

## REPORT

## Using sex ratios to estimate what limits reproduction in parasitoids

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### Abstract

The reproductive success of a foraging parasitoid may be limited by the number of eggs that she produces and/or the number of hosts that she can locate. Despite the significance for population dynamics and numerous areas of behavioural ecology, the relative importance of these factors remains an issue of contention. Attempts to resolve this controversy have been hindered because estimating the importance of factors limiting reproduction in the field can be extremely laborious and time consuming. We show how sex ratio data can be used as a relatively easy method to indirectly estimate the relative importance of the factors limiting reproduction. Sex ratio data from 48 samples of eight species suggest that: (a) the extent of host or egg limitation in a species varies between site collected and time of year; and (b) the majority of populations, and overall species means, are at an intermediate position on the egg/host limitation continuum, with a bias towards host limitation.

### Keywords

Clutch size, egg limitation, host limitation, sex ratio, trade-off.

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### INTRODUCTION

Some of the most qualitatively and quantitatively successful research in evolutionary ecology has come from studies of parasitoid wasps (Godfray 1994). Female wasps search the environment for hosts. Upon finding a host a female wasp must make a series of behavioural decisions such as whether to feed or oviposit upon the host, how many eggs to lay (clutch size) and what sex should the offspring be (sex allocation). The optimum strategy for each of these behaviours depends upon the degree to which a female's reproductive success is limited by the number of hosts she can locate and oviposit on (termed time or host limitation) or the number of eggs she is carrying (termed egg limitation) (reviewed by Godfray 1994).

However, despite the enormous amount of research on parasitoid oviposition behaviour, the relative importance of the factors limiting reproduction in natural populations remains unresolved and is a subject of recent controversy (Rosenheim 1996, 1999; Ellers 1998; Sevenster *et al.* 1998). Several theoretical models have been constructed in order to predict which type of limitation is most likely. These models are based on the assumption that limited resources must be divided between egg production and maintenance, resulting in a trade-off between reproduction and survival. The models predict how egg load should evolve in response to variation in the ecological conditions (host

encounter rate). This result is then used to predict the proportion of individuals that exhaust their egg supply before dying, and are therefore egg-limited. Rosenheim (1996, 1999) used this type of model to argue that reasonable levels of egg limitation are likely to occur. Sevenster, Ellers and colleagues (Ellers 1998; Sevenster *et al.* 1998) have, however, argued that the assumptions of Rosenheim's model are unrealistic, and that evolution should lead to individuals who are predominantly host limited.

Resolution of this controversy requires field data on the relative importance of the factors limiting reproduction in natural populations of a range of species. However, directly estimating the importance of factors limiting reproduction in the field can be extremely laborious and time consuming, and so there is currently only detailed data on single samples of three species (Driessen & Hemerik 1992; Ellers *et al.* 1998; Casas *et al.*, in press). Consequently, there is a need for indirect methods that will facilitate the study of more species, and multiple estimates from the same species.

In certain parasitoid species the optimal sex ratio depends upon the factors limiting reproduction (Godfray 1994; Hunter & Godfray 1995; Rosenheim *et al.* 1996; West *et al.* 1999). Consequently, several authors have used sex ratios to make comments on the factors that are likely to be limiting reproductive success (e.g. Godfray & Hunter 1992; Hunter 1993; Godfray 1994; Hunter &

Godfray 1995; Heimpel *et al.* 1998; Rosenheim 1999; West *et al.* 1999). However, these comments have usually not been quantified and the different authors have drawn different conclusions from the same data. In this paper we: (a) show how sex allocation data can be used as a relatively quick and easy indirect method to provide estimates of the relative importance of the factors limiting reproduction, and (b) use data from 48 samples of eight parasitoid species to see if any tentative generalizations can be made.

## USING SEX RATIOS

Several theoretical models have been developed which predict that the optimal oviposition strategy (e.g. host choice, clutch size, sex ratio) depends upon a single dimensionless combination of ecological and physiological parameters (e.g. Hunter & Godfray 1995; West *et al.* 1999). This single dimensionless parameter ( $\phi$ ) summarizes where a female lays along the continuum between pure egg limitation ( $\phi \rightarrow 0$ ) and pure host limitation ( $\phi \rightarrow \infty$ ). For proovigenic wasps that are born with their full complement of eggs,  $\phi = \mu x / \lambda$ , and for synovigenic wasps that mature eggs through their lifetime,  $\phi = y / \lambda$ . The parameters  $\mu$ ,  $x$ ,  $\lambda$  and  $y$  represent the mortality rate, the number of eggs that a proovigenic wasp is born with, the host encounter rate and the maximum number of eggs that a synovigenic wasp can mature and lay per unit time. An index can be constructed,  $\Phi = \phi / (1 + \phi)$ , that maps the egg/host limitation continuum onto the unit interval: a value of zero indicates extreme egg limitation, while a value of one indicates extreme host limitation.

