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Local mate competition, variable fecundity and information use in a parasitoid

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ABSTRACT

Experiments with sex allocation in parasitic wasps offer excellent opportunities for testing how the way in which organisms process information about their environment influences behaviour. If mating takes place in temporary patches, where only a small number of females produce offspring, then sex allocation theory predicts a female-biased sex ratio. When females lay different numbers of offspring in a patch, females that produce relatively fewer offspring should lay a less female-biased, or even male-biased, sex ratio. Recent theoretical models have predicted that the exact form of this relationship depends upon whether females know only their own clutch size (self knowledge) or also the clutch sizes laid by the other females on the patch (complete knowledge). We tested the predictions of these models by examining sex allocation when two females of the parasitoid wasp *Nasonia vitripennis* oviposited simultaneously on a patch. The offspring sex ratio (proportion of males) produced by a female was: (1) negatively correlated with the number of offspring that she laid; and (2) positively correlated with the body size of the other female on the patch. Larger females matured more eggs and laid more offspring in the experimental patch. This suggests that, as predicted by the complete knowledge model, the offspring sex ratio laid by a female became more female biased as she laid a greater proportion of the total offspring laid on the patch. Furthermore, females use the body size of other females to assess the clutch sizes that these will lay.

The study of how sexually reproducing organisms divide their resources between offspring of the two sexes (sex allocation) has proved one of the most successful areas in evolutionary biology (Charnov 1982; Leigh et al. 1985; Godfray 1994; Herre et al. 1997). A very active area of research has been the study of female-biased sex ratios in species with spatially structured populations. Hamilton (1967) was the first to demonstrate that when the offspring of one or a few mothers mate amongst themselves in their natal patch, before daughters disperse, a female-biased sex ratio is favoured by natural selection. The female bias arises because it reduces competition among brothers for mates, and because it increases the number of mates for each of the female's sons (Taylor 1981). Together these processes were called local mate competition (LMC; Hamilton 1967). Hamilton predicted that the optimal sex ratio (proportion of males) on a patch (r) would be $(n-1)/2n$, where n is the number of foundress females that contribute to the patch. Sex ratios thus decline from 0.5 for large n to 0 when n=1, the latter interpreted as meaning that the female should produce the minimum number of males required to fertilize all her daughters. In haplodiploid species, an additional factor biases the sex ratio: inbreeding causes mothers to be more related to their daughters than their sons, and so a slightly more female-biased sex ratio is favoured (Frank 1985; Herre 1985).

Most empirical support for LMC has come from work with parasitoids and fig-pollinating wasps (Werren 1987; King 1993a; Godfray 1994; Herre et al. 1997). Like other haplodiploid species, females are able to control the sex of an offspring by whether the egg is fertilized or not (Cook 1993). This has allowed natural selection to lead to sex ratios adapted to local conditions. Female-biased sex ratios have been observed in many species whose population structures are likely to lead to LMC, and differences in the average sex ratios of species appear to reflect variation in the intensity of LMC (Waage 1982; West & Herre, in press). In addition, females of several species adjust the sex ratio of their offspring in response to the number of females ovipositing in a patch (Werren 1983;

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Waage & Lane 1984; Frank 1985; Herre 1985, 1987; King & Skinner 1991a; Molbo & Parker 1996; Herre et al. 1997).

However, a growing and largely untested body of theoretical work also suggests a number of reasons why individuals ovipositing simultaneously on the same patch should produce different sex ratios. These factors include variable fecundity amongst the females ovipositing in a patch (Frank 1985; Herre 1985; Yamaguchi 1985; Stubblefield & Seger 1990; Greeff 1997a), whether females are mated to siblings (Greeff 1996), and mixed strategies favoured by the constraint that clutches have to contain integer numbers of eggs (Nagelkerke 1996; West et al. 1997). These models provide testable predictions, but also address two broader issues. First, individual variation in the sex ratio produced by females ovipositing simultaneously on a patch has been observed (Orzack et al. 1991), and it has been argued that such variation presents problems for sex allocation theory, and also for optimality models in general (Orzack & Sober 1994). A consideration of the strategies of individuals may provide an explanation for such variation. Second, the predictions of these models depend critically upon how precisely females are able to assess relevant information about their environment, such as the fecundity and number of other females on the patch (Stubblefield & Seger 1990; Taylor & Crespi 1994; Greeff 1997a; West & Herre, in press). The way in which organisms process information about their environment is a general problem that has implications for many optimality models (Parker & Maynard Smith 1990). Indeed, the lack of a mechanistic basis to most optimality models has been a major criticism of the optimality approach (Krebs & Kacelnik 1991). Local mate competition offers one of the clearest opportunities for investigating this aspect of optimality models because it provides quantitative predictions for a trait that can often be measured relatively easily.

