Variable host quality, life-history invariants, and the reproductive strategy of a parasitoid wasp that produces single sex clutches

S. A. West,[a,b] K. E. Flanagan,[a] and H. C. J. Godfray[a]
[a]Natural Environment Research Council Centre for Population Biology and Department of Biology, Imperial College, Ascot, Berkshire SL5 7PY, UK, and [b]Institute of Cell, Animal and Population Biology, University of Edinburgh, EH9 3JT, UK

The parasitic wasp *Achrysocharoides zwoelferi* (Hymenoptera, Eulophidae) produces clutches consisting of only one sex. Moreover, male clutch size is invariably one while female clutches are in the range one to four. We designed field experiments to determine the effect of host quality on clutch composition. We found that solitary male and solitary female clutches were reared from the same size mines, and that larger mines tended to produce gregarious female clutches. A higher proportion of male clutches were placed in older hosts, despite their large size. Variation in body size, both between and within clutches, was measured in order to test the predictions of models that take into account the constraint that clutch size is an integer trait, something of potential importance when absolute clutch size is low. Our data supported several predictions of these models, including the trade-off-invariant rule for optimal offspring size developed by Charnov and Downhower. However, while most invertebrate clutch size models assume equal resource share among members of the same clutch, we found an increase in inequality in larger clutches. *Key words:* body size, clutch size, Hymenoptera, sex allocation, sex ratio, trade-off. *[Behav Ecol 12:577–583 (2001)]*

Clutch size and sex ratio are major components of the life history strategy of many animals and have been studied intensively, both theoretically and experimentally (Bulmer, 1994; Charnov, 1982; Stearns, 1992; West et al., 2000). Parasitoid wasps have proved to be an extremely useful model system for testing ideas in this area (Godfray, 1994). This is chiefly because the decisions made by an ovipositing female on encountering a host are intimately related to her fitness, and also because parasitoids show a wide range of clutch size and sex ratio strategies (parasitoid wasps are haplodiploid and offspring sex is determined by whether the parent fertilizes the egg or not; Godfray, 1994). While earlier studies of parasitoids tended to be laboratory based, and concerned with either clutch size or sex ratio, there has been an increasing move in recent years to study both sex ratio and clutch size simultaneously, and to work with wasps in the field (Driessen and Hemerik, 1992; West et al., 1999).

This is the third in a series of articles concerned with the reproductive strategies of wasps in the genus *Achrysocharoides* (Hymenoptera, Chalcidoidea, Eulophidae) and in particular the species *A. zwoelferi* Delucchi (West et al., 1996, 1999). We chose to work with these wasps because of their varied and unusual oviposition strategies. All species lay small clutches of eggs (1–4) in the larvae of leaf-mining Lepidoptera, but the majority of species segregate males and females in different hosts (Bryan, 1983). In many of these species, including *A. zwoelferi,* the size of male and female clutches differ with the former being invariably one while the latter is generally one, two, or three. The obligate segregation of the sexes is very unusual in parasitoid wasps (and other animals). We do not understand why the sexes are segregated in many *Achrysocharoides* species, or why in species such as *A. zwoelferi* the size of male clutches is always one (see Discussion). Consequently, our previous work has considered this phenomenon as a constraint, and focused on predicting and testing how the oviposition behavior (sex ratio and clutch size) of these species should vary depending on the extent to which a female's reproductive success is limited by egg availability or host availability (West et al., 1999). In this article we are concerned with how a female's oviposition behavior depends on host quality.

Host quality (especially size) has been shown to have an important effect on both clutch size and sex ratio in parasitoid wasps. In species where more than one wasp can develop per host (gregarious wasps), many studies have shown that females are able to assess host size and lay more eggs on larger hosts (reviewed in Godfray, 1994), broadly as predicted by a number of theoretical models (Charnov and Skinner, 1984, 1985; Iwasa et al., 1984; Parker and Courtney, 1984; Waage and Godfray, 1985). In solitary species, where only a single wasp develops per host, females eggs are often laid on large hosts and males on small hosts. A reason for this was suggested by Charnov et al. (1981) who noted that larger hosts led to larger parasitoids and argued that females would gain more by being large than males. Other more complicated interactions between host size, clutch size, and sex ratio occur in situations where the optimal clutch size depends on the sex ratio and vice versa (Williams, 1979). In particular, differences in competitiveness between the sexes can favor biased sex ratios (Godfray, 1986), and might even lead to the evolution of segregated clutches as occurs in many *Achrysocharoides* species (Pickering, 1980; Rosenheim, 1993). Our first aim in this article is to investigate the relationship between clutch composition and host quality (size and age) using field manipulation experiments with *A. zwoelferi*.

