Anim. Behav., 1994, **47**, 687–696

Sex ratio and foundress number in the parasitoid wasp *Bracon hebetor*

J. M. COOK, A. P. RIVERO LYNCH & H. C. J. GODFRAY*
Department of Biology and NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.

(Received 9 November 1992; initial acceptance 11 January 1993; final acceptance 23 February 1993; MS. number: 4234)

Abstract. As predicted by the theory of local mate competition, the offspring sex ratios of many parasitoid wasps become increasingly male biased as the number of conspecific females ovipositing in a patch rises. The braconid wasp *Bracon hebetor* appears to be an exception. Recent experiments have suggested that wasps ovipositing in the presence of a conspecific female produce more daughters than solitary wasps. Larval competition is more intense when two females oviposit together and it has been suggested that females lay fewer sons in these circumstances because the resultant small males have poor mating success. Experiments are reported that (1) compare the sex ratio of solitary and paired *B. hebetor*; (2) investigate the importance of differential mortality and (3) explore the relative mating success of small and large wasps. Paired and solitary wasps produced the same sex ratio and there was no evidence of differential mortality. Small males were able to mate both large and small females and, at least in the laboratory, appeared to suffer no disadvantage in competition with larger males. There are statistical problems with some previous analyses of sex ratio and foundress number in *B. hebetor*, and there are also problems in making inference about adaptation from inbred strains of a naturally outbred species.

Much of the empirical support for the theory of sex allocation has been obtained through experiments with parasitoid wasps. Like other Hymenoptera, female parasitoid wasps are able to control the sex of their offspring at oviposition by fertilizing or not fertilizing the egg. The ability of the mother to determine the sex of her offspring allows natural selection to influence female behaviour to produce sex ratios adapted to local conditions. Biased sex allocation patterns are common among parasitoid wasps and, in large part, are successfully explained by sex allocation theory (Charnov 1982; Waage 1986; King 1987; Werren 1987; Godfray 1993).

One of the most important factors influencing parasitoid sex ratios is local mate competition (Hamilton 1967). Mating frequently takes place between siblings, and sons often compete together for mates. In these circumstances, the mother obtains diminishing fitness returns from the production of sons and the evolutionarily stable strategy (ESS) is for the sex ratio to be biased towards females. The extent of the female bias depends on the severity of competition between siblings. Hamilton (1967) showed that if mating occurred randomly between the progeny of n females (called foundresses), each of whom produce the same number of offspring, the ESS sex ratio is $(n-1)/2n$. When $n=1$, this expression predicts a sex ratio of zero which is interpreted as only enough sons to fertilize the female's daughters; for $n>1$ the sex ratio becomes progressively less female biased, approaching 0·5 as n becomes large. This result applies exactly to diploids. In haplodiploid species, mating between siblings causes the mother to share more genes with daughters than with sons; the increased coefficient of relatedness of daughters to mothers selects for a small extra female bias in the ESS sex ratio (Hamilton 1979; Taylor & Bulmer 1980). Hamilton's (1967) original model has been extended in many directions (e.g. Taylor 1981; Frank 1985, 1986; Nunney & Luck 1988) and has been tested both experimentally and using comparative data (for reviews see King 1987; Godfray 1993). For example, a number of workers have manipulated or observed natural variation in foundress number and found that progeny sex ratio varies in line with theoretical predictions (Werren 1983; Waage & Lane 1984; Frank 1985; Herre 1985, 1987; King & Skinner 1991; though see Orzack 1986 for a dissenting view of the explanatory power of theory).

---

*To whom all correspondence should be addressed.

0003–3472/94/030687+10 $08.00/0

Recently, Galloway & Grant (1989) reported unusual results from a foundress manipulation experiment using the wasp *Bracon hebetor* Say (=*Habrobracon juglandis*; Braconidae). This wasp attacks the larvae of stored product moths (Lepidoptera, Pyralidae) laying a clutch of eggs which develop gregariously on the host. *Bracon hebetor* has a female-biased sex ratio which has sometimes been interpreted as due to local mate competition (see discussion in Taylor 1988). However, Galloway & Grant reasoned that local mate competition is unlikely to explain the female-biased sex ratio of *B. hebetor*. This is because local matings would often involve siblings and inbreeding depression is severe in species such as *B. hebetor* that produce diploid males (discussed later). Consequently, *B. hebetor* is expected to outbreed (Whiting 1961; Galloway & Grant 1989) and this prediction has recently received strong support from observations of mating behaviour made in a semi-natural environment by Antolin & Strand (1992).