In this paper, we test the predictions of models that allow females ovipositing simultaneously in a patch to produce different clutch sizes. The importance of variable clutch size, under conditions of LMC, was first noted by Werren (1980) and Suzuki & Iwasa (1980), in studies of sequential oviposition in a single host by female parasitoids of the same species. Specifically, they showed that when a female lays eggs on a host that has already been parasitized, she should normally lay a smaller clutch, and a less female-biased, or even male-biased, sex ratio. More recently, Stubblefield & Seger (1990) constructed two LMC models in which females, who produce different clutch sizes, oviposit in a patch simultaneously. In both models females were assumed to be able to assess the number of other females ovipositing in a patch. In the 'complete knowledge model' females know both their own clutch size and also the clutch sizes of other females on the patch (see also Frank 1985; Herre 1985; Yamaguchi 1985; Greeff 1997a). In contrast, the 'self knowledge model' assumes that females know only their own clutch size. Both models make the same qualitative prediction that females laying a relatively small number of offspring should produce a less female-biased sex ratio.

The two models of Stubblefield & Seger (1990), however, also make several different predictions. The complete knowledge model predicts: (1) all the females in a patch produce the same number of males; (2) across patches, the number of males produced by each female increases linearly with the total number of offspring laid in the patch; and (3) all patches produce the same sex ratio. In contrast, the self knowledge model predicts: (1) within a patch, the number of males laid by each female initially increases with her clutch size, and then levels off and eventually declines; (2) across patches, the number of males produced by each female also initially increases, but then reaches an asymptote or even declines with increasing numbers of offspring in the patch; and (3) the sex ratio is predicted to vary between patches, and to be inversely proportional to the total number of progeny laid in the patch.

Here we test the predictions of Stubblefield & Seger's (1990) models with experiments on *Nasonia vitripennis* Walker (Hymenoptera, Pteromalidae), a chalcidoid parasitoid of blowfly larvae. *Nasonia vitripennis* is particularly suitable for testing models of LMC because its natural history closely matches the lifestyle originally considered by Hamilton (1967): hosts occur in small isolated patches, and its flightless males are unlikely to disperse between patches (Werren 1980, 1983). Facultative sex allocation in response to variable clutch size has previously been investigated in *N. vitripennis* for sequential, but not simultaneous, oviposition (Werren 1980, 1984; Orzack & Parker 1986, 1990). In addition, there is likely to have been selection for a response to variable fecundity when females oviposit simultaneously: the variation in brood sizes developing on hosts in the field and laboratory would lead to variation in body size and hence fecundity (Werren 1983; Charnov & Skinner 1984). Multiple females oviposit on patches in the field (Werren 1983; Molbo & Parker 1996) and simultaneous oviposition is common under standard culturing conditions (see Methods).

In our first experiments, we show that the clutch size laid by a female is correlated with her body size. A wide range of female body sizes can easily be produced by manipulating the number of wasps developing together on a host, and this enables us to manipulate clutch size. In our main experiment we used this procedure to investigate how, when two females oviposit simultaneously on a patch, the number of males and the sex ratio that a female produces are influenced by her own clutch size, the clutch size of the other female and the body size of the other female. Body size may be used as a cue of fecundity, and therefore clutch size, because it is unlikely that females will be able to assess accurately the number of eggs laid by another female (Werren 1984; King & Skinner 1991b).