Most optimal clutch size models treat clutch size as a continuous variable, even though only an integer number of eggs are laid. Where a fractional number of eggs are predicted,

most workers assume that natural selection will favor the nearest integer clutch size. Recently, several workers have examined models that explicitly deal with the complications that arise when a parent divides up a certain amount of resources between a small, integer, clutch of offspring (Charnov, 1997; Charnov and Downhower, 1995; Charnov et al., 1995; Downhower and Charnov, 1998; Ebert, 1994). Specifically, Charnov et al. (1995; Charnov and Downhower, 1995) have argued that if offspring size (I) is a function of the amount of resources each individual receives, then the ratio of the range of offspring sizes found for clutches of i and j offspring ($j = i - 1$) is the reciprocal of the ratio of clutch sizes. In symbols:

$$\frac{I_{\max i} - I_{\min i}}{I_{\max j} - I_{\min j}} = \frac{C_j}{C_i} \tag{1}$$

where $I_{\max i}$ and $I_{\min i}$ are the maximum and minimum size of offspring in clutches of i young. Note that this rule is only expected to hold for $j \geq 2$, because $I_{\min 1}$ depends on the minimum size of viable offspring. Equivalently, the range in sizes of offspring is proportional to the inverse of clutch size. The accuracy of this invariant rule depends on a linear relationship between resources allocated to offspring and the particular measure of offspring used (I); an equal division of resources among offspring, and the precise form of the function $S(I)$ relating offspring size to fitness. Charnov and Downhower (1995) demonstrated the widespread applicability of Equation 1 by showing that Equation 1 was true or nearly true for a wide range of functions, $S(I)$, used in the life history theory literature. We return to the reasons for, and general applicability of this rule in the Discussion.

Our second aim in this article is to test both the predictions and assumptions of the invariant rule of Charnov et al. (1995), using the small integer female clutches of *A. zwoelferi*. We examined whether resources were distributed equally among young by seeing if individuals from the same clutch differed more in size than randomly chosen individuals (from clutches of the same size). We carried out a direct test of Equation 1 by exploring whether the size range of adult wasps from different sized clutches was proportional to the inverse of clutch size. However, statistical estimators of ranges tend to converge only slowly with sample size, and so we also tested Equation 1 by determining if the variance of offspring size decreased with increasing clutch size. Finally, we observed how the average body size of offspring varied with increasing clutch size. While Charnov and Downhower (1995) predicted that this should remain constant, Ebert (1994) has shown that in some circumstances it can decrease.

METHODS

Study organism and site
A. zwoelferi is a small metallic 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. Females oviposit in first, second, or third instar *Phyllonorycter* larvae after first causing temporary paralysis (Bryan, 1980). The final instar parasitoid larvae kill the host in its fourth or fifth instar and pupate in the mine (Bryan, 1983). Both host and parasitoid have two generations a year with the peak wasp flight periods being June and September. At this time, females can be collected searching the leaves of *Salix* for hosts. Parasitoids overwinter as pupae in mines within fallen leaves.

Mine size and clutch composition
The aim of the first experiment was to find out whether the proportion of male and female clutches, and the size of female clutches, varied with host size. Leaf mine area is used as a surrogate for host size which cannot be measured directly. We collected mature mines of *P. salicicolella* at Silwood Park during September 1994, and placed them individually in corked glass tubes in an outside insectary. At the beginning of May 1995 we placed nine large muslin sleeves over branches of individual *S. cinerea* trees at Silwood Park. These sleeves prevent access by both moths and parasitoids. We placed 10 individual moths that had emerged from the mines collected in 1994 in each sleeve. Female moths lived for only a few days in these sleeves, and so all mines produced are approximately of the same age. After 3 weeks the mines had developed within the sleeves to a size at which they could be parasitised by females of *A. zwoelferi*. At this point we removed all the muslin sleeves simultaneously, labeling and measuring the size (length × width, measured in mm²) of each mine. The sleeves were replaced after 1 week to prevent further parasitoid attack, hence minimizing the risk of superparasitism. The sleeves were placed on different trees and are unlikely to have been visited by the same wasps. During July 1995 we picked all the mines that had completed development in the sleeves and stored them in an outside insectary. The wasps and moths emerged from these collections during August and September 1995, whereupon we recorded the number and sex of any emerging *A. zwoelferi*.

Mine age and clutch composition
The aim of the second experiment was to find out whether the proportion of male and female clutches, and the size of female clutches, varied with host age. During May 1994 we located very small *P. salicicolella* mines, a few days old, on *S. cinerea* trees at Silwood Park. We labeled these mines and allocated them at random to one of three treatments (total sample size = 300 mines). In the first treatment we left mines uncovered and exposed to parasitism for the first week after they were discovered and subsequently enclosed them in a small muslin envelope which prevented the entry of parasitoids. We refer to these mines as young at the time of parasitism. In the second treatment we enclosed the mines for the first and third weeks, and left them uncovered for the second week to produce mines of medium age at the time of oviposition. Similarly, in the third treatment we enclosed mines for 2 weeks and then left them uncovered for the third week of the experiment to produce old mines at the time of oviposition. Mines were added to the three treatments over a period of 30 days and consequently the day the mines were exposed to parasitism (with 5 May defined as day 0) was included in the analysis. After the third week all mines were left covered until the larvae pupated, at which time the leaves were picked and placed in corked glass tubes, and reared in an outside insectary. We recorded the number and sex of any emerging *A. zwoelferi*.