Galloway & Grant compared the brood sex ratios of two strains of wasp when one or two females oviposited on the same host. They found that in one strain, but not the other, the sex ratio was more female-biased in the two-foundress case. This is a trend in the opposite direction to that predicted by local mate competition theory. Galloway & Grant suggested an adaptive explanation for their results. When two females oviposit together, the greater number of eggs laid on the host results in increased competition for resources and, in consequence, smaller adult wasps. Grosch (1948) had previously reported that dwarf male *B. hebetor* were unable to mate with normal-size females while dwarf females can both mate and successfully produce progeny. Galloway & Grant suggested that females ovipositing on overcrowded hosts might lay fewer male eggs as these would result in adults with very low fitness.

We report here a series of experiments with *B. hebetor* designed to investigate sex allocation and foundress number. We repeat Galloway & Grant's experiments and investigate changes in clutch size when one or two females attack the same host. We manipulate the numbers of eggs per host to explore any confounding effects of differential mortality of the sexes at increased larval densities. We explore the ability of large and small males to copulate successfully with females of different size, and to compete with other males for access to females. Our results support neither Galloway & Grant's hypothesis, nor the importance of local mate competition. We discuss other factors that may influence sex ratio in *B. hebetor*.

Studies of sex allocation in *B. hebetor* are complicated by the sex determination system found in this wasp. Haploid (unfertilized) eggs always develop into males but diploid (fertilized) eggs become females only if the individual is heterozygous at a sex determination locus (Whiting 1943; Whiting 1961; reviewed by Cook, in press). Diploid, homozygous individuals normally die as embryos although some survive to become adult males (Whiting 1961; Petters & Mettus 1980). Wild populations of *B. hebetor* are probably highly polymorphic at the sex determination locus so that only a small proportion of diploid eggs develop as males. However, laboratory strains of *B. hebetor* often carry only two alleles, in which case 50% of diploids are male. Based on observed sex ratios, Galloway & Grant estimated that one of the strains they used had two alleles, the other four.

METHODS

Insects

We used two strains of *B. hebetor*: a wildtype strain (Lumberton) with normal black eyes, and a mutant strain (Peach) with peach-coloured eyes. The difference in eye colour is caused by a single recessive gene (Whiting 1961). To remove sex ratio variation due to the number of sex determination alleles, we initiated populations of the two strains of wasps from pairings of a virgin female with her haploid son. In the absence of further mutation, each strain carries two alleles segregating at the sex determination locus. All experiments were conducted with wasps from the first six generations after the mother–son cross.

The host used both in the experiments and in the stock cultures was *Corcyra cephalonica* Stainton (Pyralidae). Hosts were reared on a medium consisting of 70% wheatgerm and 30% maize meal supplemented with 50 ml glycerol and 10 g Bakers' yeast per 2·5 kg dry medium. Wasps and moths were maintained in a constant temperature room at 30°C and 70% relative humidity, the moths in darkness, the wasps in a 16:8 h light:dark cycle.

It is important that all wasps are maintained under identical conditions prior to use in an experiment. Females of several species of parasitoid are known to use contact with other females, or

Table I. The sex ratio and brood size of the progeny of single and paired females of the two strains of *B. hebetor* ($\bar{X}\pm$SE)

		Single foundress	Paired foundress
Peach	Sex ratio	0·500±0·029	0·496±0·035
	Brood size	15·53 ±0·88	9·37 ±1·36
	Replicates	41	27
Lumberton	Sex ratio	0·608±0·038	0·600±0·066
	Brood size	9·59 ±0·68	6·38 ±0·54
	Replicates	29	16

Only data from the first brood produced by each wasp are shown.

contact with the chemical traces of other females, as proximate cues to bias their sex ratio (e.g. Viktorov & Kochetova 1971, 1973; Strand 1988). Groups of 20 newly emerged females were placed in round plastic pots (12 cm diameter, 6 cm depth) with 20 newly emerged males and provided with four hosts and dried honey for food. After 24 h, females were removed and assigned randomly to experimental treatments.