METHODS

Insects

Nasonia vitripennis is a small (about 3 mm long) chalcidoid wasp that parasitizes cyclorrhaphous fly pupae (Whiting 1967). On encountering a host pupa, the female wasp drills through the puparial wall, kills the host by injecting venom and deposits a clutch of 20–40 eggs. Females also feed on the host and are synovigenic, maturing new eggs throughout their life. Male offspring emerge first from the host (after 12 days at 27.5°C), and mate with the females as they emerge. The males can inseminate many females, but females mate only once (van den Assem & Feuth-de Bruin 1977). Males have very reduced wings and are relatively short lived, so all mating is likely to be on the natal patch (King & Hopkins 1963; Werren 1983). We used two strains of *N. vitripennis*: LBII, a wild-type strain (which has purple-brown eyes) and STDR, a red-eyed mutant. We used sex-ratio data only from wild-type females in our analyses; the mutant strain lays significantly more male-biased sex ratios than the wild-type strain (Werren 1980, 1984; King & Skinner 1991a). Females do not appear to be able to assess the sex ratio of eggs in a host (Werren 1984) and so the sex-ratio behaviour of the mutant strain should not affect the behaviour of the wild type.

We obtained the original cultures of *N. vitripennis* from J. H. Werren, University of Rochester (New York State, U.S.A.). Both strains had been in culture for several years and are free from the known sex-ratio-distorting elements. These strains have been routinely cultured by placing a small number of wasps in a tube with some hosts, and so simultaneous oviposition has been frequent. The hosts we used were pupae of *Calliphora vicina*, which were obtained as final-instar larvae from an angling supplier and pupated in 3 days at 27.5°C. Twenty-four hours after pupation, an air space develops between the puparial wall and the pupa and the hosts are then suitable for parasitism. Both hosts and parasitoids were maintained at 27.5 ± 2°C, 70% RH and 16:8 h light:dark photoperiod. At this temperature *N. vitripennis* development took 12 days from oviposition to emergence. Juvenile mortality is very low in this host species, and hence the sex ratio of emerging wasps is very similar to the primary sex ratio (Velthuis et al. 1965; Walker 1967; Werren 1980, 1983, 1984). We obtained females of different sizes by manipulating the number of wasps developing together on a single host (Charnov & Skinner 1988). We did this by presenting females with different host densities: high host densities resulted in small clutches of large offspring, while low host densities resulted in large clutches of small offspring.

Experiments 1 and 2: Body Size, Clutch Size And Fecundity

Our main experiment (3) relied on our being able to manipulate clutch size by using females of different sizes. We tested this assumption in two separate experiments (1 and 2) with wild-type females. We also checked that there was a correlation between the number of eggs laid in an experimental patch and body size in our main experiment (3).

Our aim in experiment 1 was to examine if lifetime fecundity and number of offspring laid per day were correlated with body size. We allowed emerging females to mate and then placed them individually in glass tubes with moist vermiculite, honey-soaked filter paper and five hosts. We removed and replaced the hosts every other day and counted all progeny reared. Females were checked each day, the honey was refreshed and any deaths recorded. We recorded the hind tibia length of each wasp when it died.

In experiment 2 we tested if wasps of different size, treated the same way as in experiment 3, had different numbers of mature eggs at the beginning of the experiment. Females were given the opportunity to mate for 24 h and were then placed with three host pupae for a further 24 h. They were then placed in a glass tube with honey-soaked filter paper for 18 h. After this treatment we dissected the females under a microscope, counted the number of mature eggs in their ovarioles, and recorded their hind tibia length.

Experiment 3: Sex Allocation With Variable Clutch Size

Our aim in this experiment was to test the predictions of Stubblefield & Seger's (1990) two models. To do this we examined how, when two females oviposit simultaneously on a patch, the number of males and the sex ratio that a female produces are influenced by her own fecundity, the fecundity of the other female and the body size of the other female. We pretreated females as described in experiment 2. Females were sized by eye and allocated at random to a female that was either of similar size, considerably larger, or considerably smaller. Pairs of females consisted of one of each strain (STDR and LBII), so that progeny could be assigned to their mother on the basis of eye colour. We conducted the experiments in chambers that allowed females to leave the patch, but not return, so preventing unnaturally high clutch sizes (modified from Werren 1983). After 24 h, we removed the females, recorded their hind tibia length, and counted the number of eggs remaining in their ovarioles. The hosts were kept in separate glass tubes at 27.5°C until the offspring had emerged, when they were sorted by eye colour, sexed and counted.