Tests of the Charnov and Downhower invariant rule
We obtained data on the size range of *A. zwoelferi* developing in different sized clutches from two sources: naturally occurring clutches recorded in our previous study examining the relationship between fitness and body size (West et al., 1996); and clutches collected to provide the moths used in Experiment I (above). In both cases we used hind tibia length as a measure of individual size (measured in mm). The cube of hind tibia length (hereafter just called body size) was used in all analyses as a measure of wasp volume.
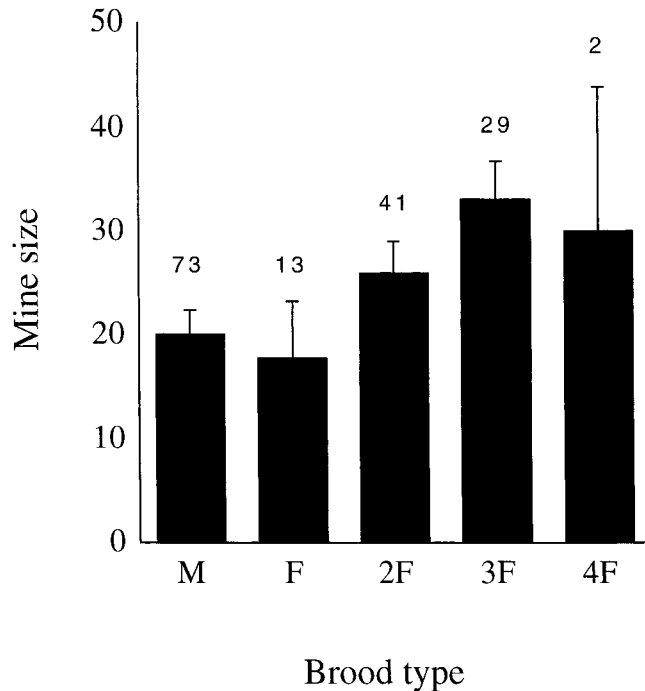
Figure 1
The average size of leaf mines (mm³) for the different types of
clutches. Shown are clutches containing a single male (M), a single
female (F), two females (2F), three females (3F) and four females
(4F). The error bars are standard errors, and the numbers above
each bar show the number of clutches of that type measured.

Statistical analyses
We analyzed the data using generalized linear modeling tech-
niques (Crawley, 1993; McCullagh and Nelder, 1983) which
are implemented in the GLIM statistical package. The sex of
the clutch was treated as a binary variable and analyzed using
a logit link function. Terms were removed from the full model
by stepwise deletion (Crawley, 1993), and whether the removal
of a term caused a significant increase in deviance was as-
sessed with a χ^2 test. We analyzed the data on body size assum-
ing normally distributed errors, checking this assumption by
standard tests on the residuals, and testing for significance
with F tests. Where the appropriate replicate was the clutch
developing in a single mine, we analyzed the average size of
an individual in order to avoid pseudoreplication (Hurlbert,
1984).

To test whether resources are allocated equally among off-
spring, we calculated the average within-clutch variance for
clutches of size two (the sample size for clutches of size three

is too small for analysis). We then created a new data set of
exactly the same size by randomly allocating individuals to
clutches, and again calculated the average within-clutch vari-
ances. We repeated this randomization procedure 1000 times
and asked whether our observed within-clutch variance was
significantly different from that expected by chance.

We tested Charnov and Downhower's (1995) invariant rule
using data on the mean body size of females for clutches of
size one ($n = 67$), two ($n = 60$), and three ($n = 35$). This
enabled us to test Equation 1 for $\{i,j\} = \{2,1\}$ and $\{3,2\}$. We
estimated confidence intervals for $(I_{\max\ i} - I_{\min\ i})/(I_{\max\ j} -
I_{\min\ j})$ by the bootstrap with 1000 resamples. A problem with
using range as a statistic is that the sample range converges
slowly from below on the true range with increasing sample
size. To control for this in calculating the ratio in Equation 1,
we used the same sample size in both the denominator and
numerator (i.e., the smallest sample size of the two, $n = 60$
for $\{i,j\} = \{2,1\}$, and $n = 35$ for $\{i,j\} = \{3,2\}$). By this means we
obtained estimates of the mean and 95% confidence intervals
of the Charnov and Downhower ratio.

RESULTS

Mine size and clutch composition
The 158 clutches of wasps that we reared in this experiment
were of five different types: single male clutches, and female
clutches containing clutches of one to four females. The num-
bers of each, and the average size of the mine at the time of
oviposition, are shown in Figure 1. In analyses of the effect of
mine size on clutch composition, we first controlled for dif-
ferences in clutch size across the different experimental units
(sleeve effects). We also tested the interaction terms between
mine size and sleeve, but as none even approached signifi-
cance they are not reported further below.