Experiment 1. Foundress Number and Sex Ratio

In this experiment we determined whether sex ratio was influenced by foundress number. Unfortunately little is known about foundress number in the field but it seems reasonable to consider cases where either one or two females oviposit together. Female wasps of the two strains were placed either alone (Lumberton or Peach female) or in pairs (Lumberton female plus Peach female) in a petri dish 5 cm in diameter with a single host and some dried honey. All hosts were approximately the same size (30–40 mg) and their weights were recorded. Wasps were allowed to remain with the host for 24 h after they commenced oviposition. They were then transferred to a new petri dish with a fresh host for another 24 h, and this procedure continued for five hosts or until one of the wasps died. Each brood was kept until the adult wasps emerged and the sex ratio of the progeny of each female recorded. If a female produced no daughters she was assumed to be unmated and her sex ratio score was discarded (although in paired treatments the sex ratio of the progeny of her partner was included in the analysis). If a female failed to lay any eggs, the data from her partner were also discarded. The resultant replication of each treatment is shown in Table I.

In a separate experiment, wasps of the Peach strain were placed alone or in pairs on a single host. In this design, it is not possible to distinguish the sex ratios of the progeny of individual females in the paired treatment; however, any effects of asymmetric competition between the two strains can be excluded.

We analysed sex ratios (proportion of males) in two ways. First, we treated the sex ratio of each female's progeny as a response variable in a 2×2 factorial experiment with strain and experimental treatment as the two factors (in the second experiment with Peach wasps treatment alone was the single factor). We used generalized linear modelling techniques (McCullagh & Nelder 1983) implemented on the GLIM statistical package to assess the importance of the explanatory variables assuming binomial error variance and a logit link function. The appropriateness of the assumption of binomial errors was checked by comparing the residual deviance with the residual degrees of freedom after fitting the full model. Large relative values of the residual deviance indicate overdispersion which may result in artefactually narrow confidence limits. Where the residual deviance exceeded the residual degrees of freedom by more than 20% we rescaled the deviance using William's algorithm (Collett 1991). Second, we follow Galloway & Grant (1989) in combining across replicates the number of offspring of each sex laid by Lumberton and Peach females in each of the two treatments. The resulting contingency table was analysed using the *G*-test. Brood size was analysed using standard ANOVA assuming normal error variance (we use clutch size to denote the number of eggs laid and brood size to describe the number of larvae or adults that emerge from the clutch).

Experiment 2. Foundress Number and Clutch Size

In experiment 2 we investigated how foundress number affects clutch size and hence the competition for host resources among parasitoid larvae. Female wasps of the Peach strain were placed either alone or in pairs in a 5 cm petri dish with a single host and some dried honey. Two sizes of host were used: small (20–35 mg) and large (45–70 mg). Wasps were allowed to remain with the host for 24 h after they began to oviposit and then the number of eggs laid were counted under a binocular microscope. The four treatments were replicated 15 times; in some cases females died or did not lay eggs leading to reduced replication in the statistical analysis.

Experiment 3. Differential Mortality

In experiment 3 we investigated whether females, haploid males or diploid males suffer disproportionate mortality at high larval densities. Peach females were mated with Lumberton males (in crosses known to involve two sex determination alleles) and allowed to oviposit on host caterpillars. This mating combination was chosen because all diploid offspring (male or female) have dark eyes and all haploid offspring peach-coloured eyes. The three sex types (haploid male, diploid male and female) are thus phenotypically distinguishable. Eighty paralysed hosts weighing 30–40 mg were cleared of parasitoid eggs and then artificial clutches of 10, 20, 30 and 40 eggs were created by transferring eggs with a pin. Eggs in each clutch were chosen randomly from a large pool and placed on the host in positions typical of natural oviposition. Parasitoids were allowed to grow to the adult stage and the number of males, diploid females and diploid males recorded. In the data analysis, the four clutch size manipulations were considered separate experimental treatments.

Experiment 4. Body Size and the Ability to Mate

In experiment 4 we investigated whether adult body size influences successful mating. Pairs of wasps of different size were placed together in a petri dish for 40 h and supplied with dried honey for food. Four size combinations were used: large male/large female; large male/small female; small male/large female; and small male/small female. Large wasps were obtained by allowing a female to lay only a few eggs on a host, small wasps by removing larvae from a host before they were fully grown. All wasps were isolated as pupae to ensure no matings occurred before the experiment. It is difficult to measure accurately the size of an adult wasp while it is still alive and so the two size categories of wasps were initially separated by eye. At the end of the experiment, all wasps were killed and their thorax length measured under a binocular microscope. Post-mortem measurements indicated virtually no overlap of the two size categories. After mating, each female was provided with a host weighing 30–40 mg. The female was given a fresh host after 24 h and the procedure repeated until death. All wasps used in this experiment were of the Peach strain.

