

Asymmetric larval competition in the parasitoid wasp *Nasonia vitripennis*: a role in sex allocation?

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Abstract Sex allocation theory offers excellent opportunities for testing how animals adjust their behaviour in response to environmental conditions. A major focus has been on instances of local mate competition (LMC), where female-biased broods are produced to maximise mating opportunities for sons. However, the predictions of LMC theory can be altered if there is both local competition for resources during development and an asymmetry between the competitive abilities of the sexes, as has been seen in animals ranging from wasps to birds. In this paper, we test the extent to which asymmetric larval competition alters the predictions of LMC theory in the parasitoid wasp *Nasonia vitripennis*. We found that the body size of both sexes was negatively correlated with the number of offspring developing within the host. Further, we found that when faced with high levels of competition, the body size of females, but not males, was influenced by the sex ratio of the competing offspring; females were smaller when a higher proportion of the brood was female. This asymmetric competition should favour less biased sex ratios than are predicted by standard LMC theory. We then develop a theoretical model that can be parameterised with our data, allowing us to determine the quantitative consequences of

the observed level of asymmetric larval competition for sex allocation. We found that although asymmetric competition selects for less biased sex ratios, this effect is negligible compared to LMC. Furthermore, a similar conclusion is reached when we re-analyse existing data from another parasitoid species where asymmetric larval competition has been observed; *Bracon hebetor*. Consequently, we suspect that asymmetric larval competition will have its greatest influence on sex ratio evolution in species that have smaller clutches and where local mate competition is not an issue, such as birds and mammals.

Keywords Local resource competition · Optimality · Adaptation · Hymenoptera

Introduction

Sex allocation theory allows some excellent opportunities for testing how animals adjust their behaviour in response to environmental conditions (Charnov 1982; Hardy 2002; West and Sheldon 2002). Fisher (1930) showed that frequency dependant selection would favour the less common sex, selecting for equal investment into male and female offspring. Since then, it has been realised that this breaks down if there are competitive interactions between relatives, termed local resource competition (LRC; Hamilton 1967; Clark 1978). If competition for resources differs between the sexes, such that the production of one sex leads to greater LRC, then selection favours over-production of the sex that leads to less LRC (Bulmer and Taylor 1980; Taylor 1981).

The form of LRC that has attracted the most attention is local mate competition (LMC; Hamilton 1967). Hamilton (1967) showed that when mating takes place between the offspring of a small number of mothers, before the

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daughters disperse, then a female biased sex ratio is favoured. This bias is favoured because it leads to reduced competition for mates between related males and provides more mates for sons (Taylor 1981). In haplodiploid species, an additional bias is favoured because inbreeding increases the relative relatedness of mothers to daughters (Hamilton 1972; Frank 1985; Herre 1985). There is a huge amount of experimental support for LMC theory, showing that species subject to LMC produce female biased sex ratios, and that individuals adjust their offspring sex ratio facultatively in response to the local level of LMC (West et al. 2005).

However, the predictions of LMC theory can be altered if there is also LRC for resources during larval development (Godfray 1986). Godfray (1986) examined the situation where offspring compete for resources, such as when a number of parasitoid wasps develop on a single host, and there can be sexual asymmetries in larval competition. In this case, when males and females differentially affect the level of competition experienced by other members of the clutch, the ESS sex ratio is biased towards the sex that causes the smaller competitive effect. Although such asymmetries have been observed in species subject to LMC such as parasitoid wasps (Ode et al. 1996; van Baaren et al. 1999), their quantitative effects on sex allocation are unclear. In addition, such asymmetries have also been observed more widely in organisms where LMC does not occur, such as birds (Oddie 2000; Arnold et al. 2003; Uller 2006).

In this paper, we test the extent to which asymmetric larval competition alters the predictions of LMC theory in the parasitoid wasp *Nasonia vitripennis*. *N. vitripennis* has proved to be an extremely useful organism for testing LMC theory, with a large number of experimental and field studies demonstrating that females adjust their offspring sex ratio in response to the extent of LMC (Werren 1980, 1983; Orzack 1986; Orzack and Parker 1986; King and Skinner 1991; King 1992; King et al. 1995; Molbo and Parker 1996; Flanagan et al. 1998; Reece et al. 2004; Shuker et al. 2004a, b; Shuker and West 2004; Shuker et al. 2005, 2006a, b). The possibility that asymmetric larval competition may be important in *N. vitripennis* has been suggested by a recent study showing that wasp size correlates with the sex ratio of wasps developing in a host (Rivero and West 2005). However, the sex ratio was not manipulated experimentally in this previous study, and so the result could be due to other correlated factors. Here, we test for asymmetric larval competition by experimentally manipulating both the number of offspring developing in a host and their sex ratio (proportion that are male). We then develop a theoretical model that can be parameterised with our data, and which allows us to determine the quantitative consequences of the observed level of asymmetric larval competition for sex allocation.