## Autoparasitoids

In some parasitoid species, termed autoparasitoids or heteronomous hyperparasitoids, females develop as primary parasitoids of a homopteran, whilst males develop as secondary parasitoids of their own or another species. For both sexes only a single wasp develops in a host. In these species the optimal sex ratio is predicted to depend upon (a) the relative encounter rate with hosts suitable for the development of male and female offspring, and (b) the extent to which they are egg- or host-limited (Godfray & Waage 1990; Godfray & Hunter 1992; Hunter & Godfray 1995). Applying Fisher's (1930) principle of equal investment in the sexes, purely egg-limited females should lay an equal number of male and female eggs, and hence have a sex ratio of 0.5. However, if females are purely host-limited they should oviposit on all host encountered, and so the sex ratio will reflect the availability of hosts suitable for males and females.

The index of host limitation can be inferred from sex ratio data as follows. Hunter & Godfray (1995) considered

the case of when a proportion  $m$  of broods are secondary hosts suitable for male development, and the remainder are primary hosts suitable for female development. A single egg is laid in a proportion  $s$  of the secondary hosts, and a proportion  $p$  of the primary hosts. Consider a synovigenic species where the index of host limitation equals the maximum number of eggs that can be laid per unit time divided by the host encounter rate ( $\phi = y / \lambda$ ). If primary hosts are most common then  $s = 1$ , and by differentiating the relevant fitness function it can be shown that the ESS is  $p = (\phi + m) / (1 - m)$  (Hunter & Godfray 1995). From this the equation for the optimal sex ratio ( $r^*$ ) can be rearranged to give the index of host limitation in terms of the sex ratio ( $r$ ) and proportion of secondary hosts ( $m$ ),

$$\phi = \frac{m}{r} - 2m. \quad (1)$$

Note that this equation is constrained by the fact that the proportion of primary hosts parasitized must be less than or equal to one ( $p \leq 1$ ), and so the sex ratio must be greater than or equal to the proportion of secondary hosts ( $0.5 \geq r \geq m$ ). If secondary hosts are more common then  $P = 1$ ,  $s = \phi / m + (1 - m) / m$  (Hunter & Godfray 1995), and a similar equation can be obtained for the index of host limitation,

$$\phi = \frac{(m - 1)(2r - 1)}{r - 1}. \quad (2)$$

Field data on autoparasitoid sex ratios have been collected for 30 samples of two species, *Coccophagus atratus* and *Encarsia pergandiella*, both of which are synovigenic (Donaldson & Walter 1991b; Hunter 1993). Our estimates of the host limitation index ( $\phi$ ) from these data are presented in Table 1. In both cases the sex ratios suggest that the extent of host- or egg-limitation varies between site collected and time of the season. In some samples the sex ratios are consistent with pure egg-limitation, whilst in others they are consistent with pure host-limitation. Overall, the data suggest an intermediate position on the egg/host limitation continuum, with a bias towards host limitation.

## Single sex broods

In some parasitoid species females produce single-sex broods containing only males or females. In this case the optimal sex ratio depends upon (a) the relative size of male and female broods, and (b) the extent to which reproductive success is limited by hosts or eggs (Godfray 1994; West *et al.* 1999). Fisher's (1930) principle states that equal investment should be made in the two sexes. If the only factor limiting reproduction is finding hosts (pure host-limitation) then females should invest equal numbers

**Table 1** Estimates of the host limitation index from autoparasitoid sex ratio data. Data for *C. atratus* were obtained from Donaldson & Walter (1991b), and for *E. pergandiella* from Hunter (1993).

