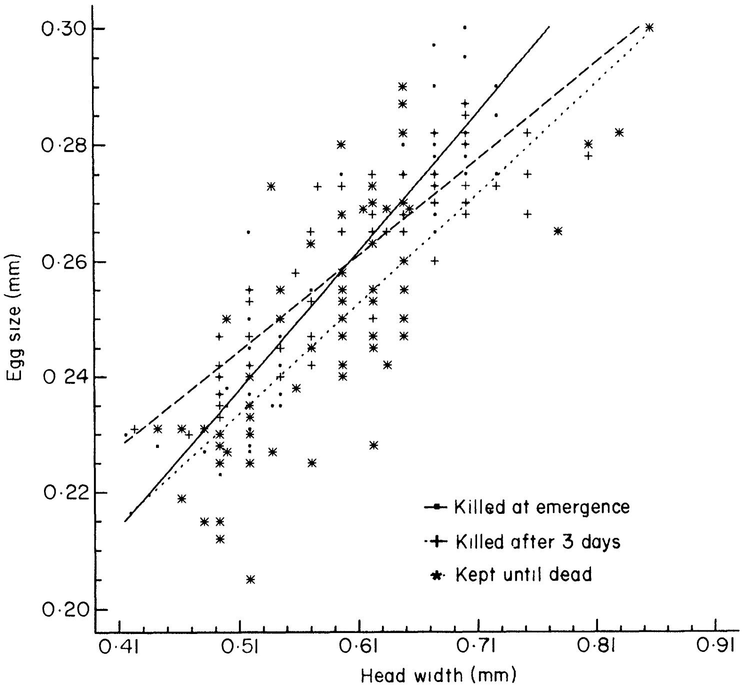

Fig. 11. The size of eggs (mean of five eggs) present in the ovarioles of parasitoids of different size (head width) when (a) killed on day of emergence [egg size (mm) = 0·116+0·238 *hw* (mm), $n = 77$], (b) killed after 3 days [egg size (mm) = 0·160+0·165 *hw* (mm), $n = 65$] and (c) kept until dead [egg size (mm) = 0·137+0·189 *hw* (mm), $n = 67$] with food, but without hosts.

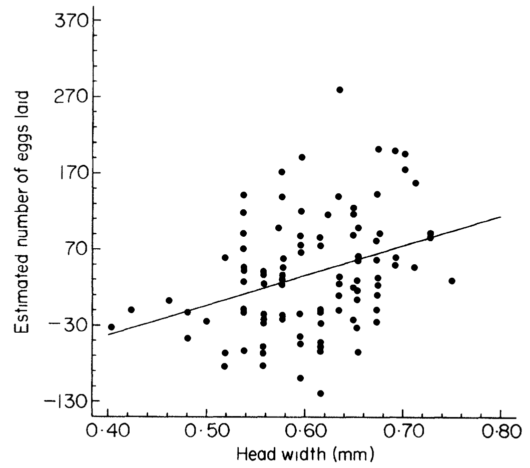

Fig. 12. The estimated number of eggs laid by parasitoids of different size (head width) between emergence and capture in the field ($n = 100$).

CONCLUSIONS AND DISCUSSION

Method A: estimating the number of eggs laid in a lifetime under field conditions

Although size had a negative influence on the number of eggs laid per hour, this method indicated a strong positive relationship between number of eggs laid in a lifetime and parasitoid size. This is due to the importance of the relationship between size and longevity in calculating this relationship, which also explains the shape of Fig. 9. Although this method is the best of the three, mark–recapture is very labour intensive. There are two comments that should be made. The rate of egg laying is assumed to be a constant, but because egg load will decrease over the lifetime of a parasitoid, and both life expectancy and egg load will influence clutch size decisions (as is also predicted by the dynamic programming model of Part 2 of this paper), the rate of egg laying might be a function of age. One hint that the rate of egg laying as measured in the experiment is too high to be an average rate is that the total number of eggs laid in a lifetime as calculated is higher than the number of eggs females have available, especially for the larger females (see Fig. 8). A second problem with this method is that good survival data from the field are necessary and such data are hard to collect. Field survival data are usually collected with capture–recapture experiments, so by measuring all parasitoids before release, it may be possible to collect both data on egg-laying rate and survival in one experiment.

