

The relationship between parasitoid size and fitness in the field, a study of *Achrysocharoides zwoelferi* (Hymenoptera: Eulophidae)

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Summary

1. A knowledge of the relationship between body size and fitness is very important in many models of parasitoid behavioural ecology. We estimated this relationship for *Achrysocharoides zwoelferi* (Hymenoptera, Eulophidae), a parasitoid of leaf mining moths (Gracillariidae) on willow (*Salix*).
2. The size distribution of female wasps emerging from their pupae was compared with the size distribution of wasps caught while searching for hosts. A parametric statistical approach was used to obtain a function relating size to fitness.
3. Laboratory estimates of the influence of size on a component of fitness, longevity, were obtained under two different sets of experimental conditions.
4. In the field, fitness increased rapidly with size over the first two-thirds of the observed size range, but plateaued (or possibly declined) in the last third of the range.
5. One laboratory experiment showed no effect of size on fitness while the other did show an effect although much weaker than that observed in the field. This suggests caution in using results from the laboratory in parameterising behavioural ecological models.
6. The results are compared with two other field estimates of the influence of size on fitness which show broadly similar patterns.

Key-words: clutch size, fitness, parasitoid, sex ratio, size.

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Introduction

Parasitoid wasps have proved excellent experimental models for testing a variety of theories from behavioural and evolutionary ecology (reviewed by Godfray 1994). This is because of the relatively simple link between the reproductive behaviour and fitness of female parasitoids, and the great flexibility in sex allocation behaviour possessed by hymenopteran parasitoids as a consequence of their haplodiploid sex determination. However, many hypotheses about parasitoid sex ratio and life history have been tested only qualitatively rather than quantitatively. The reason for this is that quantitative tests require reliable estimates of the form of the relationship between parasitoid size and fitness, and these have proved difficult or impossible to obtain in the laboratory. To give two examples, Charnov's theory of conditional sex allocation (Charnov 1979; Charnov *et al.* 1981) provides a convincing explanation for the widespread observation that parasitoid wasps tend to place male

eggs in relatively small hosts (giving rise to small adult wasps) and female eggs in relatively large hosts (giving rise to large adult wasps). The theory assumes that the marginal increase in fitness with adult size is greater for females than males, and while this has been examined in the laboratory (van den Assem, van Iersal & Los-den Hartogh 1989; Heinz 1991), these parameters have not been estimated in the field and used to predict sex ratio behaviour. Similarly, application of clutch size theory to parasitoids provides qualitative explanations of oviposition patterns (Charnov & Skinner 1984, 1985; Skinner 1985; Waage & Godfray 1985; Godfray 1987), but quantitative predictions based on laboratory-derived fitness measures are almost invariably too high, probably because the fitness penalties of being small are underestimated (e.g. Hardy, Griffiths & Godfray, 1992; Vet *et al.* 1994; Godfray 1994). Further examples of the importance of understanding the significance of adult parasitoid size could have been taken from studies of host searching behaviour (van Alphen & Vet 1986) and superparasitism

(van Alphen & Visser 1990). An understanding of the form of the relationship between wasp size and fitness is also important from an applied perspective: in inundative biological control programmes parasitoids are reared en masse in the laboratory or factory and different rearing techniques often result in different size distributions of wasps for release (Waage & Godfray 1985; Kazmer & Luck 1995).

Field estimates of size-dependent fitness can be obtained in a number of ways (Visser 1994; Godfray 1994; Kazmer & Luck 1995). First, individual wasps of different sizes can be marked and then recaptured while mating or ovipositing. Most parasitoid wasp species are small or minute insects, and there are logistic problems in marking and recapturing sufficient wasps for statistical analysis. Secondly, the size distribution of wasps at emergence and those caught mating or ovipositing can be compared. As long as the mating/ovipositing sample come from the same population as the emerging sample, differences in the two size distributions reflect size-dependent relative fitness. So far two parasitoid studies have used the second technique to estimate size-dependent fitness in the field. Visser (1994) found a significant difference in the mean size of emerging and ovipositing *Aphaereta minuta* (Braconidae), a larva-pupal parasitoid of cyclorrhaphous Diptera indicating a fitness advantage of being large. Kazmer & Luck (1995) used non-parametric methods to show that in the lepidopteran egg parasitoid *Trichogramma pretiosum* (Trichogrammatidae), both males and females benefited from being large. Herre (1989) has used similar techniques in a study of pollinating fig wasps.