Statistical Analyses

We analysed all data using generalized linear modelling techniques (McCullagh & Nelder 1983) in the GLIM statistical package (Crawley 1993). We analysed the fecundity data using the assumption of normal errors. For these analyses the explanatory variable, hind tibia length, was cubed since body volume would be more likely to be related to egg reserves. In addition, with this transformation, plots of the residuals showed no obvious patterns, and the ranked residuals against the standard normal deviates were straight lines, supporting our assumption of normal errors.

We initially analysed the sex ratio data assuming binomially distributed errors. However, after fitting the explanatory variables, the ratio of the residual deviance to the residual degrees of freedom was greater than 4, showing considerable overdispersion, suggesting that the data did not fit the assumption of binomial errors (McCullagh & Nelder 1983). Consequently, the sex ratios were arcsine square root transformed and used as the response variable in a multiple regression analysis assuming normal errors. In all subsequent analyses the residuals showed no obvious patterns, and plots of the ranked residuals against the standard normal deviates were straight lines, supporting our assumption of normal errors. The minimum adequate model was found by stepwise deletion (Crawley 1993). Although not presented, we also obtained identical results when we carried out an analysis discarding any broods that contained 100% males, which may have resulted from females constrained to produce only males (females that failed to mate or mated with a sperm-depleted male; Godfray 1988, 1990; Hardy & Godfray 1990; West et al. 1997, 1998).

RESULTS

Experiments 1–3: Body Size, Clutch Size And Fecundity

Experiment 1

Both lifetime fecundity ($F_{1,34}$=84.07, P<0.01, r^2=0.44) and the average fecundity per day ($F_{1,34}$=10.81, P<0.01, r^2=0.24) were significantly positively correlated with female body size (hind tibia length cubed).

Experiment 2

The average number ±SE of eggs in the ovarioles of a female after the experimental pretreatment was 65.67 ± 2.88 (N=61). The number of eggs was significantly positively correlated with body size (hind tibia length cubed; $F_{1,59}$=57.99, P<0.01, r^2=0.50; Fig. 1a).

Experiment 3

Females laid 51.22 ± 2.86 ($\bar{X}$ ± SE; N=86) offspring, and had 39.16 ± 2.13 (N=86) eggs in their ovarioles at the end of experiment 3. Both the number of offspring laid ($F_{1,87}$=40.03, P<0.01, r^2=0.32; Fig. 1b) by a female and the number of eggs remaining in her ovarioles when she left the experimental patch ($F_{1,87}$=48.53, P<0.01, r^2=0.36; Fig. 1c) were significantly positively correlated with her body size (hind tibia length cubed). In the experiment, females oviposited in an average ±SE of 3.35 ± 0.13 (N=86) hosts, laying a mean clutch size ±SE of 15.41 ± 0.69 (N=86). The mean clutch size laid by a female was significantly positively correlated with her body size ($F_{1,87}$=32.54, P<0.01, r^2=0.27) and with the number of eggs remaining in her ovarioles when she left the experimental patch ($F_{1,87}$=33.99, P<0.01, r^2=0.28; Fig. 2).

Experiment 3: Sex Allocation With Variable Clutch Size

The average offspring sex ratio (proportion of males) in experiment 3 was 0.31 ± 0.02 ($\bar{X}$ ± SE; N=86). Simple regression analyses showed that the offspring sex ratio produced by an individual female was: (1) significantly

