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Sex allocation and interactions between relatives in the bean beetle, *Callosobruchus maculatus*

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Abstract

When a small number of females contribute offspring to a discrete mating group, sex allocation (Local Mate Competition: LMC) theory predicts that females should bias their offspring sex ratio towards daughters, which avoids the fitness costs of their sons competing with each other. Conversely, when a large number of females contribute offspring to a patch, they are expected to invest equally in sons and daughters. Furthermore, sex ratios of species that regularly experience variable foundress numbers are closer to those predicted by LMC theory than species that encounter less variable foundress number scenarios. Due to their patterns of resource use, female *Callosobruchus maculatus* are likely to experience a broad range of foundress number scenarios. We carried out three experiments to test whether female *C. maculatus* adjust their sex ratios in response to foundress number and two other indicators of LMC: ovipositing on pre-parasitised patches and ovipositing with sisters. We did not find any evidence of the predicted sex ratio adjustment, but we did find evidence of kin biased behaviour.

Keywords: Bruchid; Kin discrimination; Local mate competition; Sex allocation

1. Introduction

The field of sex allocation is one of the most successful areas of evolutionary biology—we can explain when, why and by how much females should vary their offspring sex ratios, in a wide range of taxa (Charnov, 1982; West and Sheldon, 2002; Hardy, 2002). Hamilton's (1967) theory of local mate competition (LMC) is particularly well supported, applying to organisms ranging from protozoans to metazoans: including malaria parasites, mites, wasps, barnacles and snakes (Werren, 1980, 1983; Charnov, 1982; Herre, 1985; Madsen and Shine, 1992; Wrensch and Ebbert, 1993; Shutler and Read, 1998). LMC theory predicts that, in structured populations, offspring sex ratios should vary with foundress number (Hamilton, 1967). When one or a few foundresses contribute offspring to a patch and their daughters are likely to mate with their sons, the unbeatable sex ratio is very female

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biased (Maynard Smith, 1982). Under these conditions, a female biased sex ratio reduces competition between sons and provides more females for the sons to mate with (Taylor, 1981; Frank, 1998; Peer and Taborsky, 2004). At the other extreme, if a larger number of females contribute offspring to the mating group, offspring sex ratios closer to equality are predicted to maximise fitness.

The extent to which observed sex ratio biases match LMC predictions may depend on a number of factors. For example, fig wasp species that regularly encounter a variety of foundress numbers, produce sex ratios closest to those predicted when tested in a variety of LMC situations (Herre, 1987). These species have been selected to facultatively respond to greater levels of environmental variability than species that encounter less variation in LMC (West et al., 2000, 2002; West and Sheldon, 2002). Females can assess the level of LMC their sons will face from both the number of other foundresses and the presence of conspecific eggs on the patch (Shuker and West, 2004a). Furthermore, for a given foundress number, sisters are predicted to lay more female biased sex ratios than unrelated females because they will gain inclusive fitness benefits from reducing the level of LMC that their nephews face (Shuker et al., 2004b).

Most evidence for strong sex ratio shifts comes from members of the Hymenoptera. Their sex determination system is haplodiploidy, in which daughters are produced from fertilised eggs and sons from unfertilised eggs. In contrast, chromosomal sex determination mechanisms (CSD) have often been assumed to constrain the extent of sex ratio adjustment (Williams, 1979; Charnov, 1982). Recent studies suggest that CSD does not actually constrain the extent of sex ratio adjustment (Badyaev et al., 2002; Hardy, 2002; West et al., 2002; West and Sheldon, 2002; Sheldon and West, 2004), but more detailed data are required to evaluate the generality and extent of sex ratio adjustment from a wider range of taxa with CSD than is currently in the literature (West et al., 2005).

The bean beetle *Callosobruchus maculatus* (Bruchidae) has a chromosomal sex determination mechanism, in which males are the heterogametic sex. *C. maculatus* is a major pest of stored legume products in the tropics (Caswell, 1981; Tindall, 1983). Once a seed store is colonised, the population rapidly expands over successive generations until resources become limiting. When resources become scarce, females have to compete for oviposition sites and offspring have to compete for food (Credland et al., 1986; Smith, 1990). Females will have to choose between ovipositing on poor quality seeds (part consumed or with high larval competition) or dispersing to seek new patches. Evidence suggests that *C. maculatus* populations are usually founded by a single female (Cipollini, 1991; Tran and Credland, 1995), and LMC theory predicts that these foundresses should lay a female biased sex ratio. Given that *C. maculatus* females are likely to encounter substantial variation in foundress numbers as populations expand, we might expect them to show a close fit to predicted sex ratios in range of LMC situations (Cipollini, 1991; Tran and Credland, 1995; Colegrave, 1997). Although female-biased population sex ratios have previously been documented in Bruchids (Cipollini, 1991; Giga and Smith, 1991; Ishihara and Shimada, 1993), no study has explicitly tested whether this is due to LMC.