Experiment 5. Body Size and Competition Among Males

In experiment 5 we tested whether small wasps were disadvantaged in competition for mates. Large and small males were obtained as in experiment 4. Wasps were initially categorized by eye and their exact size measured after death. Again, post-mortem measurements indicated virtually no overlap of the two size categories. Pairs of males, one large and one small, were allowed to compete for either one, two or four females in a large petri dish (diameter 9 cm, depth 1·5 cm). To identify paternity, a Peach and a Lumberton male were used in each experiment while all females used were Peach (recall that the eye colour mutant is recessive so that Lumberton/Peach crosses have the Lumberton phenotype). To control for possible differences in the number of sex alleles in Peach × Lumberton and Peach × Peach crosses, and also for differences in the competitive ability of the two strains, two sets of experiments were performed, one with small Peach males, and one with small Lumberton males. Each of the six experimental combinations was replicated 20 times. The significance of the results was assessed using log-linear analysis.

RESULTS

Experiment 1. Foundress Number and Sex Ratio

Table I shows the sex ratio and brood size of the first broods of the two strains of wasps. We first analyse the results treating the sex ratio of the progeny of each female as the response variable.

Table II. The total numbers of males and females produced by different genotypes ovipositing alone and in pairs

Genotype		Single foundress		Paired foundress			
		Males	Females	Males	Females	*G*-test	*P*
Lumberton	1st brood	175	103	63	69	8·44	0·0037
	All broods	483	337	549	498	7·78	0·0053
Peach	1st brood	328	313	137	116	0·65	NS
	All broods	874	704	553	435	0·03	NS
Combined	1st brood	503	416	200	185	0·85	NS
	All broods	1357	1041	1082	893	1·43	NS

The data from the first brood and from all broods combined are analysed separately.

There was no significant difference between the sex ratio produced by single and paired females of either genotype although Peach females produced a significantly more female-biased sex ratio than Lumberton females ($\chi^2_1 = 12{\cdot}3$, $P < 0{\cdot}01$); the interaction between genotype and foundress number was not significant. The brood size of both genotypes was smaller when two females oviposited per host ($F_{1,109} = 23{\cdot}9$, $P < 0{\cdot}001$) and broods of Lumberton were larger than Peach ($F_{1,109} = 17{\cdot}3$, $P < 0{\cdot}001$); again, the interaction was not significant. To see if brood size might explain variation in the sex ratio we added this variable to the statistical model containing genotype and foundress number but found no significant increase in the explanatory power of the model ($\chi^2_1 = 2{\cdot}3$, NS).

We also analysed the sex ratio of all the offspring produced by each female on five hosts (fewer if the female died during the experiment). The analysis included three factors: genotype, foundress number and the number of broods produced before death. No interactions were significant and the only significant main effect was brood number: females that laid more broods tended to produce a greater proportion of males, perhaps because of sperm depletion (see Discussion). Thus Peach females produce more females in their first brood but over five broods the two genotypes on average produce the same sex ratio.

To facilitate comparison of our analysis with that of Galloway & Grant (1989), we analysed our results using a *G*-test. For both first broods and all broods combined there were no differences in the offspring sex ratio of single and paired foundresses of the Peach strain, or for both strains combined (Table II). However, there were significant differences in the sex ratio of Lumberton offspring with more females produced in the paired treatment. These findings contrast with the analysis using logistic regression, a discrepancy we return to in the Discussion.

In the experiment using wasps of a single strain (Peach), there was no significant difference between sex ratios laid by single females ($\bar{X} \pm \text{SE} = 0{\cdot}506 \pm 0{\cdot}098$) and paired females ($0{\cdot}502 \pm 0{\cdot}046$). Here, 13·46 (SE 0·78) wasps emerged on average from clutches laid by a single female while 17·07 (SE 1·92) emerged from clutches laid by two females. Clutches laid by two females were thus about 27% larger.

Experiment 2. Foundress Number and Clutch Size

Single wasps laid on average 34·31 (SE 3·23) eggs and paired wasps together laid 51·83 (SE 4·72), an increase in the number of eggs per host of just under 50%. In an analysis of variance, host weight did not significantly improve the fit of a statistical model containing foundress number, although there was a trend for wasps to lay more eggs on larger hosts ($F_{1,45} = 3{\cdot}46$, critical value ($P < 0{\cdot}05$) $= 4{\cdot}08$). Comparing these results with the number of adult wasps produced by Peach females ovipositing alone or in pairs, the survival of young on hosts attacked by one female is approximately 39% and on hosts attacked by two females 33%.