Male clutches were recorded from smaller mines than fe-
male clutches ($\chi^2_{(1)} = 7.41$, $p < .01$, $n = 158$) when female
clutches of all sizes were included in the analysis, and there
was also a strong sleeve effect ($\chi^2_{(8)} = 40.59$, $p < .001$). How-
ever, as Figure 1 suggests, there was no difference in the size
of mines that gave rise to solitary male and solitary female
clutches ($\chi^2_{(1)} = 0.007$, $p > .1$, $n = 86$; controlling for a sig-
nificant sleeve effect, $\chi^2_{(7)} = 18.22$, $p < .05$) and hence the
difference between the sexes is due to female clutches con-
taining more than one wasp. Considering only female clutch-
es, larger clutches were produced on bigger mines ($F_{(1,83)} =
5.57$, $p < .05$, $r^2 = .06$; sleeve effect not significant, $F_{(7,76)} =
0.43$, $p > .05$) though the regression explained only a rela-
tively small fraction of the variation.

The average size of individuals emerging from different
clutch types are shown in Table 1. Females were larger than
males ($F_{(1,109)} = 9.41$, $p < .01$) but neither male nor female

Table 1

**The mean and variance between clutches in body size of individuals emerging from different clutch
types**

Clutch type	West et al. (1996)			Experiment I		
	n	Mean	Variance	n	Mean	Variance
Male				52	0.0325	0.0027
Female (1)	59	0.0394	0.0090	8	0.0433	0.0011
Female (2)	36	0.0373	0.0032	24	0.0405	0.0025
Female (3)	10	0.0335	0.0002	25	0.0335	0.0006
Female (4)	1	0.0244		2	0.0272	0.0001

Body size was measured by hind tibia length cubed (mm³). The number in parentheses in the first
column is the clutch size of female clutches.

Table 2
Effect of mine age and oviposition date on the sex of a clutch laid

			Male clutches		Female clutches	
Mine age	Proportion male clutches	n	Mean (SE) oviposition date	n		Mean (SE) oviposition date
Young	0.67	10	11.9 (1.0)	5		12.0 (0.6)
Medium	0.50	7	19.3 (0.9)	7		13.29 (1.4)
Old	0.91	10	25.5 (1.5)	1		24.0 (—)

For oviposition date, day 0 represents 5 May 1995.

size was influenced by mine size ($F_{(1,49)}$ = 2.62 and $F_{(1,46)}$ = 0.26, respectively). The effect of clutch size on body size was significant in females ($F_{(1,47)}$ = 12.88, p < .01; a factor we controlled for in the analysis above). Sleeve effects were significant for females but not males ($F_{(6,47)}$ = 29.51, p < .01 and $F_{(6,44)}$ = 0.26, respectively).

Mine age and clutch composition
Of the 300 small mines included in this experiment, parasitoids emerged from 40 (13%), a fraction that did not differ significantly among treatments ($\chi^2_{(2)}$ = 0.77, NS). Table 2 shows the proportion of male clutches found in mines parasitized when young, medium-aged, or old. In a statistical analysis using treatment and oviposition date as explanatory variables, a significant interaction term was found ($\chi^2_{(2)}$ = 6.56, p < .05). Inspection of the data and step-wise deletion to obtain a minimum adequate model showed that there was a significant bias towards male clutches in the young and old mines, both absolutely ($\chi^2_{(1)}$ = 7.95, p < .005, Table 2) and relative to the medium-aged mines ($\chi^2_{(1)}$ = 8.40, p < .005, Table 2); and that oviposition date was only important for the medium-aged mines where later clutches were significantly more likely to be male ($\chi^2_{(1)}$ = 11.32, p < .001, Table 2).
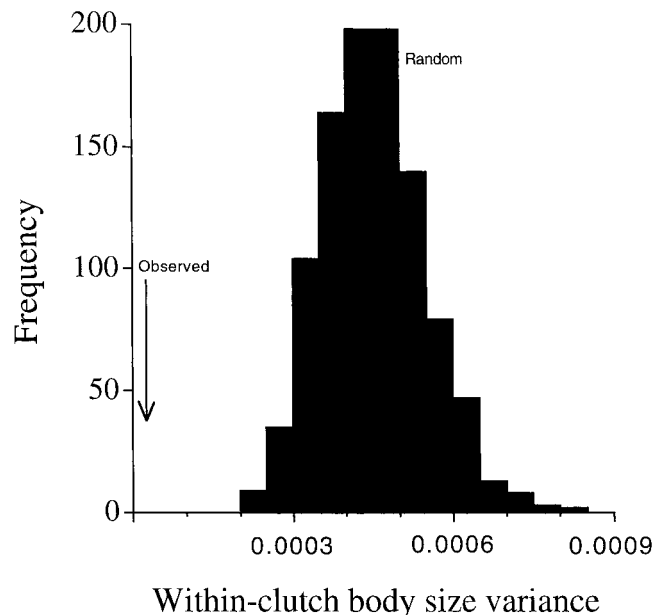

Figure 2
Randomization test, for clutches containing two females, comparing the observed within-clutch variance in body size (arrow) with that in which individuals have been randomly assigned to clutches (histogram).