Here we study the eulophid *Achrysocharoides* (= *Enaysma*) *zwoelferi* (Delucchi) and compare the size distribution of emerging females, and of females caught searching for hosts on their foodplant. We use a parametric approach to fit a size-fitness function that can subsequently be used in modelling studies. We compare the relationship obtained in the field with a standard laboratory approach to the problem. *A. zwoelferi*, in common with most other members of the genus, has an unusual reproductive strategy (Askew & Ruse 1974; Bryan 1983; Godfray & Parker 1991; Godfray 1994). Females are laid in small, single-sexed clutches of two or three, while male eggs are laid either solitarily (as in *A. zwoelferi*) or in single-sexed clutches that are normally slightly smaller than those containing females. A few species lay mixed clutches and at least one species is thelytokous. This work is part of a larger study attempting to understand the evolution of oviposition behaviour in *A. zwoelferi* and other *Achrysocharoides*.

Methods

NATURAL HISTORY

A. zwoelferi is a small metallic chalcidoid wasp approximately 2 mm in length. It is oligophagous,

attacking those species of *Phyllonorycter* (Lepidoptera, Gracillariidae) that mine the leaves of *Salix* spp.. In our study site at Silwood Park (Berkshire, UK), the wasp is the commonest parasitoid attacking *Phyllonorycter salicicolella* (Sircom) on *Salix cinerea* L. and *Salix caprea* L.. Both host and parasitoid have two generations a year with the peak wasp flight periods being in June and September. At this time, females can be collected searching the leaves of *Salix* for hosts. Like other members of the genus, it is easily recognized in the field by its habit of moving rapidly sideways across the leaf in a crab-like fashion. We found no males on the host plant and have yet to discover where mating takes place. The wasp kills the host larva prior to pupation and forms a naked pupa in the mine. Parasitoids overwinter as pupae in mines within fallen leaves.

SIZE DISTRIBUTION OF EMERGING WASPS

Mature, first generation mines of *P. salicicolella* were collected in June and July 1993 from an area of damp mixed woodland and grassland, and placed individually in corked glass tubes in an outside insectary. At the time of collection, the parasitoids would have completed development and pupated. Mines were checked daily and emerging *A. zwoelferi* were separated to be used in the laboratory experiments described below. On death, the hind tibia length of each wasp was recorded (hereafter, wasp size refers to length of the hind tibia).

SIZE DISTRIBUTION OF OVIPOSITING WASPS

In July and August 1993, *Salix cinerea* and *Salix caprea* trees were searched intensively for wasps in the act of locating hosts. We searched the same trees that provided mines for the emerging wasp sample, and the insects we collected were of the same generation. Wasps were measured in the laboratory, and their date of capture recorded.

LABORATORY EXPERIMENTS

Experiment 1

Seventy wasps from the collection reared to determine the size distribution of emerging insects were kept in the laboratory to study the relationship between size and longevity. Wasps were placed individually in a corked glass tube and provided with a piece of filter paper soaked in honey solution. The tubes were stored at 20 °C (± 2 °C) under a 16:8 light:dark regime. Humidity was not controlled and varied in the range 40–60%. Wasps were checked daily and their size and date of death recorded.

Experiment 2

The second experiment was conducted in spring 1994 using 70 wasps that emerged from mines collected in September and October 1993. Wasps were treated as before except that they were maintained at high humidity (*c.* 90–95%) and provided every second day with a fresh piece of filter paper soaked in honey solution. On death, the size of the wasp was measured in the usual way.

STATISTICAL ANALYSIS

The relationship between size and fitness can be studied using both parametric and non-parametric statistical techniques. We chose a parametric study as part of the aim of the study was to derive a function relating fitness and size that could be used in life-history modelling. We assumed that the relationship between fitness and size (x) was of the form $f(x) = \exp(a_1 + a_2x + a_3x^2)$ where a_1 , a_2 and a_3 are parameters. In the Appendix we show that if the distribution of emerging wasps is normal, analytical estimates of a_2 and a_3 can be obtained through maximum likelihood methods so that the effect of size on *relative* fitness can be examined (it is not possible to obtain estimates of a_1 and hence calculate absolute fitness). In illustrating the effect of size on fitness, we define the fitness of a wasp of mean size at emergence (\bar{x}) to be 1.0 so that $a_1 = -a_2\bar{x} - a_3\bar{x}^2$. We also obtain the standard errors for a_2 and a_3 and construct log-likelihood statistics to test the hypotheses that an exponential linear model is superior to a model with no size-related component, and that the exponential quadratic model is superior to the exponential linear.