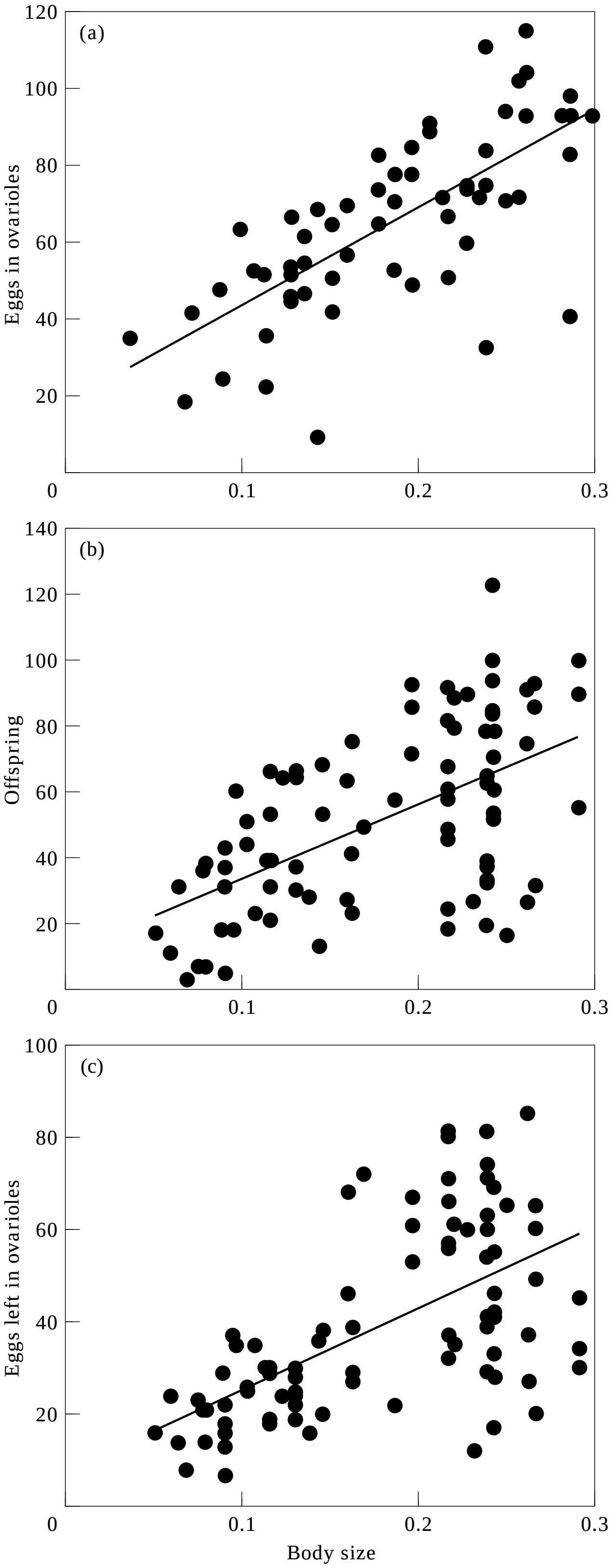

Figure 1. The relationship between a female's body size (the cube of hind tibia length (mm^3)) and: (a) the number of eggs in her ovarioles after the experimental pretreatment (see text for details); (b) the number of offspring laid in the experimental patch; (c) the number of eggs left in her ovarioles after she left the experimental patch.

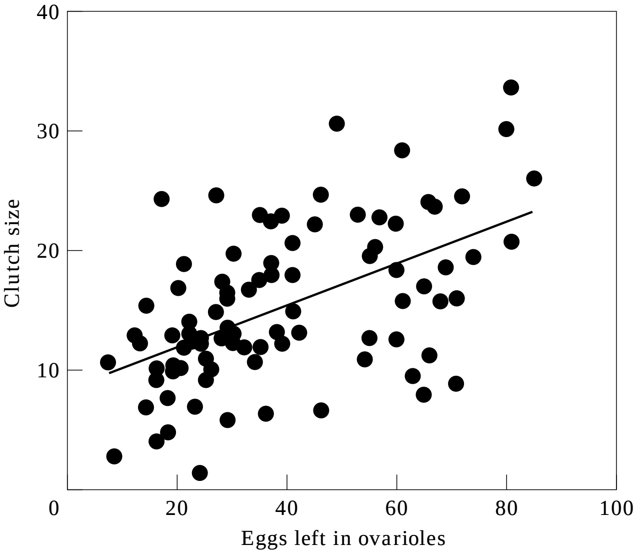

Figure 2. The relationship between the mean clutch size laid on a host by a female, and the number of eggs left in her ovarioles after she left the experimental patch.