Materials and methods

Study organism

Nasonia vitripennis is a small (females are approximately 2 mm long), gregarious, parasitoid wasp that parasitises large fly pupae (Whiting 1967). Females seek out the host puparia, paralyse the fly pupa within and can oviposit over 60 eggs on the pupa's surface. Upon emergence the males wait outside the host for the females, who develop more slowly. They then mate, and the females disperse to find new hosts. The flightless males remain behind and die. *N. vitripennis* has been used as a model organism for studying local mate competition (LMC) and its relationship with sex allocation behaviour, with females producing highly female-biased sex ratios when ovipositing alone (sex ratio = 0.1–0.2), through to highly male-biased sex ratios (>0.9) if super-parasitising previously parasitised hosts (e.g. as shown in above references). Once a host is parasitised, there is a window of approximately 48 h during which further females tend to parasitise the host (superparasitism). Super-parasitism rarely occurs after this period because by then the first brood will have developed sufficiently to start utilising the host's resources, leaving too little food for later larvae (Werren 1984; West et al. 2005).

Laboratory stock

We used wasps from strain HV7 originally collected from bird boxes in Hoge Veluwe National Park in the Netherlands by Prof. L.W. Beukeboom in the summer of 2002. Approximately 50 female mated wasps were placed in each of six glass vials (25 × 75 mm) plugged with a sponge bung. We added about 50 hosts (*Calliphora vomitoria* fly pupae) to each vial on which the females could feed and lay their eggs. The vials were kept in incubators (25°C, 16 h light, 8 dark), and after approximately 14 days, hundreds of new offspring emerged and mated for 3–5 days. We then again allowed approximately 50 mated females per vial to climb into a new vial and thus repeat the whole process.

Experimental design

To test how siblings affect each other, we created a range of competitive environments by manipulating the number (1–3) and mating status (mated or virgin) of females ovipositing on the host. This influenced both the number of offspring competing for resources in each host and the sex ratio of these offspring.

The experimental females were generated from a large sample of females collected from the stock culture as either mated (allowed to emerge and mate in mass culture

for 24 h, $N=500$) or as virgin females (collected as 12-day-old pupae from a random sample of hosts from the mass culture; $N=500$). Each female was individually placed in a 10×75 mm vial stopped with cotton wool. Each female was given a host for 24 h and then a disc of honey-soaked filter paper for a further 24 h; this period gave the wasps time to feed and then develop and mature their eggs. We then allocated females to one of six treatments (40–50 replicates per treatment): 1 \times mated female; 1 \times mated and 1 \times virgin female; 2 \times mated females; 1 \times mated and 2 \times virgin females; 2 \times mated females and 1 \times virgin female; 3 \times mated females. These treatments successfully generated clutches with a wide range of clutch sizes and sex ratios (see Table 1). We excluded clutches containing only diapause individuals (as occurred in 5.5% of cases) or ones where supposedly mated females produced all-male broods (as occurred in 15% of cases). This resulted in the removal of 60 clutches so that our treatments varied in replicate number from 29 to 44 (a total of 218 samples). Each vial was labelled blind with the help of a colleague who allocated a unique symbol to each treatment, only revealing the allocations after the experiment. A single host was added to each vial for a period of 6 h, after which the ovipositing females were removed and the hosts were placed in the incubator at 25°C (16L:8d) until the focal offspring emerged.