The effect of size on longevity in the laboratory was studied using general linear modelling techniques available in the GLIM statistical package (McCullagh & Nelder 1989). A Weibull distribution is fitted to the data with constant rate and shape parameter. The significance of the improvement of the explanatory power of the model when the rate parameter is made a linear, quadratic or higher function of body size can be calculated and provides a measure of size-specific fitness (Aitkin *et al.* 1989). Only a linear term is required below in which case the expected longevity of wasps of different size is $\Gamma[1 + (\alpha)^{-1}][1/\exp(b_1 + b_2x)]$ where α is the shape parameter and b_1 and b_2 are the two fitted coefficients of the rate parameters, $\exp(b_1 + b_2x)$. To compare the fitness estimates derived in the laboratory and field we again define the fitness of an average sized wasp as one in which case relative fitness is $\exp(b_1 + b_2\bar{x})/\exp(b_1 + b_2x)$.

Results

SIZE-RELATED FITNESS IN THE FIELD

The size distribution of emerging ($n = 163$) and searching ($n = 119$) wasps is shown in Fig. 1. The size

of emerging wasps is well-approximated by a normal distribution (Shapiro & Francia $W' = 0.988$, $P = 0.14$; Shapiro & Francia 1972) while that of searching wasps deviates from normality (Shapiro & Francia $W' = 0.977$, $P = 0.035$) because of an over-representation of large individuals. There was no statistically significant relationship between body size and the date of emergence ($F_{1,68} = 1.20$, $P = 0.28$), nor body size and the date of capture of searching wasps ($F_{1,119} < 0.01$, $P > 0.9$).

The exponential linear model provided a significantly better fit to the data than a model that did not include the effect of size ($\chi^2_1 \approx 10.30$, $P = 0.0013$) while including a quadratic term further improved the explanatory power of the model ($\chi^2_1 \approx 8.55$, $P = 0.0035$). The maximum likelihood estimate for a_2 is 178.5 (SE 67.1) and for a_3 is -248.7 (SE 98.54). The shape of the relationship between size and relative fitness is shown in Fig. 2 which is plotted for a range of wasp sizes spanning the 10th to 90th percentiles of the data. The estimates of a_2 and a_3 are negatively correlated and two curves representing relationships with parameters $\{a_2 + \text{SE}, a_3 - \text{SE}\}$ and $\{a_2 - \text{SE}, a_3 + \text{SE}\}$ are also plotted to describe the uncertainty in the shape of the function. It can be seen that fitness increases roughly linearly over a range of sizes up to about a hind tibia length of approximately 0.35. Beyond this point, the advantages of being larger asymptote or possibly even begin to decline.

SIZE-RELATED FITNESS IN THE LABORATORY

Experiment 1

The average life span of a female wasp was 3.07 days (SE 0.68; $n = 70$) and her average size 0.338 mm (SE 0.004). The Weibull model provided a significantly better fit to the data than an exponential model ($\chi^2_1 \approx 40.0$, $P < 0.001$) with an estimated shape parameter of 2.35 showing that mortality accelerated with age. Making the rate parameter a function of body size failed to improve the explanatory power of the model ($\chi^2_1 \approx 0.34$, $P > 0.1$). We were thus unable to detect a relationship between body size and longevity in this experiment (Fig. 3).

Experiment 2

The average size of wasps used in this experiment was 0.334 mm (SE 0.004; $n = 70$). There was no significant difference in the sizes of the wasps used in the two experiments ($F_{1,138} = 0.61$, $P = 0.44$), nor their variability (Bartlett's statistic = 2.42, d.f. = 1, $P > 0.1$). Under this more benign regime, wasps on average lived over three times longer (9.61 days, SE 0.49). Again, a Weibull model was superior to an exponential model ($\chi^2_1 \approx 64.2$, $P < 0.001$). However, in contrast to the previous experiment, making the rate parameter a function of body size did improve the fit