Method B: comparing the size distribution of emerging females and females found searching on patches in the field

There is a significant difference in the size distributions of females that have emerged from samples and females that are found searching on substrates. The difference in the mean sizes of the two groups is however very small, indicating that small females are spending not much less time searching than large females. As already mentioned in the introduction several assumptions are needed to interpret the results from this method. These assumptions are that there is no variation in size of parasitoids over time, that there is a stable age distribution and that there is an equal probability of immigration/emigration from the sample site for the different sized females. How many of these assumption are violated in the *A. minuta* data is unclear. At the time of sampling, late in the season, many overlapping generations had been completed, and the assumption of a stable age distribution is likely to be realistic. Also, relative to the high density of hosts present at the field site, the availability of hosts outside the tomato field appeared limited, and so high levels of emigration and immigration are unlikely.

Method C: estimating the number of eggs laid by wild caught females

A. minuta, although it emerges with a large number of eggs in its ovarioles, develops some new eggs over its lifetime. From the experiment it cannot be concluded whether this is an age effect or due to the availability of food. Comparing the figures for egg load and egg size for females kept without food until dead (Figs 1 & 2) with those for females kept with food (Figs 10 & 11, line for females kept until dead) indicates that it is mainly an age effect because these females have the same number and the same size of eggs at death.

This field experiment indicates that the number of eggs laid until capture increases with female size, although not very strongly. The method can easily be combined with the previous method. It also assumes a stable age distribution, in which case there is no relationship between female size and age when caught. In the results (Fig. 12), females, the small ones in particular, sometimes have a calculated number of eggs laid that is negative. It is unclear what causes this artefact, especially since the relationship between size and number of eggs is estimated from animals from the same population, differing at most by one generation from the ones caught in the field. One explanation might be that the relationship found is assumed to be linear, but in fact is not.

General discussion

This paper discusses the relationship between female size and fitness. In *A. minuta*, not only the number of eggs and longevity are influenced by female size, but also one of the components of the female's ability to find hosts: searching efficiency on a patch. There was no indication that larger parasitoids were better in locating patches or travel faster. The size-dependent constraints were combined in one fitness measure using a dynamic programming model. This technique proved to be useful for calculating the differences in fitness of animals with different constraints. The model showed a clear increase in fitness with increasing parasitoid size. Lastly, three field experiments were carried out, all of which showed a fitness increase with female size. From comparing the results from the laboratory and field experiments, it seems that the fitness increase with increasing female size is much stronger in the laboratory than in the field.

Before discussing the implications of these results, one topic needs some discussion. In both the dynamic programming model and the first of the field experiments, the relationship between size and longevity plays a crucial role. The relationship used is based on experiments in which parasitoids were individually stored in jars with an agar base, but without food or hosts. Obviously, parasitoids in the field and in the field cage experiment have access to both food and hosts, but will also suffer mortality due to predation or bad weather conditions. The overall effect of these factors on the longevity of the parasitoids is unclear. In another experiment, I studied the effect of size on longevity when food was available. A number of males and females were kept in a small cage with tomatoes as a food source but without hosts. Dead animals were collected daily, and their size measured. The experiment was done in the laboratory, at 20°C. It is, however, impossible to analyse the data from this experiment properly because they cannot be fitted to a Weibull (or any other) distribution. The problem being that on some days no parasitoids died while on other days many died. It is unclear why there are such large differences between days, but the consequence is that it is not possible to relate parasitoid longevity to size, as for the data of the animals kept without food. What can be concluded when comparing the small cage experiment with that in which the parasitoids were kept in vials without food is that in the former experiment the parasitoids lived longer (see Table 3).

It is, however, debatable whether realistic data on

Table 3. Average longevity in days (SD) of female *A. minuta* in two laboratory experiments (n = the number of females in a category)

Size class (head width, mm)	<0·45	0·45–0·49	0·49–0·53	0·53–0·57	0·57–0·61	>0·61
Females kept alone in vial without food	3·8 (1·86) $n = 15$	6·5 (1·33) $n = 17$	6·69 (1·30) $n = 11$	9·6 (1·63) $n = 11$	8·6 (1·82) $n = 5$	8·9 (3·63) $n = 7$
Females kept together in small cage with food	6·0 (0·00) $n = 1$	5·8 (2·05) $n = 5$	14·2 (6·04) $n = 18$	12·0 (7·30) $n = 7$	15·1 (4·90) $n = 18$	17·2 (5·37) $n = 32$
Mann-Whitney *U*-test, *P*	>0·05	= 0·33	<0·01	= 0·43	<0·01	<0·01