Tests of the Charnov and Downhower invariant rule
Charnov and Downhower (1995) assume that resources are equally divided among individuals within a clutch. If this is true then the within-clutch variance in body size will be small, and much lower than the overall variance in body size. Our randomization procedure in which individuals were allocated at random to clutches (within clutch size classes) allows the relative magnitude of the two variance components to be assessed. The results for a clutch size of two, using data collected by West et al. (1996), are shown in Figure 2. The average within-clutch variance in body size (with variance in a clutch of two calculated as $(x_1 - x_2)^2/4$ where x_1 and x_2 are the two sizes) was 3.7×10^{-5} (95% confidence limits ± 1.2×10^{-5}, n = 34) which is significantly lower than the value we obtained from our resampling procedure (4.5×10^{-4}, 95% confidence limits 2.7–6.6×10^{-4}, p < .001, Figure 2). Thus the within-clutch component of variance in body size is very small compared to the overall variance in body size for individuals emerging from a clutch of size two, suggesting resources are shared relatively equally between individuals in a clutch. We then tested whether resources were shared less equally in larger clutches. The variance in body size within clutches was significantly greater in clutches from which three wasps emerged compared with those giving rise to just two insects ($F_{(1,40)}$ = 28.17, p < .01, n = 42, Figure 3), suggesting that resources were shared less equitably in larger clutches.

In order to test the invariant rule of Charnov and Downhower's (1995; Charnov et al., 1995) invariant rule (Equation 1) we examined the mean body size of females from different sized clutches and calculated $(I_{\max\ i} - I_{\min\ i})/(I_{\max\ j} - I_{\min\ j})$ with bootstrap confidence intervals. We observed ratios of 0.759 (95% C.I.: 0.601, 0.954) and 0.503 (95% C.I.: 0.358, 0.681) for $\{i,j\}$ = {2,1} and {3,2} respectively. The 95% C.I. for $\{i,j\}$ = {3,2} includes the theoretical prediction of 0.67. This pattern in ranges is also reflected by the observed variance in body sizes: both data collected by West et al. (1996; Bartlett's test, $\chi^2_{(3)}$ = 19.69, p < .001, n = 106) and the mines collected as part of experiment I (Bartlett's test, $\chi^2_{(3)}$ = 9.42, p < .025, n = 57) showed that the variance in female body size decreased significantly with clutch size (Table 1), as predicted.

Finally, we tested the prediction that mean body size is unaffected by clutch size. Both data from the mines collected by West et al. (1996) (Spearman correlation coefficient, (r^s) = .18, p < .05, n = 106) and the mines collected as part of Experiment I (r^s = .90, p < .001, n = 57) showed that female body size was negatively correlated with clutch size (Table 1). In these analyses a nonparametric test was used because the variance in body size changed significantly with clutch size (see above).

DISCUSSION

The parasitoid wasp *A. zwoelferi* lays clutches containing eggs of only one sex: males always develop alone in a clutch while
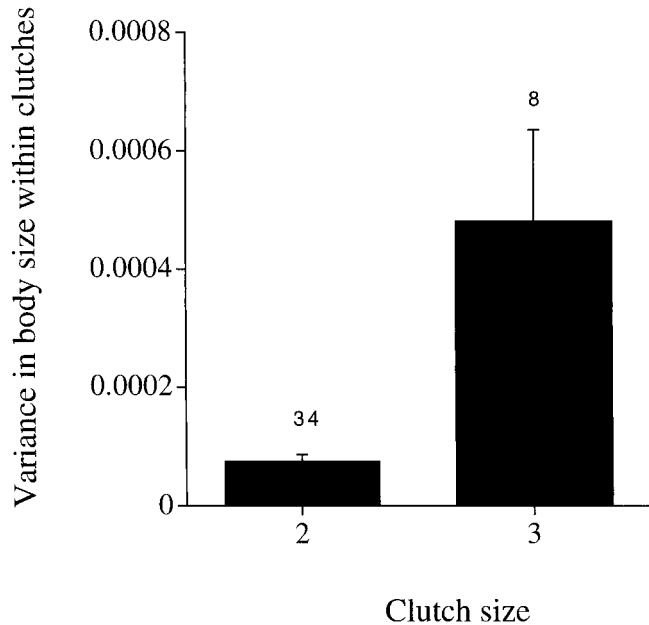
Figure 3
The within-clutch variance in body size plotted against clutch size. The error bars are standard errors, and the numbers above each bar show the number of clutches of that type measured.

female clutches consist of one to four eggs. We carried out experiments in the field to examine the influence of host quality on clutch composition. We found that a combination of host size and age influenced the wasp's oviposition strategy. In addition, we found that the variation in body size both between and within clutches supported the predictions and assumptions of a suite of clutch size models appropriate to organisms that lay only a few eggs per clutch (Charnov and Downhower, 1995; Charnov et al., 1995; Ebert, 1994).

Solitary females were laid in the same size mines as solitary males (Figure 1), but had larger body sizes. The smaller size of males is probably a reflection of their faster development time leading to less efficient use of host resources (Bryan, 1983). The observation that females were laid in the same size hosts as males contrasts with a large number of previous studies where females were laid in larger hosts (though in species where both sexes are solitary; Godfray, 1994), presumably because they gain a larger fitness benefit from increased body size (Charnov et al., 1981). We have not been able to test this assumption in *A. zwoelferi* because although we have previously estimated the relationship between fitness and size for females in the field (West et al., 1996), we do not know where mating takes place, and so have been unable to estimate this relationship for males.