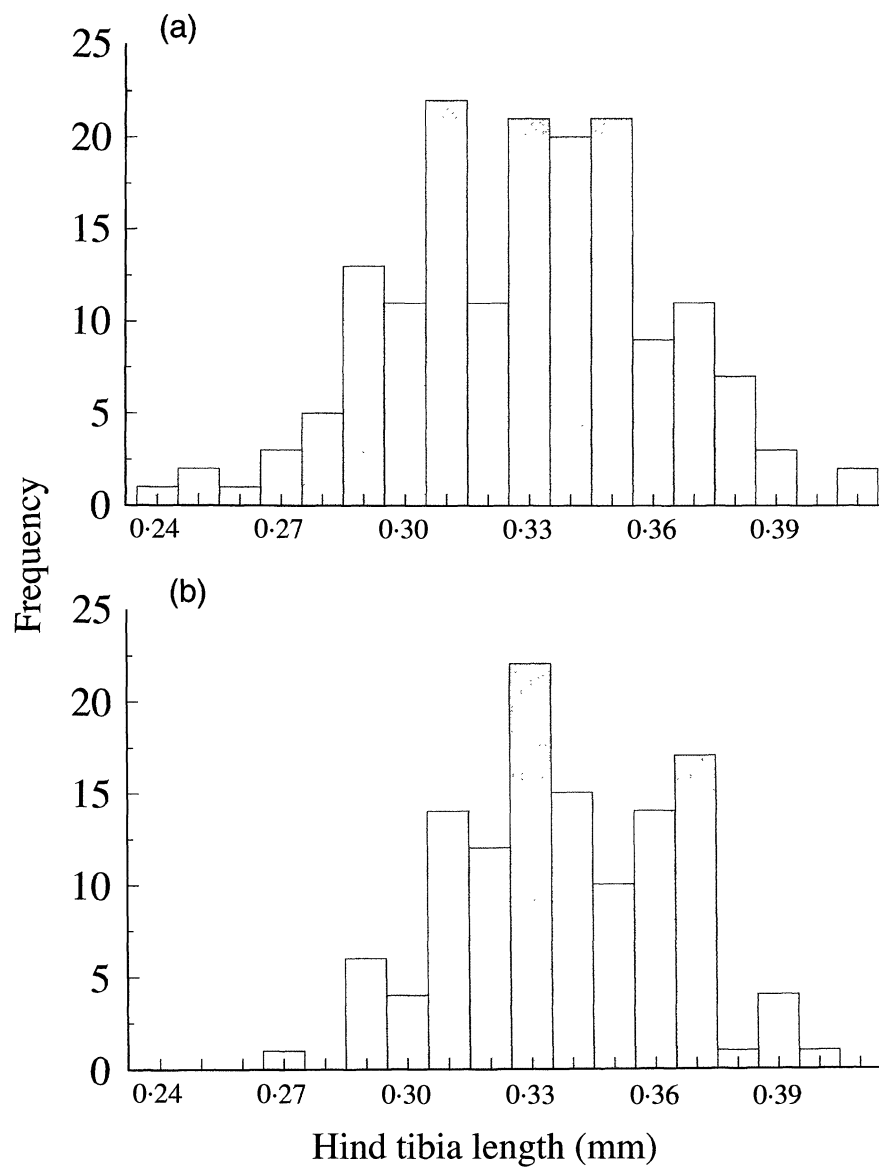


Fig. 1. The size distributions of (a) emerging *A. zwoelferi* and (b) those caught searching for hosts in the field.

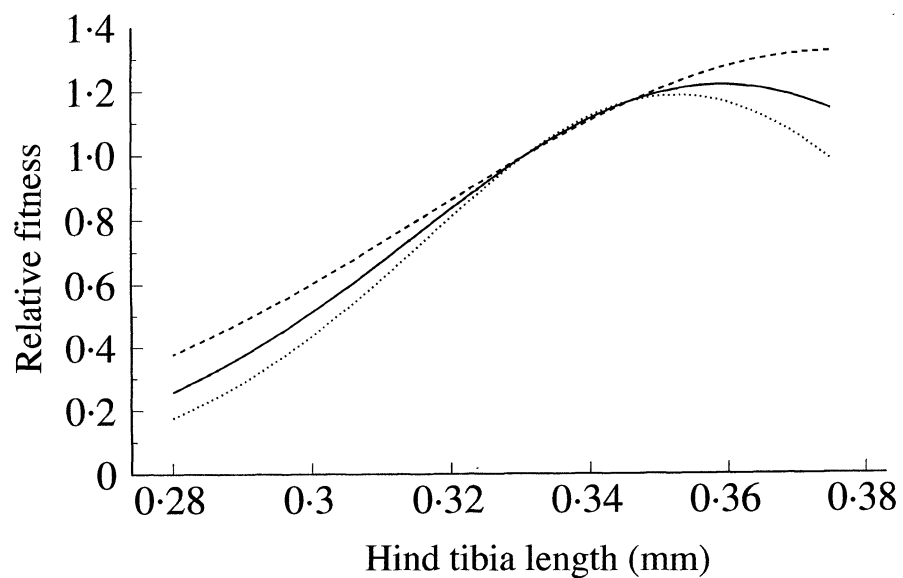


Fig. 2. The estimated relationship between size (hind tibia length) and fitness in the field for *A. zwoelferi* (with fitness of wasps of average size defined as one). The dotted and dashed lines represent the standard errors of this estimate.