Experiment 3. Differential Mortality

Table III shows the numbers and proportions of adult females, haploid males and diploid males. Because there were only two sex determination

Table III. The average number and proportion of females, haploid males and diploid males that developed successfully on hosts with different egg densities

	Egg density			
	10	20	30	40
Females	2·89 ± 0·26 0·54	4·80 ± 0·61 0·53	6·68 ± 0·32 0·55	6·78 ± 0·41 0·60
Haploid males	2·42 ± 0·29 0·45	3·75 ± 0·13 0·41	5·05 ± 0·38 0·42	4·26 ± 0·29 0·37
Diploid males	0·05 ± 0·05 0·01	0·57 ± 0·16 0·06	0·36 ± 0·74 0·03	0·31 ± 0·57 0·03

Table IV. Results of the experiment to determine the mating success of large and small males

	No eggs laid	Unmated	Mated	Total
Small male/small female	3	1	14	18
Small male/large female	1	3	28	32
Large male/small female	1	1	16	18
Large male/large female	1	2	27	30
Total	6	7	85	98

The number of females that failed to lay any eggs, the numbers laying only male eggs and hence assumed to be unmated, and the numbers laying eggs of both sexes are shown.

alleles present in each strain, females laid equal numbers of daughters and diploid males. The much smaller proportion of diploid males among the adult progeny indicates that, as expected, they are particularly susceptible to juvenile mortality. However, the proportion of the three sex types was not significantly influenced by egg density. As expected there was a strong effect of egg number on overall survival ($\chi^2_3 = 30{\cdot}14$, $P < 0{\cdot}01$). The adult size of wasps of each sex type was not significantly different, but clutch size had a strong influence on adult size ($F_{3,165} = 183{\cdot}5$, $P < 0{\cdot}001$); the interaction between sex type and clutch size was not significant.

Experiment 4. Body Size and the Ability to Mate

Table IV shows the mating success of the four combinations of large and small males and females. Eighty-seven per cent of females mated successfully and laid eggs. There was no significant effect of either the difference in male and female size, or the absolute size of either sex, on the probability of failing to oviposit, or the probability of being mated. We also found that neither the lifetime production of offspring, nor the lifetime production of daughters (a measure of the father's reproductive success), was influenced by the absolute or relative size of the parent.

Experiment 5. Body Size and Competition Among Males

There were four outcomes to the competition experiment (Table V). In 15% of replicates the females either died before presentation with a host or laid no eggs; in a further 8% of replicates the female laid only male eggs and hence was probably unmated; in 2% of cases the female produced eggs of both phenotypes and was thus definitely mated by both males, while in the remaining 75% of replicates the female produced uniform broods of one phenotype indicating that a single male inseminated all the female's eggs. The ratio of the four outcomes was statistically independent of the strain of the large and small wasps.

Table V. The reproductive success of females in the male competition experiments

Males	Females No eggs laid	Unmated	Uniform broods	Mixed broods	Total
Small wasp Peach	11	4	54	2	72
Small wasp Lumberton	10	8	53	1	71
Totals	*21*	*12*	*107*	*3*	*143*

Females either lay no eggs, lay only male eggs (unmated), produce uniform broods of one phenotype, or mixed broods of both phenotypes.

Table VI. The genotype of the successful wasp in the uniform broods of the male competition experiment

No. of females	Successful male Large Lumberton	 Large Peach	 Small Lumberton	 Small Peach
1	7	4	5	2
2	12	5	10	4
4	21	5	24	8
Total	40	14	39	14

Table VI shows the genotype of the successful male in the replicates that produced uniform broods. Size, or the interaction between size and the number of females, had no significant effect on the outcome of competition ($\chi^2_4=3{\cdot}18$). However, Lumberton males were significantly more successful in competition than Peach males, and their advantage was independent of the number of females in the mating group ($\chi^2_3=25{\cdot}37$, $P<0{\cdot}001$). We also analysed the influence of male genotype and male size (thorax length) on the number of daughters produced by mated females with uniform broods. Females mated with Lumberton males produced significantly more daughters ($\chi^2_1=60{\cdot}79$, $P<0{\cdot}001$) but size and the interaction of size and genotype had no significant influence on the number of female progeny.