longevity are obtained by keeping parasitoids under laboratory conditions with food and hosts. It is likely that parasitoid mortality in the field will be influenced by predation and weather conditions. Predation of *A. minuta* by spiders (*Xysticus* sp.) was for instance observed in the field cage experiment on two occasions. In fact, the field cage experiment can serve as a control for how realistic the longevity data are from the experiment in which parasitoids were kept without food and hosts. The necessary calculations have already been made in the discussion of Part 1 (see p. 968). In Table 4 the observed number of parasitoids on the patches in the field cage experiment, 12 days after their release, is compared to the number calculated to be alive, using the survival data from the experiment in which parasitoids were kept without food and hosts. During the last round (12 days after release) two females were observed on the patches in the field cage, while the number calculated to be still alive in the cage is 9·55, and the number calculated to be seen on patches is 1·72. These figures are remarkably close, from which it can be concluded that the survival data used, although obtained from an experiment in which parasitoids were kept in a vial without food or hosts, are realistic for *A. minuta* under field conditions, and it is valid to use these data in both the dynamic programming model and the first of the field experiments.

The results from the three field experiments to estimate the relationship between female size and fitness indicate that there are fitness differences between small and large females in *A. minuta*, but that they are much smaller in the field than in the laboratory. If this is also found to be the case for other species, this will have important consequences for a number of models. In optimal clutch size theory it has been suggested (Hardy *et al.* 1992) that the reason why predicted Lack clutch sizes are larger than the observed clutch size (for conditions under which animals are expected to lay the Lack clutch size) is because the relationship between female size and female fitness is estimated with laboratory experiments. However, if laboratory experiments show a steeper fitness increase with increasing size than field experiments, as the results suggest, this would make the predicted clutch sizes even larger, thereby enlarging the discrepancy between predicted and observed clutch sizes.

For sex allocation models when host quality varies, not only the relationship between female size and female fitness is important, but also that between male size and fitness. In such models, it is important that female fitness increases more with size than male fitness (Charnov 1979; King 1987). In the experiments, the relationship between male size and fitness was not explicitly considered, but the longevity data (Fig. 3) indicate the opposite: male longevity increases more with increasing size than female longevity. Similar to female fitness, it is unclear whether these laboratory data are representative for the size-fitness relationship in the field. It is therefore interesting to look at the data collected on males in one of the field experiments. In the tomato field in Greece, 61 males were collected on tomatoes. These males were caught while sitting on uninvested tomatoes with their wings spread out, and high on their legs, a behaviour that is related to attracting females (R. A. Wharton, personal communication). In one case, mating was observed on a tomato. The size of these caught males (measured as head width and as tibia length) can be compared to that of males that emerged from the pupae collected in the field (125 emerged males). There was no significant difference between these size distributions (Kolmogorov-Smirnov two-sample test; head width: $P = 0{\cdot}38$, tibia length: $P = 0{\cdot}72$). This indicates that, in the field, male fitness, opposite to female fitness, does not depend on size, as is usually assumed in models on sex allocation when host quality varies.

This paper is the first to compare laboratory and field data on the relationship between female size and fitness in parasitoids, and more studies are needed in order to evaluate whether data obtained in the laboratory can be used to estimate this relationship. Modelling parasitoid behavioural ecology is important in understanding the biology of this diverse group. Often, models are also used to reveal which relationships should be measured because they are critical for the outcome of these models. Such relationships, and without doubt the relationship between size and fitness is one of them, should then be measured. Only then can models be tested with experimental data

Table 4. The number of females observed on patches in the field cage on day 12 of the experiment (for six size classes), the number calculated to be alive and the number calculated to be seen on patches on day 12, when the longevity data of the laboratory experiment are used

Size class (head width, mm)	<0·45	0·45–0·49	0·49–0·53	0·53–0·57	0·57–0·61	>0·61	Total
Number of females on patches after 12 days—observed	0	0	1	1	0	1	2
Number of females alive in cage after 12 days—calculated	0	0	0·11	1·77	3·04	4·63	9·55
Number of females on patches after 12 days—calculated	0	0	0·02	0·32	0·55	0·83	1·72

and will the field get new input for further development.

Acknowledgements

Charles Godfray is gratefully acknowledged for his support and for stimulating discussions. Lucie Peijnenburg helped out during the field work, Chantalle Jay carried out the travel speed experiment and Jane Hodgson assisted with keeping the cultures alive. Gerard Driessen collected the *A. minuta* to initiate the culture, Bob Wharton is acknowledged for his helpful information on braconid biology and Ian Maclean for identifying the *Muscina* flies. The work has greatly benefited from many discussions with Molly Hunter, Gerard Driessen and Hefin Jones. Lastly, I want to thank Demetra Prophetou for her kind hospitality during the field work in Greece. This study was supported by a grant from the EC Science programme (grant number ERB4001GT910445).

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Received 14 September 1993; revision received 2 March 1994