Testing for asymmetric larval competition

We used three measures to assess the consequences of larval competition: body size, longevity and, in the case of females, fecundity. We scanned the tubes three times per day and recorded the time when five females had emerged from the host as our estimate of emergence time to measure

adult longevity. All wasps from a clutch normally eclose and then emerge from the host within 24 h of each other (Whiting 1967) even when super-parasitism occurs (Werren 1980). Directly measuring eclosion times for individual wasps would have required invasively opening hosts, risking pupal mortality. After emergence, we allowed the wasps to mate for 24 h, and then individuals from each clutch were sorted into separate 10×75 mm vials and stopped with cotton wool. We collected up to five males and five females to measure lifespan in the absence of hosts and two females to record lifetime fecundity. The remaining wasps from each clutch were left to die, whereupon we counted the number of males, females and diapause larvae (we added this data to the number of each sex used for assessing fecundity and lifespan). We also measured the right-hind tibia of up to 5 males and 5 females from each clutch as an estimate of body size. Variation within a group decreases with greater sampling. Previous work indicates that sampling between three and five individuals from a group gives a high level of accuracy (unpublished data). To do this, we dissected each leg and used a Leica dissecting microscope with $\times 100$ magnification. Males have longer hind-tibias than females, although they are smaller in other morphological traits (Whiting 1967).

When measuring the longevity of wasps in the absence of hosts, we supplied each individual with a fresh disc of honey-soaked filter paper every 48 h until they died. We checked for and recorded deaths three times per day and calculated the mean longevity of males and females from each clutch to avoid pseudo-replication. To assess lifetime fecundity of female wasps, we gave them six fresh hosts every 48 h until they died. These parasitised hosts were then placed in a new vial so that the offspring could emerge, be counted, sexed and, in a sample of cases, have their tibia measured as before. We recorded the number of males, females and diapause larvae found in each vial.

Table 1 The mean clutch sizes and sex ratios of broods produced in the varying treatments

Number of ovipositing females		Initial clutch sizes		Initial sex ratios		<i>n</i>
Mated	Virgin	Mean	Standard Deviation	Mean	Standard Deviation	
1	0	19.28	8.41	0.14	0.17	36
1	1	32.93	13.73	0.57	0.20	29
1	2	45.88	11.41	0.74	0.14	34
2	0	34.33	11.09	0.36	0.21	40
2	1	45.68	13.19	0.57	0.13	44
3	0	47.11	11.88	0.35	0.17	35

The test offspring were collected from these broods.

Analysis

To assess the effects of larval competition and the sex ratio of the competing larvae, we collapsed the six treatments together to provide a continuous range of clutch sizes and sex ratios, using each as a main effect. We then assessed the significance of these main effects and their interaction on size, longevity and fecundity using general linear models with model simplification (Crawley 2002). When assessing the causes of variation in longevity, we considered the possible effects of body size along with the main effects of the experiment. Our sex ratio data were taken as the proportion of males and were arcsine square root transformed before analysis. All analyses were undertaken with the statistical package JMP IN 5.1 (SAS Institute).

Results

Competition and body size

Male offspring were smaller when they had to share a host with more competitors, as might be expected from resource limitation ($F_{1,125}=92.06$, $R^2=0.42$, $\beta=-0.247$, $SE=0.026$, $P<0.0001$; Fig. 1a). However, the sex ratio of the larval competitors had no effect ($F_{1,124}=1.26$, $P=0.26$), and the interaction between sex ratio and clutch size was also not significant ($F_{1,123}=2.17$, $P=0.14$). Female offspring were also smaller when they had to share a host with more competitors ($F_{1,128}=142.55$, $R^2=0.527$, $\beta=-0.293$, $SE=0.025$, $P<0.0001$; Fig. 1b). However, the size of female offspring also varied with the sex ratio of the wasps developing in a host; in larger clutches females were smaller when sex ratios were female biased (interaction between sex ratio and brood size: $F_{1,127}=5.70$, $R^2=0.55$, $P=0.019$) although sex ratio was not a main effect ($F_{1,127}<0.01$, $P=0.98$). We examined this further by splitting the dataset into individuals that came from large or small clutches, using the median of 40 individuals as the cut-off. In large clutches female offspring were smaller when they were competing with a higher proportion of females ($F_{1,65}=8.91$, $R^2=0.41$,

$\beta=3.702$, $SE=1.240$, $P=0.004$; Fig. 2); in small clutches, sex ratio had no effect ($F_{1,63}=1.86$, $P=0.18$). The males had longer tibias than females ($F_{1,253}=11.00$, $R^2=0.50$, $p=0.001$), but when we analysed both sexes simultaneously, we found qualitatively identical results as those above.