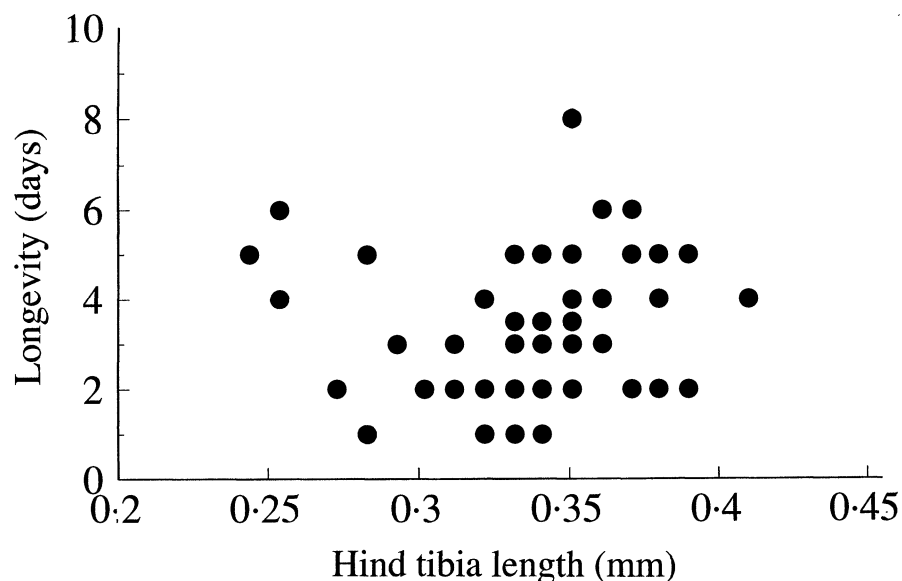


Fig. 3. The longevity of females of different size in Experiment 1. Females were kept in an environment with relatively low humidity and fed honey once, upon emergence. There was no significant relationship between longevity and size.

of the model (coefficients of rate parameters: $b_1 = -1.04$, SE 0.47; $b_2 = -3.99$, SE 1.40; shape parameter, 2.66; $\chi^2_1 \approx 7.19$; $P = 0.007$). The inclusion of a quadratic term led to little increase in the explanatory power of the model ($\chi^2_1 \approx 0.94$). Figure 4 shows the results of the experiment with the expected longevity of wasps of different sizes. There is a weak linear increase with size.

Discussion

Figure 5 shows our best estimate of the relationship between size and fitness for the two laboratory experiments and from the field data. The laboratory experiments use longevity as a measure of fitness while the

field study assumes that fitness can be measured by the time spent searching on the host's foodplant. The relationships are plotted, as before, for a range of sizes representing the 10th to 90th percentile of emerging wasps. It is clear that the field derived estimate accords a much higher importance to size than the laboratory studies, one of which found no effect of size. The field estimate suggests that a wasp in the 90th percentile of the size distribution of emerging wasps has a fitness 3.1 times greater than a 10th percentile wasp while the second laboratory estimate suggests the larger wasp would have a fitness only 1.4 time that of the smaller.

Why do laboratory and field estimates of the importance of size on fitness agree so poorly? Lab-

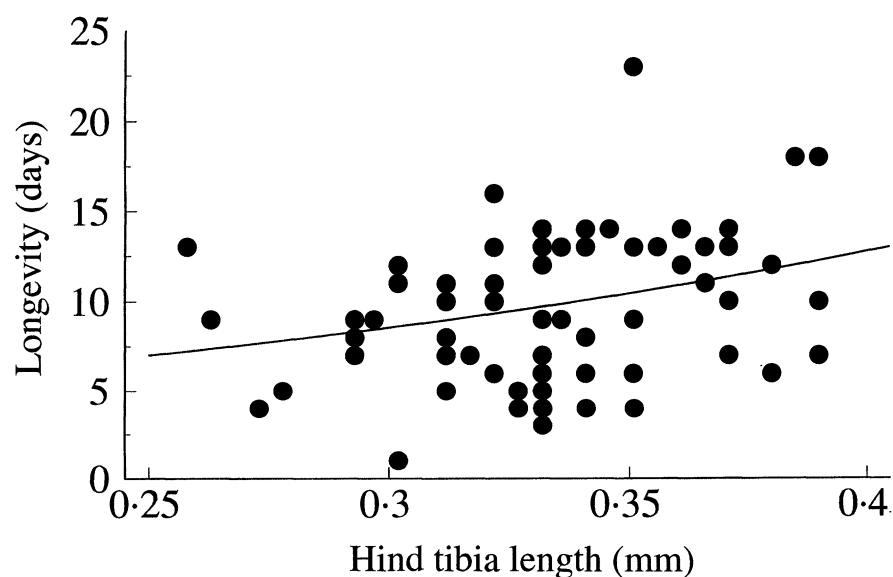


Fig. 4. The longevity of females of different size in Experiment 2. Females were kept under high humidity and provided with an excess of honey. There was a significant positive correlation between longevity and size. The line represents the results of the Weibull analysis described in the text.