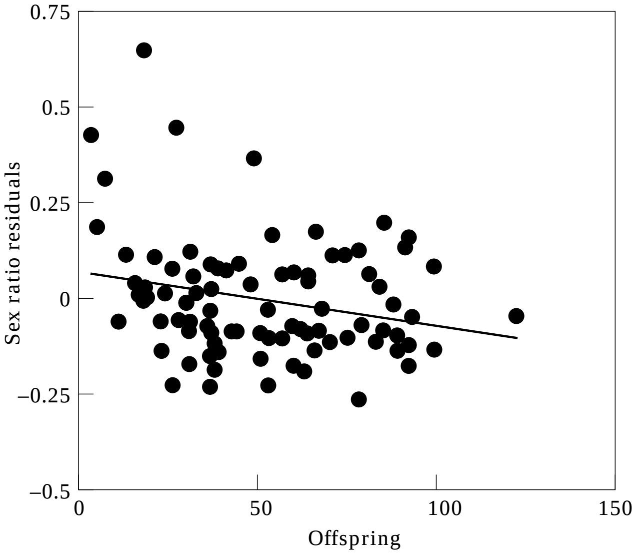

Figure 3. The relationship between the offspring sex ratio produced by a female and the number of offspring that she laid. The figure shows the residuals of sex ratio (arcsine square root transformed) after controlling for the body size (cube of hind tibia length (mm^3)) of the other female on the patch.

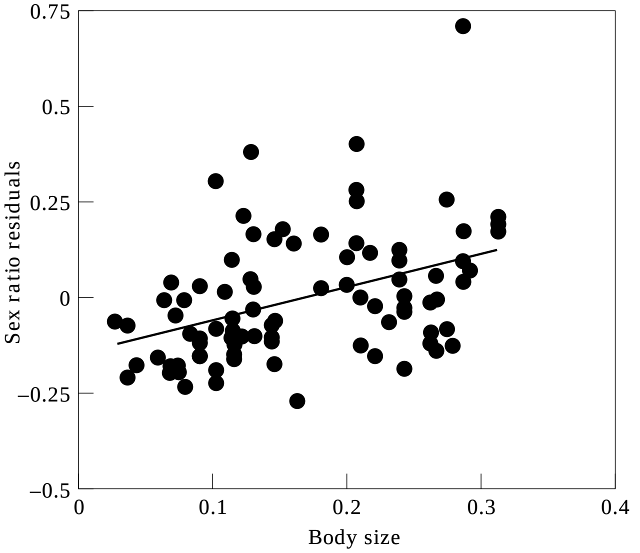

Figure 4. The relationship between the offspring sex ratio produced by a female and the body size (the cube of hind tibia length (mm^3)) of the other female on the patch. The figure shows the residuals of sex ratio (arcsine square root transformed) after controlling for the number of offspring laid by the females whose sex ratios are being considered.

negatively related to the number of eggs that she laid ($F_{1,84}=4.26$, $P<0.05$, $r^2=0.05$); (2) significantly negatively related to the relative number of eggs that she laid on the patch (defined as number of eggs that she laid/number of eggs that the other female laid; $F_{1,84}=7.84$, $P<0.01$, $r^2=0.09$); (3) significantly positively related to the body size (hind tibia length cubed) of the other female ($F_{1,84}=15.72$, $P<0.01$, $r^2=0.16$); and (4) showed no significant relationship with the number of eggs that the other female laid ($F_{1,84}=1.90$, NS, $r^2=0.02$), her own body size (hind tibia length cubed; $F_{1,84}=0.36$, NS, $r^2<0.01$), or her average clutch size ($F_{1,84}=0.79$, NS, $r^2=0.01$).

Multiple regression analyses showed that two variables were the most important, and significant. The offspring sex ratio produced by an individual female was significantly negatively related to the number of eggs that she laid ($F_{1,83}=7.82$, $P<0.01$; Fig. 3), and significantly positively related to the body size (hind tibia length cubed) of the other female on the patch ($F_{1,83}=15.14$, $P<0.01$; Fig. 4). Together these variables explained 20% of the variation in the data. In contrast, the offspring sex ratio produced by a female showed no significant relationship with her body size (hind tibia length cubed; $F_{1,82}=1.34$, NS), the relative number of eggs that she laid ($F_{1,82}=0.44$, NS), her average clutch size ($F_{1,82}=0.06$, NS) or the number of offspring laid by the other female on the patch ($F_{1,82}=0.26$, NS). The interaction term between the number of eggs that a female laid and the size of the other female was also not significant ($F_{1,82}=0.19$, NS).