Competition and longevity

We found no relationship between longevity and the level of larval competition or larval sex ratio. This result held when analysing males (clutch size: $F_{1,88}=18.09$, $P=0.48$; sex ratio: $F_{1,88}=1.14$, $P=0.29$), females (clutch size: $F_{1,182}=3.13$, $P=0.08$; sex ratio: $F_{1,182}=0.37$, $P=0.55$), or both sexes together (clutch size: $F_{1,272}=2.24$, $P=0.14$; sex ratio: $F_{1,272}=0.08$, $P=0.77$).

Larger wasps lived longer. This result held when analysing males ($F_{1,44}=7.29$, $R^2=0.15$, $\beta=0.420$, $SE=0.155$, $P=0.010$; Fig. 3), females ($F_{1,119}=11.65$, $R^2=0.09$, $\beta=0.254$, $SE=0.074$, $P=0.001$; Fig. 3), or both sexes together ($F_{1,164}=19.05$, $R^2=0.14$, $\beta=0.300$, $SE=0.067$, $P<0.0001$). Males lived longer than females ($F_{1,164}=5.23$, $R^2=0.14$, $P=0.023$), and there was no significant interaction between sex and body size on longevity ($F_{1,156}=0.35$, $P=0.55$).

Competition and lifetime female fecundity

Females with more competitors have lower lifetime fecundity ($F_{1,23}=6.86$, $R^2=0.23$, $\beta=-2.489$, $SE=0.950$, $P=0.015$; Fig. 4), but the sex ratio of their competitors was not important ($F_{1,23}=0.18$, $P=0.69$) even when considered as an interaction with number of competitors ($F_{1,22}=0.95$, $P=0.34$). This effect of the number of competitors was via its influence on body size, as shown by the fact that if body size was included in the model, body size was positively associated with lifetime fecundity ($F_{1,24}=6.97$, $R^2=0.23$, $\beta=7.158$, $SE=2.712$, $P=0.015$), and competitor number is no longer significant ($F_{1,23}=0.31$, $P=0.58$).

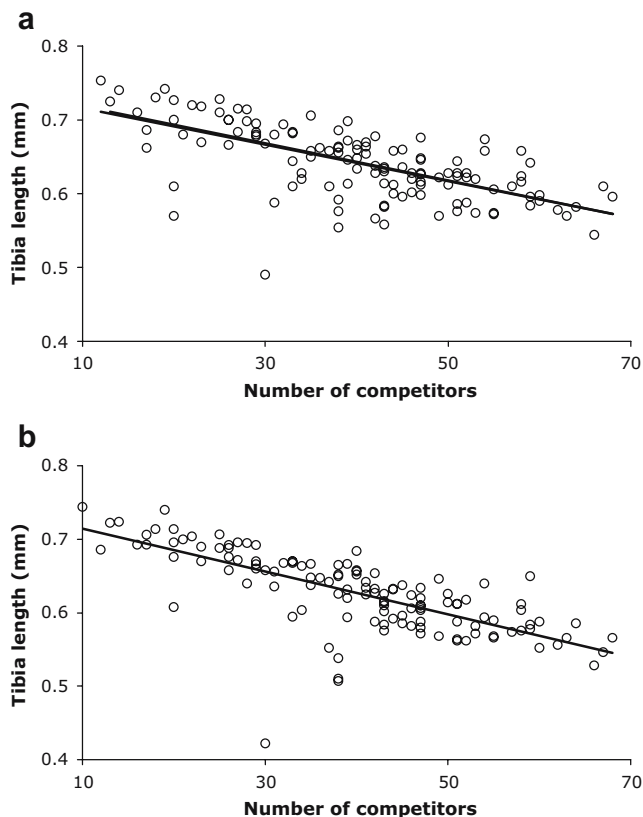


Fig. 1 Larval competition influences tibia length. **a** Males: male body size decreases as the number of competitors increases **b** Females: female body size also decreases as the number of competitors increases

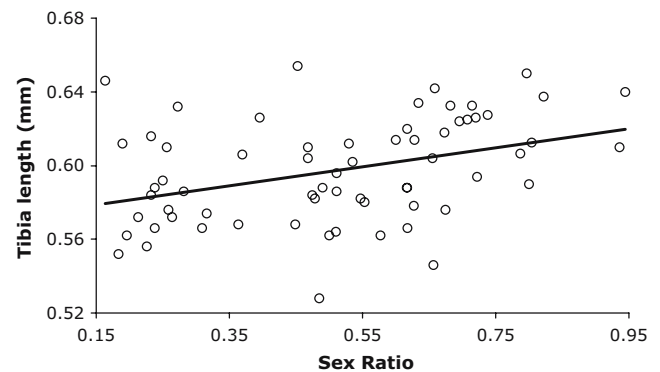


Fig. 2 Larval competition interacts with larval sex ratio to influence female tibia length. For large clutches (above the median of 40 offspring) sex ratio is positively correlated with female body size such that females are larger the fewer females they are competing with