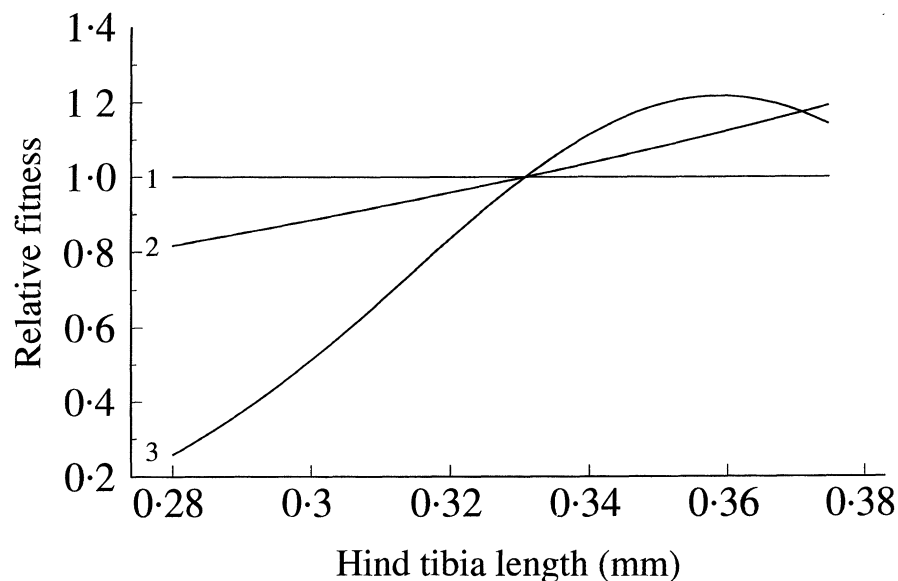


Fig. 5. A comparison of the field and laboratory estimates of the relationship between size and fitness for female *A. zwoelferi*. Line 1 (fitness constant) represents the conclusions from Experiment 1 where no influence of wasp size on longevity was detected. Line 2 is the inferred relationship between fitness (measured by relative longevity) and wasp size from Experiment 2. Line 3 is the field estimate of the relationship between size and fitness. In all cases, the fitness of wasps of mean size is defined as one.

oratory estimates of longevity are likely to be correlated with lifespan in the field, and the latter is probably correlated with fitness. However, the correlation may not be strong, and estimates of longevity will be strongly influenced by experimental conditions. The importance of experimental conditions is illustrated by a comparison of our Experiments 1 and 2. One possible factor that may confound this comparison is that the two experiments were conducted using wasps from different generations, although we see no particular reason why this should have a strong effect on our results. A second measure of fitness often used in the laboratory is fecundity (a measure not open to us because the host of *A. zwoelferi* cannot be cultured). Again, estimates of fitness are strongly influenced by laboratory protocols making their interpretation difficult.

How valid is the measure of fitness that we used in the field study? Time spent searching on the host plant is likely to be strongly correlated with the number of hosts located and hence fitness. There are, however, some factors that might weaken the correlation. First, there may be an experimental bias if the size of the insect influences its probability of capture. In the present case we believe this to be unlikely as *A. zwoelferi* of all sizes are easily seen and captured in the field. Secondly, wasps of different sizes may differ in their efficiency of host location, or in their ability to attack a host once located (Hurlbutt 1987; Visser 1994; Godfray 1994). We have no information about whether these problems apply to *A. zwoelferi*. Finally, the fitness of wasps may not be limited by their ability to locate hosts but by their fecundity which in turn may be influenced by their size (egg limitation rather than

host limitation). This would not be a problem if wasps only visited the host plant when they had mature eggs to lay, but would distort the fitness if wasps remained on the host plant while they matured eggs (the wasps are synovigenic, maturing eggs throughout their life). While we cannot rule out the last possibility, the behaviour of the wasps we encountered on the host plant suggested they were actively searching for hosts that occurred on the trees at low density, which indicates that they are unlikely to have run out of eggs. A second piece of evidence that suggests *A. zwoelferi* is host-limited comes from their unusual reproductive strategy: wasps always lay clutches of single male eggs but of one to three female eggs. If wasps are host limited then equal numbers of male and female clutches are expected while if wasps are egg limited equal numbers of male and female eggs are predicted (Godfray 1994). Both our data (unpublished results) and those of Bryan (1983) show roughly equal numbers of male and female clutches (and a consequent female biased sex ratio) providing indirect evidence for host limitation.