The positive correlation between the clutch size of female clutches and mine size is predicted by clutch size theory if larger mines provide more resources for developing parasitoid larvae (Godfray, 1987). This has been shown to be the case for numerous parasitoid species, including several koinobiont species, like *A. zwoelferi,* where the host continues to grow after oviposition (Godfray, 1994; King, 1989). Body size was not influenced by mine size, but in gregarious species where the main effect of varying host size is to change the number of eggs laid by the parent, the residual effect of host size on parasitoid size can be hard to predict (Godfray, 1994).

In the mine age experiment we found that a greater proportion of females, and therefore of larger clutches, were laid in medium-aged mines. A possible explanation for this is that medium-aged mines represent the best quality host for devel-

oping larvae. The age of a host can affect its quality through its potential to grow and support parasitoid growth (Kouame and Mackauer, 1991). For example, parasitizing a young mine may cause it to die early and hence yield less resources for larvae, while older mines may contain more differentiated morphological structures which are harder for larvae to metabolize (Strand, 1986). Detailed studies are required to examine how parasitoid mortality and growth rates vary with mine age; such studies would be extremely hard to carry out on a species such as *A. zwoelferi* which so far has not successfully been brought into laboratory culture.

The results of the mine size and mine age experiments have implications for the interpretation of our previous work examining how the reproductive strategy of a female should depend on the extent to which she is egg- or host-limited (West et al., 1999). Purely host-limited females are predicted to produce the clutch size that maximizes the fitness return per clutch (termed the Lack clutch size; Charnov and Skinner, 1984, 1985), and smaller clutch sizes are predicted as females become more egg-limited. However, clutch sizes above the Lack value were occasionally observed in the field (about 5% of the time). The Lack clutch size (three) we predicted was based on a host of average size. The results of this study suggest that the female wasp modulates clutch size in response to host size, and so clutches of four or even higher might be laid on exceptionally large hosts.

Numerous models for the evolution of clutch size, especially in invertebrates, assume that resources are shared equally between the members of a clutch. We found some support for this in clutches of size two, where individuals were more similar in body size to other members of the same clutch than expected by chance (Figure 2; see Charnov et al., 1995, for a similar result in a fish). However, resources were shared less equally in larger clutches (Figure 3), a pattern that was also found in a study on another parasitoid wasp, *Laelius pedatus* Say (Hymenoptera: Bethylidae), by Mayhew (1997). Increased variability has a complex effect on optimal clutch size, chiefly determined by the manner in which fitness declines on either side of the optimum (Godfray and Ives, 1988). If the total fitness costs for laying a clutch size larger than the optimum are less than the costs of laying a smaller than optimal clutch, increased variation selects for higher clutch size and vice versa. For *A. zwoelferi* (and the other species of wasp whose fitness has been measured in the field), the penalties for the individual of being slightly smaller than the optimum are greater than the advantages of being slightly bigger (West et al., 1996), suggesting that increased variability may select for lower clutch sizes, though this effect is not likely to be big.

Our results largely support Charnov and Downhower's (1995; Charnov et al., 1995) invariant rule. We found that the variance in body size between clutches decreased significantly with clutch size (Table 1; see also Mayhew, 1997). Furthermore, our estimate of the $(I_{\max i} - I_{\min i})/(I_{\max j} - I_{\min j})$ ratio for $\{i,j\} = \{2,3\}$ was not significantly different from Charnov and Downhower's (1995) theoretical prediction of 0.67. In contrast, Mayhew (1998), also working with parasitoid wasps, found that the range of body sizes did not decrease as predicted by this invariant rule. One important difference between the two studies is that we examined a species that produces single sex clutches while the species studied by Mayhew (1998) had mixed sex clutches where there may be different levels of optimum investment in sons and daughters. Other possible factors that might contribute to the failure of the invariant rule include: (1) the assumption that females are host-limited—field studies on parasitoids suggest partial egg and host limitation to be most common (Casas et al., 2000; Driessen and Hemerik, 1992; Ellers et al., 1998; West and Rivero, 2000; West et al., 1999); (2) parent-offspring conflict over

clutch size, and (3) inequality of resource share that changes with clutch size (this study and Mayhew, 1997).