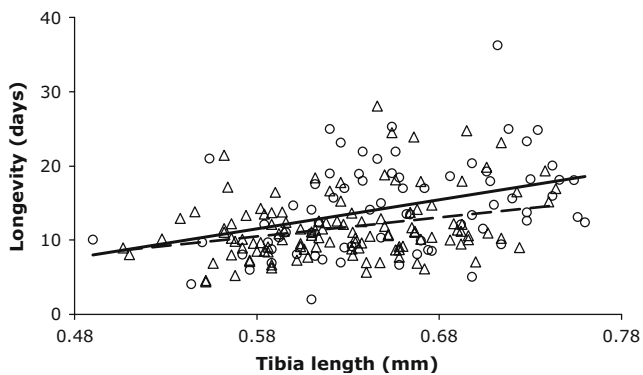


Fig. 3 Larger wasps live longer and males live longer than females (males: circles, continuous line; females: triangles, broken line)

Discussion

We investigated how the number and sex of *N. vitripennis* offspring developing within a host influenced larval competition for resources. We found that body size of both male and female offspring was negatively correlated with the number of offspring developing within their host (Fig. 1). In addition, we found that size of females, but not males, was influenced by the sex ratio of wasps developing within the host. Specifically, females were smaller in hosts where a higher proportion of the offspring were female, and this effect was greater at larger clutch sizes (Fig. 2). This asymmetric larval competition would reduce the marginal benefit of producing females and so favour a less female biased sex ratio than predicted by standard LMC theory (see below; Godfray 1986). Body size was positively correlated with longevity in males and females (Fig. 3), and fecundity in females (Fig. 4; see also Flanagan et al. 1998; Rivero and West 2002, 2005). Males were found to live longer than females although there was no interaction between sex and body size. Whilst competitor number affected body size and body size was linked to longevity, we found no direct relationship between competitor number and longevity,

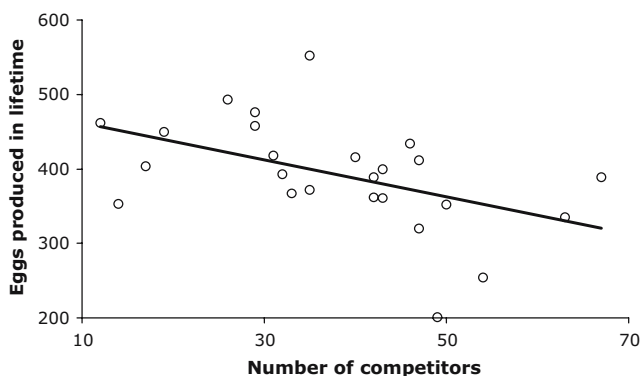


Fig. 4 Larval competition is negatively correlated with female lifetime fecundity

presumably because we lacked statistical power to link these two effects in just one step.

What are the consequences of the observed level of asymmetric larval competition for sex ratio evolution in *N. vitripennis*? In the appendix, we develop a theoretical model for the evolutionary stable (ES) sex ratio, which can be parameterised with our data. We assume the classic LMC structure of N mated females laying eggs per patch, the offspring of which then develop and mate, before only the females disperse (Hamilton 1967, 1979). However, we also allow the fitness of females to depend upon the size and the sex ratio of the brood in which they develop (Godfray 1986). To parameterise this model it is necessary to do two things. First, we use the relationships provided in Table 2 to calculate how fitness depends upon brood size and sex ratio. It is thought the fitness of a female parasitoid wasp will be limited by either the number of hosts that she can find (host limitation) or the number of eggs that she can produce (egg limitation), or some intermediate between these extremes (Driessen and Hemerik 1992; Rosenheim 1996; Sevenster et al. 1998; Rosenheim 1999a, b; West et al. 1999; West and Rivero 2000). We can investigate the two extreme cases by assuming fitness is proportional to longevity and fecundity. These correspond to host and egg limitation respectively. Second, we used field data on *N. vitripennis* from (Molbo and Parker 1996) to determine the range of parameter values that are useful to investigate. Their data give a mean brood size of approximately 25 (range 7–51), which does not vary significantly with foundress number ($F_{1,11}=1.9$; $p=0.19$).