Comparisons of the size distributions of wasps at emergence sites and at oviposition or mating sites is a powerful tool for estimating size-specific fitness in the field. It is, however, essential that the two samples of insects come from the same population. The technique is thus easiest to implement for species such as *A. zwoelferi* that have discrete generations and which do not disperse great distances within a generation. Once the data is collected, there are a number of ways to analyse it. Comparing the mean size of the two samples shows the presence of size-specific fitness but provides little extra information. To proceed further, one

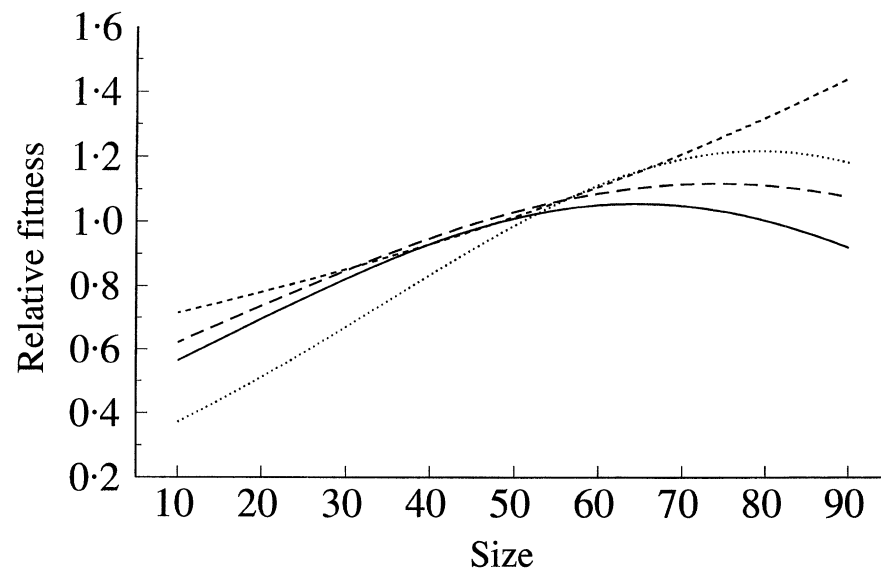


Fig. 6. Field estimates of the relationship between body size and fitness for three species of parasitoids. All relationships are calculated using the parametric approach described in the text. The dotted line represents the relationship for *A. zwoelferi* (this study). The short-dashed and solid lines depict, respectively, the 1988 and 1990 estimates of the relationship for *Trichogramma pretiosum* (Kazmer & Luck 1995). The long-dashed line shows the relationship for *Aphaerata minuta* (based on Visser 1994). Size is measured in percentiles of the distribution of emerging wasps. The fitness of wasps of mean size is defined as one (note, curves do not all intercept at a relative fitness of one because the median and the mean do not coincide).

has the choice of parametric methods such as those used here, or non-parametric methods such as those used by Kazmer & Luck (1995) which were based on Schluter (1988). There are advantages and disadvantages to both methods. The parametric approach is computationally simpler, statistically more powerful, and provides a functional form for fitness that can be incorporated in behavioural ecological models. However, to use a parametric approach, assumptions have to be made about the underlying distribution of emerging parasitoids, and about the form of the model to be fitted. The main assumption of the parametric technique we used is that the distribution of emerging wasps is normal (or can be transformed to a normal distribution).

We now have four data sets (from three studies) in which the size-related fitness of female parasitoids has been measured in the field and already some patterns are discernible. Kazmer & Luck's 1988 data show a fairly linear increase in fitness with size. However, both our study and Kazmer & Luck's (1995) data for 1990 shown an initial linear increase in fitness with size followed by an asymptote or even decline in fitness (not distinguishable with the current data) for the largest wasps. Visser's (1994) study possibly also shows this pattern: we fitted our parametric model to his data although with the strong caveat that we detected a deviation from normality in the distribution of the sizes (head capsule width) of emerging wasps. The results are shown in Fig. 6, together with our data and those of Kazmer & Luck (again using our parametric model which gives similar results to their non-parametric model). To facilitate comparison, we have defined the fitness of average-sized wasp of all

three species to be 1.0, and plot size in units of the percentiles of the distribution of emerging wasps. It will be fascinating to see whether the non-linear relationship between fitness and size shown by three out of four of these data sets holds for other species and whether field derived estimates of size-dependent fitness improve the quantitative fit of models of parasitoid reproductive strategies.

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Appendix

Let the size of wasps collected at emergence be represented by y_i ($i = 1 \dots n_e$) and those collected at the oviposition site

be x_i ($i = 1 \dots n_o$). We assume that the sizes of emerging wasps are normally distributed $N(y; \mu, \sigma)$. We consider a suite of models f_1 , $f_2(x)$, and $f_3(x)$ that describe the amount of time spent at the oviposition site as a function of wasp size (x),

$$f_3(x) = \exp(a_1 + a_2x + a_3x^2), \quad \text{eqn A1}$$

The function f_2 is obtained by setting $a_3 = 0$ and f_1 is obtained by setting both a_2 and a_3 to zero. Manley (1985) discusses previous uses of this equation as a model of Darwinian fitness.