We now turn to analysing the number of males produced by each female. These analyses are not statistically independent of the previous sex ratio analyses, but it is useful to look at the data both ways to test different predictions of Stubblefield & Seger (1990). In these analyses the *X* variable (total number of offspring laid in the patch) includes the *Y* variable (number of male eggs laid by a female) and so they are not independent. However, we are interested in the exact quantitative form of the relationship, not merely whether there is a correlation. The number of male eggs laid by a female was significantly positively related to the total number of offspring laid by both females in the patch ($F_{1,87}=89.95$, $P<0.01$, $r^2=0.51$). The intercept of this line was not significantly different from the origin ($F_{1,87}=0.67$, NS). In addition, two further analyses suggest that the relationship between number of sons laid by a female and the total

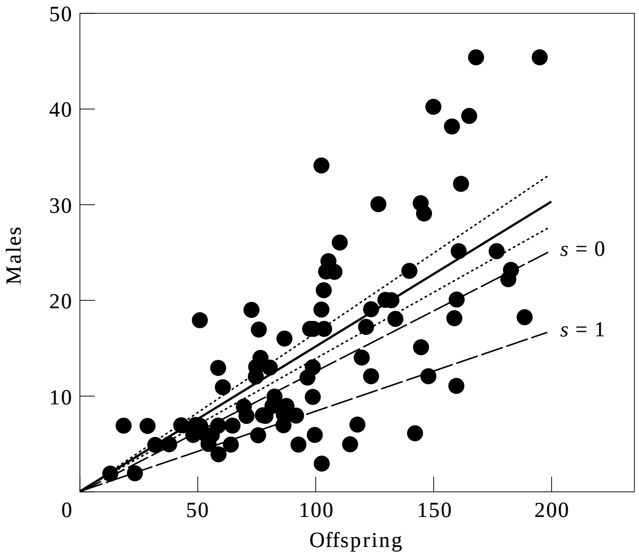

Figure 5. The relationship between the number of males produced by a female and the total number of offspring laid in the patch. The solid line is the regression line through the data, and the dotted lines its 95% confidence intervals. The dashed lines represent the range of slopes predicted by Stubblefield & Seger's (1990) complete knowledge model for no (s=0) and total (s=1) inbreeding, respectively.

number of offspring laid was linear: (1) the inclusion of a quadratic term (total number of offspring laid in the patch squared) was not significant ($F_{1,87}$=1.53, NS); and (2) a plot of the residuals against the total number of offspring in a patch showed no pattern ($F_{1,87}$=0.56, NS, r^2=0.006). Consequently, the relationship between the number of males laid by a female (m) and the total number of offspring laid by both females in the patch (x) was best described by the equation m=0.151 (±0.014) x (±95% confidence interval; Fig. 5).

DISCUSSION

We have shown that, when two *N. vitripennis* females oviposited in a patch, the offspring sex ratio produced by individual females was: (1) negatively correlated with the number of offspring that she laid (Fig. 3); and (2) positively correlated with the body size of the other female on the patch (Fig. 4). In addition, we have shown that larger females produced greater numbers of eggs and laid more offspring in the experimental patch (Fig. 1). Consequently, the offspring sex ratio produced by a female became more female-biased as she produced a greater proportion of the total offspring laid on the patch. This sex ratio adjustment agrees qualitatively with that predicted by local mate competition models which allow for females producing variable clutch sizes (Frank 1985; Herre 1985; Yamaguchi 1985; Stubblefield & Seger 1990).

Two circumstances are required for females to be selected to adjust their sex ratio in response to the body size of the other female on the patch. The first condition is that females cannot directly assess the exact number of eggs laid by another female. *Nasonia vitripennis* females appear to be able to assess the number of eggs laid in a previously parasitized host, but only after a delay of 48 h between ovipositions (Werren 1980, 1984; King & Skinner 1991b). Consequently, it is unlikely that a female would be able to count the eggs laid by another female that is ovipositing simultaneously. The second condition is that body size provides a reliable estimate of the clutch size that a female is likely to produce. We have shown that a female's body size is positively correlated with the number of eggs she produces, the number of offspring that she lays on an experimental patch, the number of offspring that she lays on each host, and the number of eggs left in her ovarioles when she leaves the experimental patch. The high number of physical contacts between females ovipositing simultaneously on a patch (King et al. 1995) would provide opportunities to assess the size of other females. These results suggest that the cues used to adjust the offspring sex ratio in response to relative investment are different when females oviposit simultaneously on a patch to those used when they oviposit sequentially on a host (Wylie 1965, 1973; Werren 1984; King & Skinner 1991b).