Putting our data into our theoretical model, we find that asymmetric larval competition has a negligible effect on the ES sex ratio (Fig. 5). Figure 5 shows the predicted ES sex ratio for *N. vitripennis* assuming that fitness is determined by longevity, but practically identical results were obtained assuming fitness is determined by fecundity. The solid line shows the classic prediction provided by the original equation of Hamilton (1979). The dashed lines show the predictions for a brood size of 70. We have not shown predictions for the range of brood sizes observed in nature because these could not be distinguished from the original LMC curve. Consequently, whilst our model predicts that females should produce a sex ratio less biased than predicted by Hamilton's original model, the magnitude of this effect is negligible for the range of brood size observed in *N. vitripennis*. The reason for this small effect is that any effect of asymmetric larval competition is dwarfed by the effect of LMC. Our model also predicts that the sex ratio should vary with brood size, but this effect will also be negligible. Variable brood size is likely to be far more important through its influence on the extent of LMC (Werren 1980; Stubblefield and Seger 1990; Flanagan et al. 1998; Shuker et al. 2005).

Table 2 Parameters from the experiment used to quantify the expected influence on sex ratio of asymmetric larval competition in *Nasonia vitripennis*

Trait	Affected by	Intercept	Factors
Female body size	larval competition(c)×sex ratio(sr)	73.17	$-0.27 \times c - 0.03 \times sr + 0.2 \times c \times sr$
Female longevity	female body size(fb)	-4.22	$+0.25 \times fb$
Female fecundity	female body size(fb)	-63.62	$+7.16 \times fb$
Male body size	larval competition(c)	74.07	$-0.25 \times c$
Male longevity	male body size(mb)	-12.92	$+0.42 \times mb$

Parameters are derived from the general linear model analysis.

Our results show that females suffer from asymmetric larval competition, as suggested by Rivero and West (2005), but in the opposite direction to their prediction. A possible explanation for this difference is that our experiment was specifically designed to address this issue and had greater power. We (1) manipulated sex ratio experimentally, whereas they relied on natural variation; we (2) produced more variable sex ratios and brood sizes. However, another possibility is that the previous experiment was assessing the impact of host feeding, and that this may have different consequences for males and females (Rivero and West 2005). If male and female larvae require different nutrients, as occurs in other insect taxa (Stockhoff 1993; Telang et al. 2001; Dubois et al. 2002; Telang et al. 2002; Moreau et al. 2003; Telang et al. 2003), then numerous complications can emerge. For example, host feeding may use up resources that are preferentially used by one sex, leading to that sex facing greater competition, or having to switch its resource use. Further asymmetry in response could come from the fact that males develop more quickly than females, allowing them to

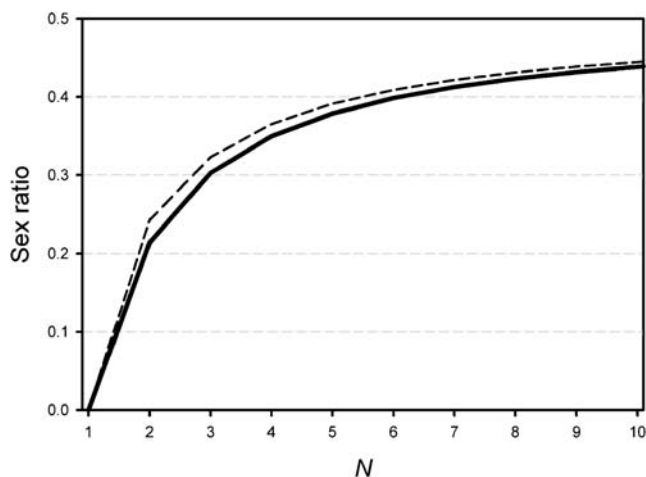


Fig. 5 The predicted consequences of asymmetric larval competition for offspring sex ratios in *N. vitripennis* where N is the number of ovipositing females on a host. The solid line shows the classic prediction for haplodiploids (Hamilton 1979), and the dashed lines show the prediction from our model and data, for a brood size of 70 (the effect with smaller brood sizes was not distinguishable from the original LMC prediction). We predict that asymmetric larval competition leads to a less female biased sex ratio, but this effect is negligible compared to the consequences of LMC

use resources and develop whilst resources are relatively less limiting (Godfray 1986, 1994; Rivero and West 2005). This suggests the possibility that females could adjust their clutch size and sex ratio behaviour dependent upon the extent to which they feed upon a host. Another surprising result was that we found that males lived longer than females.

