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

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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. zwelferi 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. zwelferi, 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. zwelferi 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. zwelferi.

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:

\[
\frac{I_{\text{max}, i} - I_{\text{min}, i}}{I_{\text{max}, j} - I_{\text{min}, j}} = \frac{C_j}{C_i}
\]

where \( I_{\text{max}, i} \) and \( I_{\text{min}, i} \) 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 \( I_{\text{min}, i} \) 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 differed more in size than randomly chosen individuals (from clutches of the same size). We obtained data on the size range of \( A. zwoelferi \). We then placed the wasps and parasitoids in a small muslin envelope which prevented the entry of parasites. 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 larvae were picked and placed in corkscrew glass tubes, and reared in an outside insectary. We recorded the number and sex of any emerging \( A. zwoelferi \).

**Mine size 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 size. Leaf mine area is used as a surrogate for host size which cannot be measured directly. We collected mature mines of \( P. salicicola \) at Silwood Park during September 1994, and placed them individually in corkscrew glass tubes in an outdoor 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 \( \times \) width, measured in mm\(^2\)) 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 \( A. zwoelferi \).

**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, Gracillaridae) that mine the leaves of \( Salix \) spp. In our study site at Silwood Park (Berkshire, UK), the wasp is the commonest parasitoid attacking \( Phyllonorycter salicicola \) (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.

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**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 1 (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.
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.

Because the clutch sizes were not normally distributed in the data (Shapiro-Wilk test, p < .05), we applied 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 assessed with a \( \chi^2 \) test. We analyzed the data on body size assuming 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 (F), the error bars are standard errors, and the numbers above each bar show the number of clutches of that type measured.

**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 numbers 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 differences 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 significance they are not reported further below.

Male clutches were recorded from smaller mines than female clutches (\( \chi^2 = 7.41, p < .01, n = 158 \)) when female clutches of all sizes were included in the analysis, and there was also a strong sleeve effect (\( \chi^2 = 40.59, p < .001 \)). However, as Figure 1 suggests, there was no difference in the size of mines that gave rise to solitary male and solitary female clutches (\( \chi^2 = 0.007, p > .1, n = 86 \)); controlling for a significant sleeve effect, \( \chi^2 = 18.22, p < .05 \) and hence the difference between the sexes is due to female clutches containing more than one wasp. Considering only female clutches, larger clutches were produced on bigger mines (\( F_{1,85} = 5.57, p < .05, r^2 = .06 \); sleeve effect not significant, \( F_{7,76} = 0.43, p > .05 \)) though the regression explained only a relatively 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**

<table>
<thead>
<tr>
<th>Clutch type</th>
<th>West et al. (1996)</th>
<th>Experiment I</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( n )</td>
<td>Mean</td>
</tr>
<tr>
<td>Male</td>
<td>59</td>
<td>0.0394</td>
</tr>
<tr>
<td>Female (1)</td>
<td>36</td>
<td>0.0373</td>
</tr>
<tr>
<td>Female (2)</td>
<td>10</td>
<td>0.0335</td>
</tr>
<tr>
<td>Female (3)</td>
<td>1</td>
<td>0.0244</td>
</tr>
<tr>
<td>Female (4)</td>
<td>2</td>
<td>0.0272</td>
</tr>
</tbody>
</table>

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.
size was influenced by mine size ($F_{(1.49)} = 2.62$ and $F_{(1.40)} = 0.26$, 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).

**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 $(\bar{x} - x)^2/4$ where $x_i$ and $x_j$ are the two sizes) was $3.7 \times 10^{-5}$ (95% confidence limits $1.2 \times 10^{-5}$, $n = 34$) which is significantly lower than the value we obtained from our resampling procedure ($4.5 \times 10^{-4}$, 95% confidence limits $2.7 \sim 6.6 \times 10^{-4}$, $p < .001$, 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 ($F_{(4.40)} = 28.17$, $p < .01$, $n = 42$, 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 $(I_{max} - I_{min})/(I_{max} - I_{min})$ 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 $i = 2$ and $i = 3$ respectively. The 95% C.I. for $i = 3$ 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, $\chi^2(3) = 4.92$, $p < .025$, $n = 57$) 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 ($r^2 = .90$, $p < .001$, $n = 57$) 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. zwelferi* lays clutches containing eggs of only one sex: males always develop alone in a clutch while...
for numerous parasitoid species, including several koinobiont larvae (Godfray, 1987). This has been shown to be the case—larger mines provide more resources for developing parasitoid clutches and mine size is predicted by clutch size theory if the relationship for males. If mating takes place, and so have been unable to estimate this portion of females, and therefore of larger clutches, were laid in medium-aged mines (West et al., 1996), we do not know where females in the field (West et al., 1999); (2) parent-offspring conflict over egg 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 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 \( \frac{(I_{\text{max}} - I_{\text{min}})}{(I_{\text{max}} + I_{\text{min}})} \) 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 oviposition 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.

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 developing 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.

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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 $P_i = S(P_i)/S'(P_i)$ 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 $P_i/2$ extra resources and then add another offspring, the deficit this time being shared by $i + 1$ offspring (see also Ricklefs, 1968). This means that $L_{min} = P_i/2$ and $L_{max} = P_i + P_i/2$ (and similarly $l_{min}$ and $l_{max}$, and so on) of the Charnov and Downhower (1995) rule follows immediately. In fact, the rule follows if the switch point occurs for any constant fraction of $P_i$, 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 $P_i$) but at $\sqrt{\pi I + \sqrt{i} - i}$. 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 $L_{min}$ and so on, terms are calculated using these switch points then the Charnov and Downhower (1995) rule becomes ($\sqrt{i}/2$) where $C$ is a complicated function of $i$. The best case is $i = 3$ where $C = 0.98$. 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 more 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 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 $\Delta_i/i$ 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 $S(x)$, then at the switch point the fitness of the two strategies should be the same:

$$iS(1 + \Delta_i/i) = (i + 1)S(1 - \Delta_i/i + 1)$$

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:

$$0 = S' - S''(i - 2\Delta_i - \Delta_i^2).$$

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

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

Note that as $i$ becomes very large the last term can be ignored and $\Delta_i \rightarrow 0$. Solving explicitly for $\Delta_i$, 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

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

$C$ 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.

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