DISCUSSION

There are now many examples of parasitoids that produce a less female-biased sex ratio in the presence of conspecifics. Galloway & Grant's (1989) experimental result with *B. hebetor* is an interesting exception to this rule. To explain their results, Galloway & Grant (1989) argued that local mate competition does not occur in *B. hebetor* and proposed that females produce more daughters in circumstances that adversely affect the fitness of sons. This is a special case of conditional sex expression first suggested by Trivers & Willard (1973) and rigorously modelled by Charnov (1979). In our experiments we have tried to replicate the original result, to investigate whether differential mortality of one sex or of diploid males occurs, and to examine whether male mating success is influenced by adult size.

We were unable to find a difference in the sex ratio produced by females ovipositing singly and in pairs. Our procedures differed from Galloway & Grant in two ways: we used a smaller host, and we analysed our results using logistic regression. Today *B. hebetor* is normally collected from grain silos and similar artificial habitats where it parasitizes a variety of pyraustine pyralids, especially those in the genera *Ephestia* and *Plodia*. Both the hosts used by us (*Corcyra cephalonica*) and by Galloway & Grant (*Galleria mellonella*) are galleriine pyralids that are readily parasitized by the wasp. We chose *C. cephalonica* as it is a similar size to the more normal hosts of this parasitoid while *G. mellonella* is distinctly larger. If females lay more males in circumstances where resource competition among their larvae is relatively severe, more biased sex ratios should be found on *C. cephalonica* in comparison with *G. mellonella*.

There is a problem in using log-linear analysis (*G*-test) of eggs summed across replicates to assess the significance of the sex ratio adjustment. In experiments such as these the independent statistical unit is the sex ratio of the female's offspring and this should be analysed using logistic regression (or equivalent parametric or non-parametric procedures). Performing a *G*-test on the total number of eggs implicitly assumes that the probability of each egg being male or female is determined by a systematic component and an error component, and that the distribution of errors is identical and independent. Unfortunately, eggs from the same parent are not independent and this reduces the degrees of freedom. Suppose that an experiment is carried out with only one female in each treatment. Without replication no statistical inference can be made about the effect of treatment on the sex ratio. However, if the female lays enough eggs it is possible to get a significant *G*-test. Galloway & Grant of course replicated their experiment but we fear that these problems may have led to an erroneously significant result. It is interesting that for the Lumberton strain we found no significant difference in the sex ratio using logistic regression, yet were able to obtain a highly significant *G*-test.

The sex ratio of broods laid by single and paired females may differ if greater competition for host resources results in the differential mortality of one sex or, in the case of *B. hebetor*, in the differential mortality of diploid males. We found that pairs of females laid more eggs than single females (although less than twice as many) and that mortality is greater in broods produced by two females. However, in our egg manipulation experiment, we found no evidence of a relationship between egg density and differential mortality of females, haploid males, or diploid males. Differential mortality has been implicated in several studies of competition in gregarious parasitoids but typically female larvae suffer more than males. Benson (1973) and Taylor (1988) observed differential mortality of females in *B. hebetor*, but Galloway & Grant noted that increased female mortality at high densities could not explain their results.

Grosch (1948) observed that dwarf males were sometimes produced in *B. hebetor* that were physically incapable of mating. We tested the ability of *B. hebetor* to mate using small males that had been artificially created by removing larvae from hosts before they were fully grown. Most of the small wasps obtained in this way were considerably smaller than those emerging from hosts naturally parasitized by the wasps. We found no evidence that small males were unable to mate with either large or small females. We also found no evidence that small males were at a disadvantage in competition for mates with large males, although experiments on mate competition in unnatural environments must obviously be interpreted with caution. Wasps of the Lumberton strain were consistently more successful at obtaining matings than wasps of the Peach strain. We have no explanation for this result: possibly Lumberton males are intrinsically superior competitors to the Peach strain. Alternatively, females may prefer to mate with a different phenotype to reduce the probability of inbreeding (Grant et al. 1980) or may avoid mutant males. Peach females produced more daughters when crossed with Lumberton males than when crossed with Peach males. The reason for this is that while Peach × Peach crosses always contain two sex alleles, Peach × Lumberton crosses may contain three alleles and thus produce no diploid males.