Why exactly does the invariant rule (Charnov and Downhower, 1995; Charnov et al., 1995) work? In their original paper they justify the rule by the observation that it works remarkably well for a range of possible functions, $S(I)$, relating offspring size to fitness. We provide an intuitive argument for the invariant rule using a ''rule of thumb'' approach, and then show why this rule of thumb can be justified theoretically. Let total parental resources be R so that investment per offspring in a clutch of i eggs is $I = R/i$. The optimum investment per offspring is given implicitly by $I^* = S(I^*)/S'(I^*)$ where the prime denotes a derivative (Smith and Fretwell, 1974). But what happens when R/i is not an integer? A rule of thumb might be that as resources accumulate keep the current clutch size and share the extra resources amongst your i offspring until you have $I^*/2$ extra resources and then add another offspring, the deficit this time being shared by $i + 1$ offspring (see also Ricklefs, 1968). This means that $I_{\min i} = I^* - I^*/2i$ and $I_{\max i} = I^* + I^*/2i$ (and similarly $I_{\min j}$ and so on) and the Charnov and Downhower (1995) rule follows immediately. In fact, the rule follows if the switch point occurs for any constant fraction of I^*, as this means that the resource spectrum, R, can be divided into intervals of equal length in which clutch sizes of 2, 3 . . . i, and so on, are produced and, as Charnov and Downhower (1995) note, this automatically leads to the rule.

But can this rule of thumb be justified? The precise point at which the mother should switch from i to $i+1$ offspring depends on $S(I)$. In the appendix we show that if we approximate this function by a second order Taylor expansion the switch point is not at 0.5 (expressed in units of I^*) but at $\sqrt{i(1 + i)} - i$. Clearly this is not equal to 0.5 and independent of clutch size, as required for the invariant rule, but it is very close: the switch point between 2 and 3 is at 0.45 and the expression quickly asymptotes to 0.5 as i increases. Moreover, if the $I_{\min I}$, and so on, terms are calculated using these switch points then the Charnov and Downhower (1995) rule becomes $(j/i)C$ where C is a complicated (dimensionless) function of i that is smaller than, but very near, 1. For $\{i,j\} = \{3,2\}$ (the worst case), $C = 0.98$. Thus, to second order, an optimality argument predicts that the Charnov and Downhower (1995) rule should never be more than about 2% in error.

To conclude, this article extends our knowledge of *A. zwoelferi,* a species that is of more than entomological interest because of its unusual habit of segregating its offspring in single sex clutches, with solitary male and gregarious female clutches. In previous papers we have shown that female fitness increases with body size in the field, that the majority (>95%) of clutches are equal to or less than the most productive clutch size, and that if the wasp is host limited a simple Fisherian argument predicting equal allocation of limiting resources to male and female function predicts a female biased sex ratio (West et al., 1996, 1999). Here we have found that host quality also influences clutch composition, and have examined the consequences of the wasp being constrained to produce a small, integer number of eggs per clutch. However, all this work has been based on the assumption that *A. zwoelferi* is constrained to produce segregated clutches, with solitary males, and has not attempted to explain it. We see this as the next challenge, and are currently addressing this problem by constructing a molecular based phylogeny which will allow us to map the evolution of reproductive strategies within *Achrysocharoides* and related genera.

APPENDIX

Calculation of optimum switch point

Without loss of generality, measure resources in units such that the optimum allocation to offspring is 1. Where total resources (R) are non-integer, $I < R < I + 1$ where i is an integer, the question is whether to lay a clutch of i or $i+1$ offspring. Let $R = i + \Delta_i$ where $0 < \Delta_i < 1$; the question can be rephrased as whether the extra resources should be divided such that all offspring receive an extra Δ_i/i resources, or if one more offspring should be laid so that everyone receives $(1 - \Delta_i)/(I + 1)$ less resources than the optimum. If fitness as a function of resource share is denoted by the function $S(.)$, then at the switch point the fitness of the two strategies should be the same:

$$iS\left(1 + \frac{\Delta_i}{i}\right) = (i + 1)S\left(1 - \frac{1 - \Delta_i}{i + 1}\right)$$

Taylor expanding the function S about 1 and denoting the first and second derivatives of the function at 1 as S' and S'', we obtain after some simplification, the second order approximation:

$$0 = S - S' + \frac{S''}{2}(i - 2\Delta_i i - \Delta_i^2).$$

Now $S/S'' = 1$ (the definition of the optimum) and hence $S - S'' = 0$. Thus dividing by $S'''/2$ we obtain:

$$i - 2\Delta_i i - \Delta_i^2 = 0.$$

Note that as i becomes very large the last term can be ignored and $\Delta_\infty \to 0$. Solving explicitly for Δ_i we obtain:

$$\Delta_i = -i + \sqrt{i(1 + i)}.$$

According to Charnov and Downhower, the range in sizes (or resource share) of offspring in a clutch size of i divided by that in a clutch of $i-1$ is simply $(i-1)/i$ (Equation 1). This ratio now becomes

$$\frac{i - 1}{i} \frac{1 + (\Delta_i - \Delta_{i-1})}{1 + (\Delta_{i-1} - \Delta_{i-2})} = \frac{i - 1}{i}C.$$

C describes the deviation of the second order optimal switch point from the Charnov and Downhower rule. The greatest deviation is found for the comparison of clutches of size 2 and 3 where $C = 0.98$, but as clutch size increases C approaches 1. Thus the Charnov and Downhower rule is nearly always met for reasonably smooth functions.

REFERENCES

Bryan G, 1980. Courtship behaviour, size differences between the sexes and oviposition in some *Achrysocharoides* species (Hymenoptera, Eulophidae). Netherlands J Zool 30:611–621.