| Collection date                                                                  | Proportion secondary hosts ( <i>m</i> ) | Sex ratio ( <i>r</i> ) limitation | G-test on egg limitation | G-test on host limitation ( $\phi$ ) | Index of host   |
|----------------------------------------------------------------------------------|-----------------------------------------|-----------------------------------|--------------------------|--------------------------------------|-----------------|
| Parasitoid = <i>C. atratus</i> . Host plant = <i>Chrysanthemoides monilifera</i> |                                         |                                   |                          |                                      |                 |
| 15/5/84                                                                          | 0.10                                    | 0.19                              | 29.9***                  | 2.7                                  | 0.35 (0.35–1.0) |
| 29/5/84                                                                          | 0.10                                    | 0.18                              | 42.4***                  | 3.3                                  | 0.37 (0.37–1.0) |
| 13/6/84                                                                          | 0.23                                    | 0.21                              | 42.6***                  | 0.2                                  | 0.53–1.0        |
| 27/6/84                                                                          | 0.60                                    | 0.39                              | 5.1*                     | 11.4***                              | NC              |
| 11/7/84                                                                          | 0.78                                    | 0.79                              | 14.6***                  | 0.01                                 | 0.56–1.0        |
| 28/7/84                                                                          | 0.90                                    | 0.79                              | 4.9*                     | 1.36                                 | 0.30 (0.30–1.0) |
| Parasitoid = <i>C. atratus</i> . Host plant = <i>Cliffortia strobilifera</i>     |                                         |                                   |                          |                                      |                 |
| 22/6/84                                                                          | 0.70                                    | 0.12                              | 27.0***                  | 57.0***                              | NC              |
| 29/6/84                                                                          | 0.60                                    | 0.17                              | 8.7**                    | 3.4                                  | 1.0             |
| 5/7/84                                                                           | 0.19                                    | 0.20                              | 9.6**                    | 0.0                                  | 0.58 (0.58–1.0) |
| 12/7/84                                                                          | 0.30                                    | 0.38                              | 1.2                      | 0.6                                  | 0.19 (0.0–1.0)  |
| 19/7/84                                                                          | 0.30                                    | 0.50                              | 0.0                      | 5.3*                                 | 0               |
| 26/7/84                                                                          | 0.30                                    | 0.58                              | 0.5                      | 5.6*                                 | 0               |
| 2/8/84                                                                           | 0.28                                    | 0.60                              | 0.2                      | 2.2                                  | 0.0–1.0         |
| 31/8/84                                                                          | 0.10                                    | 0.10                              | 69.8***                  | 0.0                                  | 0.81 (0.81–1.0) |
| 7/9/84                                                                           | 0.12                                    | 0.11                              | 24.8***                  | 0.0                                  | 0.77–1.0        |
| 14/9/84                                                                          | 0.19                                    | 0.08                              | 30.5***                  | 3.4                                  | 0.61–1.0        |
| 21/9/84                                                                          | 0.23                                    | 0.20                              | 18.3***                  | 0.9                                  | 0.54–1.0        |
| 28/9/84                                                                          | 0.41                                    | 0.24                              | 13.2***                  | 4.9*                                 | NC              |
| 5/10/84                                                                          | 0.47                                    | 0.39                              | 3.0                      | 1.2                                  | 0.0–1.0         |
| 12/10/84                                                                         | 0.60                                    | 0.50                              | 0.0                      | 1.8                                  | 0.0–1.0         |
| 18/10/84                                                                         | 0.80                                    | 0.53                              | 0.2                      | 34.1***                              | 0.03 (0.0–0.03) |
| 26/10/84                                                                         | 0.80                                    | 0.59                              | 0.9                      | 9.2**                                | 0.08 (0.0–0.08) |
| Parasitoid = <i>E. pergandiella</i> .                                            |                                         |                                   |                          |                                      |                 |
|                                                                                  | 0.12                                    | 0.37                              |                          |                                      | 0.09            |
|                                                                                  | 0.09                                    | 0.29                              |                          |                                      | 0.13            |
|                                                                                  | 0.12                                    | 0.17                              |                          |                                      | 0.76            |
|                                                                                  | 0.08                                    | 0.15                              |                          |                                      | 0.37            |
|                                                                                  | 0.02                                    | 0.10                              |                          |                                      | 0.12            |
|                                                                                  | 0.02                                    | 0.05                              |                          |                                      | 0.37            |
|                                                                                  | 0.02                                    | 0.06                              |                          |                                      | 0.37            |
|                                                                                  | 0.07                                    | 0.07                              |                          |                                      | 0.83            |

The *G*-test on egg limitation tests the hypothesis of equal numbers of males and females. The *G*-test on host limitation tests the hypothesis that the sex ratio equals the proportion of secondary hosts. The index of host limitation is estimated from the observed sex ratio and proportion of secondary hosts. This is given a range to include (a) 0.0 when a *G*-test on egg limitation is not significant, and (b) 1.0 (and the point at which the sex ratio asymptotes at the proportion of secondary broods; see Fig. 1 of Hunter & Godfray 1995) when a *G*-test on host limitation is not significant. NC indicates that an index could not be calculated from that sample, which occurs when the *G*-tests on egg and host limitation are significant, but the sex ratio does not lay between 0.5 and the proportion of secondary hosts. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

of hosts into female and male production, leading to equal numbers of male and female clutches. A host-limited female is predicted to produce the clutch size that maximizes fitness returns per clutch (termed the Lack clutch size). Consequently, if the Lack clutch size differs between the sexes a biased sex ratio is predicted. In contrast, a purely egg-limited female should produce an equal number of male and female eggs (assuming they are equally costly to produce) and hence an unbiased sex ratio. Assuming that the fitness of individuals of both sexes

decreases monotonically with clutch size, an egg-limited female is predicted to produce a clutch size of one for broods of both sexes.