In many ways, laboratory populations of *B. hebetor* are poor experimental models to investigate sex ratio adaptations. Strains that have been kept for many generations in the laboratory may have been subject to artificial selection. In *B. hebetor*, these problems are compounded by the origin of many laboratory strains which are derived from wasps caught in warehouses and other sites that may have been colonized relatively recently. Another problem is that laboratory strains tend to be inbred and to have very few alleles at the sex determination locus (Petters & Mettus 1980) leading to high diploid male production. Galloway & Grant estimated their wasps to have two to four alleles while we deliberately reduced the number to two. This action maximizes diploid male production, which is probably low in natural populations, but is preferable to having an unknown but potentially large variance between broods due to diploid male production. While diploid males are a potential complicating factor, our experiments indicated that they had a uniform high mortality in the different experimental treatments.

Most studies of *B. hebetor* have found that wasps produce a female-biased sex ratio (e.g. Whiting 1961; Benson 1973; Rotary & Gerling 1973; Taylor 1988; Strand & Godfray 1989). Local mate competition is an important factor leading to female-biased sex ratios in other species of gregarious parasitoids and is an obvious candidate to explain the bias found in *B. hebetor*. However, in species with the type of sex determination found in *B. hebetor*, mating between siblings leads to the production of diploid males and a substantial drop in fitness (Whiting 1960; Galloway & Grant 1989). This paradox has been partially resolved by Antolin & Strand (1992) who studied the mating behaviour of *B. hebetor* in semi-natural conditions in large grain silos. They found that males congregated at the tops of small 'hills' of grain which females visited to obtain matings. These observations strongly suggest that outbreeding is normal in this wasp, and thus the fitness penalties of producing many diploid males are avoided. This still leaves the problem of why this species produces a female-biased sex ratio (Antolin & Strand 1992). One possibility is asymmetric competition between male and female larvae on a host (Benson 1973; Godfray 1986). To predict sex ratio in such circumstances, it is important to consider simultaneously selection acting on both clutch size and sex ratio (Suzuki & Iwasa 1980; Werren 1980; Godfray 1986; Frank 1990). Alternatively, mated females may be selected to produce a female-biased sex ratio in response to the presence of unmated or sperm-depleted females laying broods consisting only of sons (Godfray 1988). Interestingly, Antolin & Strand (1992) found both categories of females among individuals caught in grain silos. Further progress towards understanding sex ratio in *B. hebetor*, and in similar species, is most likely to occur by following Antolin & Strand's example and attempting to study mating systems and larval competition under natural and semi-natural conditions.

ACKNOWLEDGMENTS

We are very grateful to Mike Strand for providing us with cultures of *B. hebetor*. We thank Ross Crozier, Ian Hardy, Molly Hunter, Sally Power, Mike Schwarz, Mike Strand and Marcel Visser for helpful advice. JMC was supported by SERC and APRL by the Ministerio de Educacion y Ciencia, Spain.

REFERENCES

Antolin, M. F. & Strand, M. R. 1992. Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). *Ecol. Entomol.*, **17**, 1–7.

Benson, J. F. 1973. Intraspecific competition in the population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae). *J. Anim. Ecol.*, **42**, 105–124.

Charnov, E. L. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. *Am. Nat.*, **113**, 465–480.

Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton, New Jersey: Princeton University Press.

Collett, D. 1991. *The Analysis of Binary Data using GLIM*. London: Chapman & Hall.

Cook, J. M. In press. Sex determination in the Hymenoptera: a review of models and evidence. *Heredity*.

Frank, S. A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution*, **39**, 949–964.

Frank, S. A. 1986. Hierarchical selection theory and sex ratios. I. General solution for structured populations. *Theor. Pop. Biol.*, **29**, 312–342.

Frank, S. A. 1990. Sex allocation theory for birds and mammals. *A. Rev. Ecol. Syst.*, **21**, 13–35.

Galloway, K. S. & Grant, B. 1989. Reverse sex ratio adjustment in an apparently outbreeding wasp. *Bracon hebetor*. *Evolution*, **43**, 465–468.

Godfray, H. C. J. 1986. Models for clutch size and sex ratio with sibling interaction. *Theor. Pop. Biol.*, **30**, 215–231.

Godfray, H. C. J. 1988. Virginity in haplodiploid populations: a study on fig wasps. *Ecol. Entomol.*, **13**, 283–291.

Godfray, H. C. J. 1993. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton, New Jersey: Princeton University Press.