Bryan G, 1983. Seasonal biological variation in some leaf-miner parasites in the genus *Achrysocharoides* (Hymenoptera, Eulophidae). Ecol Entomol 8:259–270.

Bulmer M, 1994. Theoretical evolutionary ecology. Sunderland, Massachusetts: Sinauer Associates.

Casas J, Nisbet RM, Swarbrick S, Murdoch WM, 2000. Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. J Anim Ecol 69:185–193.

Charnov EL, 1982. The theory of sex allocation. Princeton, New Jersey: Princeton University Press.

Charnov EL, 1997. Trade-off-invariant rules for evolutionarily stable life histories. Nature 387:393–394.

Charnov EL, Downhower JF, 1995. A trade-off-invariant life-history rule for optimal offspring size. Nature 376:418–419.

Charnov EL, Downhower JF, Brown LP, 1995. Optimal offspring sizes in small litters. Evol Ecol 9:57–63.

Charnov EL, Los-den Hartogh RL, Jones WT, van den Assem J, 1981. Sex ratio evolution in a variable environment. Nature 289:27–33.

Charnov EL, Skinner SW, 1984. Evolution of host selection and clutch size in parasitoid wasps. Fla Entomol 67:5–21.

Charnov EL, Skinner SW, 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. Environ Entomol 14:383–391.

Crawley M, 1993. GLIM for ecologists. Oxford: Blackwell Scientific.

Downhower JF, Charnov EL, 1998. A resource range invariance rule for optimal offspring size predicts patterns of variability in parental genotypes. Proc Natl Acad Sci USA 95:6208–6211.

Driessen G, Hemerik L, 1992. The time and egg budget of *Leptopilina clavipes,* a parasitoid of larval *Drosophila.* Ecol Entomol 17:17–27.

Ebert D, 1994. Fractional resource allocation into few eggs: *Daphnia* as an example. Ecology 75:568–571.

Ellers J, van Alphen JJM, Sevenster JG, 1998. A field study of size-fitness relationships in the parasitoid *Asobara tabida.* J Anim Ecol 67:318–324.

Godfray HCJ, 1986. Models for clutch size and sex ratio with sibling interactions. Theor Pop Biol 30:215–231.

Godfray HCJ, 1987. The evolution of clutch size in invertebrates. Oxf Surv Evol Biol 4:117–154.

Godfray HCJ, 1994. Parasitoids. Behavioural and Evolutionary Ecology. Princeton, New Jersey: Princeton University Press.

Godfray HCJ, Ives AR, 1988. Stochasticity in invertebrate clutch-size models. Theor Pop Biol 33:79–101.

Hurlbert SH, 1984. Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211.

Iwasa Y, Suzuki Y, Matsuda H, 1984. Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. Theor Pop Biol 26:205–227.

King BH, 1989. Host-size-dependent sex-ratios among parasitoid wasps—does host growth matter. Oecologia 78:420–426.

Kouame KL, Mackauer M, 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. Oecologia 88:197–203.

Mayhew PJ, 1998. Offspring size-number strategy in the bethylid parasitoid *Laelius pedatus.* Behav Ecol 9:54–59.

McCullagh P, Nelder JA, 1983. Generalized linear models. London: Chapman and Hall.

Parker GA, Courtney SP, 1984. Models of clutch size in insect oviposition. Theor Pop Biol 26:27–48.

Pickering J, 1980. Larval competition and clutch sex ratios in the gregarious parasitoid *Pachysomoides stupidus.* Nature 283:291–292.

Ricklefs RE, 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. Proc Natl Acad Sci USA 61:847–851.

Rosenheim JA, 1993. Single-sex clutches and the evolution of nonsiblicidal parasitoid wasps. Am Nat 141:90–104.

Smith CC, Fretwell SD, 1974. The optimal balance between size and number of offspring. Am Nat 108:499–506.

Stearns SC, 1992. Evolution of life histories. Oxford: Oxford University Press.

Strand MR, 1986. The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. In: Insect parasitoids (Waage JK, Greathead D, eds). London: Academic Press; 97–136.

Waage JK, Godfray HCJ, 1985. Reproductive strategies and population ecology of insect parasitoids. In: Behavioural ecology: ecological consequences of adaptive behaviour (Sibley RM, Smith RH, eds). Oxford: Blackwell Scientific Publications; 449–470.

West SA, Flanagan KE, Godfray HCJ, 1996. The relationship between parasitoid size and fitness in the field, a study of *Achrysocharoides zwoelferi* (Hymenoptera, Eulophidae). J Anim Ecol 65:631–639.

West SA, Flanagan KE, Godfray HCJ, 1999. Sex allocation and clutch size in parasitoid wasps that produce single sex clutches. Anim Behav 57:265–275.

West SA, Herre EA, Sheldon BC, 2000. The benefits of allocating sex. Science 290:288–290.

West SA, Rivero A, 2000. Using sex ratios to estimate what limits reproduction in parasitoids. Ecol Lett 3:294–299.

Williams GC, 1979. The question of adaptive variation in sex ratio in out-crossed vertebrates. Proc R Soc Lond B 205:567–580.