Our model also allows us to use existing data to determine the quantitative effect of asymmetric larval competition in another species — the parasitoid *B. hebetor*. In this species, there is also asymmetric larval competition, in the same direction as we found with *N. vitripennis*, with females suffering an increased competition for resources when the brood is more female biased (Ode et al. 1996). We used the data collected by Ode et al. (1996) and Antolin and Strand (1992) to parameterise our model (see Fig. 6 legend). As with *N. vitripennis*, this led to the prediction of

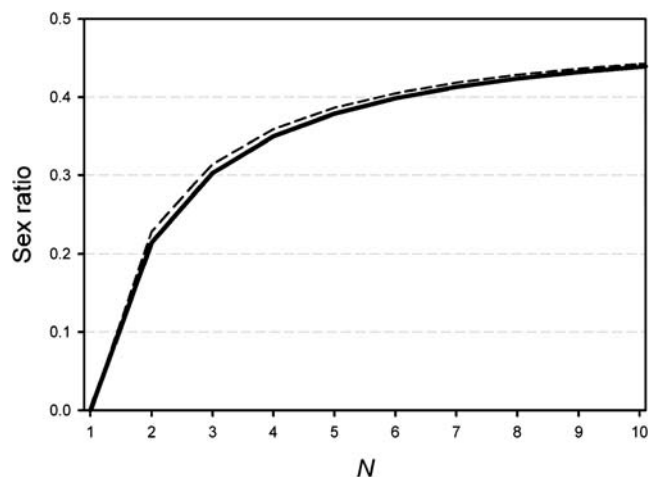


Fig. 6 The predicted consequences of asymmetric larval competition for offspring sex ratios in *B. hebetor* where N is the number of ovipositing females on a host. The solid line shows the classic prediction for haplodiploids (Hamilton 1979), and the dashed lines show the prediction from our model, parameterised with data collected by Antolin and Strand (1992) and Ode et al. (1996). From Ode et al. (1996) we obtained the relationships: $Body\ size = 0.5475 + (0.0046 \times host\ weight) - (0.0099 \times clutch\ size) + (0.043 \times sex\ ratio)$; $Longevity = -17.53 + (102.30 \times size)$; $Lifetime\ fecundity = -734.72 + (2,509.55 \times body\ size)$. From Antolin and Strand (1992) obtained an average brood size of 9.1, and an average host size of 20 mg. We predict that asymmetric larval competition leads to a less female biased sex ratio. Although the effect is greater than in *N. vitripennis*, it is still very small compared to the consequences of LMC

a less female biased sex ratio (Fig. 6). Although the effect of asymmetric larval competition was again small, it was at least visible for the average brood size. The extent of LMC in *B. hebetor* is unclear. Whilst related males could compete for mates, and the sex ratio is female biased, inbreeding avoidance reduces the possible importance of LMC (Antolin and Strand 1992; Cook et al. 1994; Ode et al. 1995, 1996, 1998). Nonetheless, as illustrated by Fig. 6, the influence of asymmetric larval competition will be low, even when LMC is weak.

We conclude by considering the importance of asymmetric larval competition more generally. In other parasitoids and insects where LMC occurs (West et al. 2005), we suspect that effects of LMC will frequently be the overriding factor, as we have found with *N. vitripennis* and *B. hebetor*. Asymmetric larval competition will therefore be relatively unimportant. Consequently, we suspect that the possibilities for asymmetric larval competition to have significant influences on sex ratio evolution will be in species that have smaller clutches and where local mate competition is not an issue, such as birds and mammals (Oddie 2000; Arnold et al. 2003).

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Asymmetric larval competition in the parasitoid wasp *Nasonia vitripennis*: a role in sex allocation?

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The original publication did not include the appendix to the article. The missing material is supplied here.

Appendix

Here we extend a standard model of sex ratio evolution under local mate competition (LMC) to take into account effects of clutch size and sex ratio on female fecundity or longevity, as we have observed in our experiments. We will then parameterize the model with empirical estimates of these relationships to generate quantitative predictions of sex ratios.

The model is built around the standard life cycle of N mated females breeding in a patch. The mated females produce offspring that mate randomly among themselves within the patch, followed by dispersal of the newly mated females to random patches.