The index of host limitation can be inferred from sex ratio data as follows. West *et al.* (1999) showed how the optimal proportion of male broods, as well as the size of male and female broods, could be calculated. From these the optimal sex ratio can be calculated. For both a proovigenic and a synovigenic model the optimal strategy is obtained by numerically solving three equations

simultaneously (see equation (A4) or (A6) in West *et al.* 1999), and so there are no simple relationships as in the autoparasitoid case (eqns 1 and 2 above). Instead the equations given by West *et al.* (1999) must be solved numerically to find the index of host limitation that gives the observed sex ratio. Note that  $\phi$  is the relevant index to use for autoparasitoids which produce solitary broods (see Hunter & Godfray 1995), whilst  $\Phi$  is the relevant index to use for *Achrysocharoides* species which produce gregarious broods (see West *et al.* 1999).

Sex ratio data have been collected which allow this methodology to be applied to 18 samples of six species in the genus *Achrysocharoides*, all of which are synovigenic (West *et al.* 1999). These data provide species averages for the sex ratio because each of these samples were taken from several areas or over several years. In all of these species the clutch size of female broods is greater than that in male broods. In order to predict the extent of egg- or host-limitation from natural sex ratio data we must know the Lack clutch size for female and male broods. In one species, *A. zwoelferi*, this has been done directly, by estimating the size–fitness relationship and the consequences of clutch size for body size (West *et al.* 1996,

1999). In the other species the Lack clutch size of broods can be inferred if we assume that the majority (> 96%) of broods are up to and including the Lack solution: this was found to be the case with *A. zwoelferi*. This places a lower limit on the importance of egg limitation because there is the possibility that females are too egg limited to ever lay the Lack clutch size. Our estimates of the host limitation index ( $\Phi$ ) from the *Achrysocharoides* data are given in Table 2. Overall the data suggest an intermediate position on the egg/host limitation continuum, with a bias towards host limitation. Unsurprisingly, these results are similar, although slightly higher, than estimates based on the distribution of brood sizes in female broods (see p. 273 of West *et al.* 1999).

## DISCUSSION

We have shown how sex allocation data can be used to provide estimates of the relative importance of the factors limiting reproduction. This methodology relies on the assumption that the theoretical models used capture the most important determinants of sex allocation in the species considered. We believe this to be justified because

**Table 2** Estimates of the host limitation index from sex ratio data in *Achrysocharoides* species that produce single sex broods.

| Species name | Generation | Sex ratio | Lack (male) | Lack (female) | G-test on egg limitation | Index of host limitation ( $\Phi$ ) |
|--------------|------------|-----------|-------------|---------------|--------------------------|-------------------------------------|
| butus        | both       | 0.36      | 1           | 2             | 0.8                      | 0.83 (0.0–0.83)                     |
| cilla        | both       | 0.35      | 2           | 4             | 96.8***                  | 0.89                                |
| latreilli    | both       | 0.29      | 1           | 4             | 70.5***                  | 0.81                                |
|              | summer     | 0.39      | 2           | 4             | 29.2***                  | 0.85                                |
|              | autumn     | 0.40      | 2           | 4             | 12.7***                  | 0.81                                |
| niveipes     | both       | 0.40      | 1           | 4             | 23.6***                  | 0.62                                |
|              | summer     | 0.26      | 1           | 4             | 5.5*                     | 0.85                                |
|              | autumn     | 0.2       | 1           | 4             | 54.0***                  | 0.94                                |
| splendens    | both       | 0.28      | 2           | 4             | 14.7***                  | NC                                  |
|              | summer     | 0.19      | 1           | 4             | 83.7***                  | NC                                  |
|              | autumn     | 0.30      | 1           | 4             | 14.2***                  | 0.80                                |
|              | summer     | 0.11      | 1           | 4             | 49.3***                  | NC                                  |
|              | autumn     | 0.42      | 1           | 4             | 9.5**                    | 0.57                                |
| zwoelferi    | both       | 0.28      | 1           | 3             | 94.3***                  | 0.87                                |
|              | summer     | 0.36      | 1           | 3             | 34.4***                  | 0.74                                |
|              | autumn     | 0.31      | 1           | 3             | 100.0***                 | 0.83                                |
|              | summer     | 0.31      | 1           | 3             | 128.2***                 | 0.82                                |
|              | autumn     | 0.32      | 1           | 3             | 120.0***                 | 0.81                                |