Grant, B., Burton, S., Contoreggi, C. & Rothstein, M. 1980. Outbreeding via frequency-dependent mate selection in the parasitoid wasp, *Nasonia (= Mormoniella) vitripennis*. *Evolution*, **34**, 983–992.

Grosch, D. S. 1948. Dwarfism and differential mortality in *Habrobracon*. *J. exp. Zool.*, **107**, 289–313.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science*, **156**, 477–488.

Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects. In: *Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 167–220. London: Academic Press.

Herre, E. A. 1985. Sex ratio adjustment in fig wasps. *Science*, **228**, 896–898.

Herre, E. A. 1987. Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature, Lond.*, **329**, 627–629.

King, B. H. 1987. Offspring sex ratios in parasitoid wasps. *Q. Rev. Biol.*, **62**, 367–396.

King, B. H. & Skinner, S. W. 1991. Sex ratio in a new species of *Nasonia* with fully-winged males. *Evolution*, **45**, 225–228.

McCullagh, P. & Nelder, J. A. 1983. *Generalized Linear Models*. London: Chapman & Hall.

Nunney, L. & Luck, R. F. 1988. Factors influencing the optimum sex ratio in structured populations. *J. theor. Biol.*, **33**, 1–30.

Orzack, S. H. 1986. Sex-ratio control in a parasitic wasp, *Nasonia vitripennis* II. Experimental analysis of an optimal sex ratio model. *Evolution*, **40**, 341–356.

Petters, R. M. & Mettus, R. V. 1980. Decreased diploid viability in the parasitoid wasp, *Bracon hebetor*. *J. Hered.*, **71**, 353–356.

Rotary, N. & Gerling, D. 1973. The influence of some external factors upon the sex ratio of *Bracon hebetor*

Say (Hymenoptera: Braconidae). *Environ. Entomol.*, **2,** 134–138.

Strand, M. R. 1988. Variable sex ratio strategy of *Telenomus heliothidis* (Hymenoptera: Scelionidae): adaptation to host and conspecific density. *Oecologia (Berl.)*, **77,** 219–224.

Strand, M. R. & Godfray, H. C. J. 1989. Superparasitism and ovicide in parasitic Hymenoptera: a case study of the ectoparasitoid *Bracon hebetor*. *Behav. Ecol. Sociobiol.*, **24,** 421–432.

Suzuki, Y. & Iwasa, Y. 1980. A sex ratio theory of gregarious parasitoids. *Res. Pop. Ecol.*, **22,** 366–382.

Taylor, A. S. 1988. Host effects on larval competition in the gregarious parasitoid *Bracon hebetor*. *J. Anim. Ecol.*, **57,** 163–172.

Taylor, P. D. 1981. Intra-sex and inter-sex sibling interactions as sex ratio determinants. *Nature, Lond.*, **291,** 64–66.

Taylor, P. D. & Bulmer, M. G. 1980. Local mate competition and the sex ratio. *J. theor. Biol.*, **86,** 409–419.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179,** 90–92.

Viktorov, G. A. & Kochetova, N. I. 1971. [The significance of population density in the regulation of the sex ratio of *Trissolcus volgensis* (Hymenopterea, Scelionidae).] *Zool. Zhur.*, **50,** 1753–1755 [in Russian].

Viktorov, G. A. & Kochetova, N. I. 1973. [The role of trace pheromones in regulating sex ratio in *Trissolcus grandis* (Hymenoptera, Scelionidae).] *Zh. Obsch. Biol.*, **34,** 559–562 [in Russian].

Waage, J. K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: *Insect Parasitoids* (Ed. by J. K. Waage & D. Greathead), pp. 63–95. London: Academic Press.

Waage, J. K. & Lane, J. A. 1984. The reproductive strategy of a parasitic wasp. II. Sex allocation and local mate competition in *Trichogramma evanescens*. *J. Anim. Ecol.*, **53,** 417–426.

Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science*, **208,** 1157–1159.

Werren, J. H. 1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution*, **37,** 116–124.

Werren, J. H. 1987. Labile sex ratios in wasps and bees. *Bioscience*, **37,** 498–506.

Whiting, A. R. 1961. Genetics of *Habrobracon*. *Adv. Gen.*, **10,** 333–406.

Whiting, P. W. 1943. Multiple alleles in complementary sex determination of *Habrobracon*. *Genetics*, **28,** 365–382.

Whiting, P. W. 1960. Polyploidy in *Mormoniella*. *Genetics*, **45,** 949–970.