We use the direct fitness approach as developed by Taylor and Frank (1996) and Frank (1998), as we have

done in previous papers on *Nasonia* sex ratios (Reece et al. 2004, Shuker et al. 2005).

A mother's total fitness is given by

$$W = c_f W_f + c_m W_m \quad (\text{A1})$$

where W_i is her fitness through sex- i offspring ($i = m, f$) and c_i is the class reproductive value of sex i . For haplodiploids, the reproductive value of females is twice that of males ($c_f = 2c_m$), which is another way of saying that a random gene from a population in the far future is twice as likely to be present today in a female as in a male (Taylor 1988). A focal female with sex ratio x (proportion sons) and clutch size k has fitness through daughters proportional to

$$W_f = (1 - x)F \quad (\text{A2})$$

where $F = F(\bar{x}, k)$ is a daughter's expected reproductive success, which may depend on the average sex ratio \bar{x} produced by the females in the patch and their clutch size k . We assume that k is fixed, not being under selection, unlike in the models of Godfray (1986), where simultaneous selection on sex ratio and clutch size was studied. We will consider two extreme situations, one where F is estimated by a female's fecundity and one where F is estimated by her life expectancy. However, it turns out that the numerical predictions for both scenarios are virtually identical, and we will therefore show only the results for fecundity.

The focal female's fitness through sons is given by

$$W_m = x \frac{1 - \bar{x}}{\bar{x}} F \quad (\text{A3})$$

The ratio $(1 - \bar{x})/\bar{x}$ is the expected number of mates per son and $F = F(\bar{x}, k)$ is the expected reproductive success of those mates.

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The direction and strength of selection on the sex ratio is given by the selection gradient

$$\frac{dW}{dx} = r_f c_f \frac{\partial W_f}{\partial x} + R_f c_f \frac{\partial W_f}{\partial \bar{x}} + r_m c_m \frac{\partial W_m}{\partial x} + R_m c_m \frac{\partial W_m}{\partial \bar{x}} \quad (\text{A4})$$

where r_i is the relatedness of sex- i offspring to the focal female and R_i the relatedness to the focal female of random sex- i offspring born in the same patch. The relatedness coefficients can be calculated from standard population genetic recursions (Taylor 1988, Reece et al. 2004). For haplodiploids with random dispersal of mated females, the results are

$$r_f = 1/(2 - 1/N), R_f = r_f/N, r_m = 1, R_m = r_m/N. \quad (\text{A5})$$

Working out the partial derivatives gives the selection gradient

$$\frac{dW}{dx} = -r_f c_f F + R_f c_f (1 - \hat{x}) F_x + r_m c_m \frac{1 - \hat{x}}{\hat{x}} F - R_m c_m \left[\frac{F}{\hat{x}} - (1 - \hat{x}) F_x \right] \quad (\text{A6})$$

where all expressions on the right are evaluated at $x = \bar{x} = \hat{x}$. F_x represents the partial derivative of F with

respect to the average patch sex ratio \bar{x} , again evaluated at $x = \bar{x} = \hat{x}$.

Female reproductive success F as a function of body size y was estimated with a linear model of the form

$$F = \beta_0 + \beta_1 y. \quad (\text{A7})$$

Body size y , in turn, was estimated as a function of sex ratio x and clutch size k by a model of the form

$$y = \gamma_0 + \gamma_1 k + \gamma_2 \arcsin(\sqrt{x}) + \gamma_3 k \cdot \arcsin(\sqrt{x}). \quad (\text{A8})$$

Plugging this relationship into (A7) and taking the derivative with respect to x yields the following estimate for F_x :

$$F_x = \frac{\beta_1(\gamma_2 + \gamma_3 k)}{2\sqrt{x(1-x)}}. \quad (\text{A9})$$

Predicted sex ratios were calculated numerically with Maple 9.5 as the \hat{x} roots of the right-hand side of (A6) after plugging in (A7) and (A9) and estimates of the various parameters. Figure 5 shows the standard predicted sex ratio $N(2N - 1)/N(4N - 1)$ (Hamilton 1979) and the predicted sex ratios from our model for *Nasonia vitripennis* (parameter estimates from table 2), assuming a total number of competitors of $k=70$. For smaller clutch sizes, the deviation from the standard model is even smaller. Figure 6 shows the very similar predictions for *Bracon hebetor* (data in the figure legend).