The probability distribution of wasp sizes on the oviposition site under model 3 is

$$\int_{-\infty}^{\infty} f_3(x)N(x; \mu, \sigma)dx, \quad \text{eqn A2}$$

$$\Rightarrow \sqrt{\frac{1-2a_3\sigma^2}{2\pi\sigma^2}}$$

$$\times \exp\left(a_2x + a_3x^2 + \frac{\mu^2}{2\sigma^2} + \frac{(\mu + a_2\sigma^2)^2}{4a_3\sigma^4 - 2\sigma^2} - \frac{(x-\mu)^2}{2\sigma^2}\right) \quad \text{eqn A3}$$

A similar expression for model 2 is obtained by setting $a_3 = 0$. Note the parameter a_1 does not appear in eqn A3 and cannot be estimated. Model 1 implies no size-dependent fitness and is thus the null model.

We estimate the four parameters μ , σ^2 , a_2 and a_3 using the data sets for emerging and ovipositing wasps. The joint log-likelihood function for model 3, L_3 , is

$$L_3 = \sum_y \left(-\frac{1}{2} \ln(2\pi\sigma^2) - \frac{(y_i - \mu)^2}{2\sigma^2} \right) + \sum_x \left(-\frac{1}{2} \ln\left(\frac{2\pi\sigma^2}{1-2a_3\sigma^2} \right) + a_2x_i + a_3x_i^2 + \frac{\mu^2}{2\sigma^2} + \frac{(\mu + a_2\sigma^2)^2}{4a_3\sigma^4 - 2\sigma^2} - \frac{(x_i - \mu)^2}{2\sigma^2} \right). \quad \text{eqn A4}$$

The log-likelihood function for model 2 is obtained by setting $a_3 = 0$.

Maximum likelihood estimates for each parameter are obtained in the normal way by differentiating the log-likelihood with respect to the parameter and setting the result equal to zero. We have made no attempt to correct for bias (see Manly 1985) as we are dealing with sample sizes in excess of 100. The matrix of second derivatives is the information matrix from which the variance-covariance matrix can be constructed and hence the standard errors obtained. Under model 3, μ and σ^2 are just the mean and variance of the distribution of y_i . The estimate of a_2 is

$$\frac{\bar{x}}{s^2} - \frac{\mu}{\sigma^2}$$

with standard error

$$\sqrt{\frac{2\bar{x}^2 + s^2}{n_e s^4} + \frac{2\mu^2 + \sigma^2}{n_e \sigma^4}}$$

where \bar{x} and s^2 are the mean and variance of the wasps collected on the oviposition site. The estimate of a_3 is

$$\frac{1}{2} \left(\frac{1}{\sigma^2} - \frac{1}{s^2} \right)$$

with standard error

$$\sqrt{\frac{1}{2n_e \sigma^4} + \frac{1}{2n_e s^4}}$$

For model 2, we can use both the data sets to obtain an estimate of the variance,

$$\sigma^2 = \frac{1}{(n_e + n_c)} \left(\sum_y (y_i - \mu)^2 + \sum_x (x_i - \bar{x})^2 \right).$$

We seek only an estimate of the one parameter

$$a_2 = \frac{\bar{x} - \mu}{\sigma^2}$$

with standard error

$$\sqrt{\frac{1}{n_e n_c \sigma^2} \frac{(n_c + n_e)^2 - 2n_c (\mu - \bar{x})^2 / \sigma^2}{(n_c + n_e) - 2n_c (\mu - \bar{x})^2 / \sigma^2}}$$

(the slightly more complex form of the standard error results

from both distributions being used to estimate a common variance).

A measure of the significance of moving from model 1 to 2 (i.e. adding an exponential linear term) and from model 2 to 3 (adding an exponential quadratic term) can be obtained by constructing the likelihood ratio statistics,

$$\Lambda_1 = -2(L_1 - L_2) = \frac{n_c (\bar{x} - \mu)^2}{\sigma^2}, \quad \text{eqn A5}$$

$$\Lambda_2 = -2(L_2 - L_3) = n_c \left(\frac{s^2 - \sigma^2}{\sigma^2} + \ln \left(\frac{\sigma^2}{s^2} \right) \right), \quad \text{eqn A6}$$

both of which are asymptotically chi-square distributed with one degree of freedom. Note that eqn A5 approaches zero as the means of the two wasp distributions converge, and eqn A6 approaches zero as the variances of the two distributions converge.