We also tested a quantitative prediction of Stubblefield & Seger's (1990) two models. Specifically, the complete knowledge model predicts that the relationship between the number of males produced by a female and the total number of offspring laid in that patch should be linear and pass through the origin. In contrast, the self knowledge model predicts that this relationship is nonlinear, reaching an asymptote at high total offspring number. Our data showed a linear relationship through the origin, as predicted by the complete knowledge model (Fig. 5). However, the complete knowledge model also predicts that the slope of this line should be given by the equation m=bx/4, where m is the number of males produced by a female, x is the total number of offspring produced on the patch, and b is a mother's proportional relatedness to her sons (for haplodiploids $b=(2-s)/(4-s)$, where s is the probability of mating with a sibling; Stubblefield & Seger 1990). The slope is therefore expected to fall between 0.083 (mating only with siblings) and 0.125 (no mating with siblings). Our data gave a slope of 0.151 ± 0.014 (±95% confidence interval), which is significantly steeper than that predicted by Stubblefield & Seger's complete knowledge model.

A possible explanation for this steeper slope would be if the fitness function around the optimal strategy is not symmetrical: the decrease in fitness for producing too few females may be greater than that for producing too many males (Greeff 1997b; West & Herre 1998). In this case variation, which is substantial, would lead to a greater number of males being favoured. Another possibility is that females have partial and not complete knowledge: our results suggest that females indirectly estimated the fecundity of other females by their body size. The theoretical consequences of partial knowledge are unknown, although we might expect it to lie between the extremes of self and complete. An alternative possibility is that although simultaneous oviposition does occur in nature and laboratory cultures, it happens too infrequently for females to respond perfectly (Herre 1987; Herre et al. 1997). Although multiple foundress patches do occur in nature (Werren 1983; Molbo & Parker 1996), we have no estimate of the relative frequency of simultaneous and sequential oviposition. Another possibility is that, in nature, some mating occurs away from the natal patch (Hardy 1994).

Our data also support one of the predictions of clutch size theory. Numerous theoretical models predict that females with greater egg reserves should lay larger clutches (Charnov & Skinner 1984, 1985, 1988; Parker & Courtney 1984; Skinner 1985; Waage & Godfray 1985; Mangel 1987; Wilson & Lessells 1994). We have shown that larger females had greater egg reserves before and after ovipositing on a patch, and that they laid larger clutches (Fig. 1). Furthermore, the mean clutch size laid on a host by a female was significantly positively correlated with the number of eggs remaining in her ovarioles when she left the patch (Fig. 1). This suggests females are facultatively laying smaller clutches when they have fewer mature eggs (see also Rosenheim & Rosen 1991). If females commonly have limited egg reserves in laboratory conditions, then this may help explain why observed parasitoid clutch sizes are consistently below that predicted to maximize the fitness return from each host (termed the Lack clutch size; Charnov & Skinner 1984, 1985; Waage & Godfray 1985; Hardy et al. 1992; Vet et al. 1994; see also Godfray 1994; West et al. 1996).

Nasonia vitripennis females adjust their offspring sex ratio facultatively in response to a number of factors (Werren 1980, 1983, 1984; Parker & Orzack 1985; Orzack & Parker 1986, 1990; King & Skinner 1991a, b; Orzack et al. 1991; King 1992, 1993b; Molbo & Parker 1996). Here we have demonstrated that females also adjust their offspring sex ratio as predicted by LMC models in which simultaneously ovipositing females lay different numbers of offspring. Specifically we have shown that females adjust their offspring sex ratio according to the number of offspring they lay, and also in response to the size (and hence fecundity) of another female ovipositing on the patch. This result may help explain the existence of the much-debated variation in offspring sex ratios between *N. vitripennis* females ovipositing in small groups (Orzack et al. 1991; see also Godfray 1994; Herre 1995; Nagelkerke 1996; Herre et al. 1997; West et al. 1997). Our results also stress the importance of understanding how individuals obtain information about their environment. How individuals process information about their environment, and with what accuracy, is an important part of investigating the evolution of animal behaviour in different environments.

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