Data were obtained from West *et al.* (1999). The Lack (male) and Lack (female) columns are the assumed Lack solutions for broods containing males and females, respectively. These were estimated based upon distribution of clutch sizes in nature (see text for further details). The G-test on egg limitation tests the hypothesis of equal numbers of males and females. G-tests on host limitation (equal numbers of male and female broods) were not carried out because developmental mortality and differences in the size of male and female broods will alter the proportion of broods that are male (see p. 272 of West *et al.* 1999). The index of host limitation is that estimated from the observed sex ratio and assumed Lack clutch sizes of male and female broods. This is given a range to include 0.0 when the G-tests on egg limitation are not significant. NC indicates that an index could not be calculated from that sample, which occurs when the sex ratio is too female biased to be explained even if females were completely host limited. \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

(a) experimental data from autoparasitoids (Hunter & Godfray 1995) and *Achrysocharoides* species with single sex broods (West *et al.* 1999) have provided support for the assumptions and predictions of these models, and (b) the segregated nature of male and female broods makes local mate competition (Hamilton 1967), the best documented cause of extremely biased sex ratios in parasitoids (Godfray 1994), extremely unlikely in these species (Donaldson & Walter 1991a; Godfray 1994; West *et al.* 1999). In addition, although the models make many simplifying assumptions, such as ignoring host feeding and whether host distributions are structured, the consequences (for the optimal sex ratio) of relaxing these assumptions are likely to be relatively minor (Godfray & Hunter 1992; Hunter & Godfray 1995; West *et al.* submitted), in which case they would not change the general conclusions that we are able to make. Field studies that examined sex allocation and the relative importance of egg and host limitation would be extremely instructive.

The sex ratio is predicted to depend upon the extent of host or egg limitation for a number of species with different life histories (e.g. Hardy *et al.* 1993; Ode & Strand 1995; Rosenheim *et al.* 1996). However, in other cases it is not so easy to infer levels of host limitation from sex ratio data. For example, consider the case when females provide different amounts of resources to male and female offspring (Rosenheim *et al.* 1996). In this case the optimal sex ratio also depends upon parameters that are not easily quantified, such as male and female fitness functions, and the distribution of resources (Frank 1995). It may, however, be feasible to infer something about these parameters from the relative size of males and females.

We have used sex ratio data from 48 samples of eight species to estimate the factors limiting reproduction in natural populations. These data illustrate two points. First, the extent of host or egg limitation in a species varies between site collected and time of year. In different samples the sex ratios are consistent with pure host limitation, pure egg limitation and intermediates between these extremes. Second, the majority of samples, and overall species means, suggest an intermediate position on the egg/host limitation continuum and/or a mixture of egg- and host-limited individuals, with a bias towards host limitation. These conclusions are consistent with previous studies that directly estimated the relative importance of egg and host limitation (see Driessen & Hemerik 1992; Ellers *et al.* 1998; Casas *et al.*, in press). Intermediate and variable levels of host or egg limitation are not surprising given the observation that individuals will facultatively alter their behaviour in response to the relative risk of becoming egg- or host-limited (e.g. Rosenheim & Rosen 1991; Roitberg *et al.* 1992; Godfray 1994; Prokopy *et al.* 1994; Hunter & Godfray 1995;

Rosenheim *et al.* 1996; Flanagan *et al.* 1998; West *et al.* 1999). Such facultative behaviour would only be selected for and maintained in an environment where the level of egg and host limitation fluctuated (Herre 1987).

More generally, this paper demonstrates how sex allocation may be used as a tool to indirectly infer characteristics of a population. This is an approach that can be applied to a number of areas (West and Herre, in press); the most notable previous examples are the use of sex ratios to estimate selfing rates in parasitic protozoa (Read *et al.* 1992; West *et al.* 2000) and plants (Cruden 1977). The feature shared by all these studies is that sex ratio data can be obtained much more easily, and at less cost, than direct measurements of the parameter we are interested in. Consequently, data can be collected from a relatively large number of populations and species, allowing generalizations to be made.

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#### BIOSKETCH

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