We carried out three experiments to investigate whether female *C. maculatus* respond to LMC. In the first experiment, we manipulated the number of foundresses contributing offspring to a patch by allowing focal females to oviposit with marker females that have different coloured elytra. This is a powerful way to test for an LMC response as it allows both brood sex ratios from focal females and patch sex ratios to be measured. In the second experiment, we tested whether female *C. maculatus* alter their sex ratios in response to the presence of conspecific eggs (superparasitism) as has been documented in parasitoid wasps (Werren, 1980). In the third experiment, we tested whether females alter their sex ratios in response to ovipositing with a sister or a non-relative. This experiment also allowed us to ask several more general questions about *C. maculatus*: whether females show kin discrimination; whether oviposition behaviour is altered more generally in response to kin; whether larvae modulate their competitive interactions in response to kin.

2. Methods

2.1. Study organism

Two strains of *C. maculatus* (Coleoptera: Bruchidae) were reared: a ‘wild type’ strain (material originating from Blades Biological, Kent, UK) used as focal females, and a black strain (original material kindly provided by P. Eady, UK) used as marker females. These two strains have different phenotypes: ‘wild type’ beetles have brown/tan elytra with distinct markings whereas the black strain has much darker pigmented elytra, which can obscure their markings. Nonetheless, the two strains show no significant differences in size, single foundress sex ratio or fecundity (Bloor, unpublished data). Black colouration is not a fixed trait in our marker population so there may have been some error when assigning strain identity to the offspring in experiments one and two. However, the strong correlation between patch and focal female sex ratios indicates that this had a very limited quantitative effect on our results.

All cultures of *C. maculatus* were mass reared, in large jars, on *Vigna unguiculata* and maintained in a L16:D8 photoperiod at a temperature of 30 °C. Animals from generations three to six were used in experiments and previous generations had been reared in similar conditions for at least five years (Blades Biological: pers. comm.). To avoid problems associated with pseudoreplication within families, all focal females in experiments one and two were non-relatives. To do this we removed mated females from stock and allowed them to oviposit on 10 seeds in individual patches (Petri dishes) for 24 h. Only one female from each of these ‘families’ were used as experimental replicates. In experiment three, we set up three replicates per family and analysed family averages.

2.2. *Experiment 1: varying foundress number*

Patches of 10 evenly-sized *V. unguiculata* seeds were established in Petri-dishes. We set up 20 replicate patches for each of the following foundress treatments: single female; 2; 4; 8; 16 females. In all patches, there was a single focal female that had been randomly chosen from one of 100 families. The remaining females were taken from the marker strain stock after mating. Focal females were isolated as virgins and individually provided with a randomly chosen male, from the same strain, to mate with for 24 h. Once mated, females were randomly assigned to a treatment and were left in their Petri dish patches for 24 h before being removed. Offspring were allowed to develop at 30 °C in each patch, and were assigned to a strain, counted and sexed upon emergence.

2.3. *Experiment 2: superparasitism*

We set up 20 Petri dish patches of 10 unparasitised *V. unguiculata* seeds and 20 patches containing 10 *V. unguiculata* seeds that had been oviposited on by marker females 24 h previously (pre-parasitised). To create the pre-parasitised seeds we allowed 20 mated marker females to oviposit on 200 seeds for 24 h as this combination of seeds, females and duration results in, on average, one to five eggs per seed (Ofuya, 1987). We then removed the marker females from the pre-parasitised seeds and randomly assigned 10 seeds to each of the patches in the superparasitism treatment. As for experiment one, we isolated one virgin focal female from each of 40 different families, allowed them to mate with a randomly chosen wild type male for 24 h and then allowed them to oviposit on their patches for 24 h. After this period, females were removed and the offspring were allowed to develop at 30 °C. Offspring were assigned to a strain, counted and sexed upon emergence.

2.4. *Experiment 3: ovipositing with a sister*

Using 36 families of the focal strain, we set up two relatedness treatments: two sisters and two unrelated females (‘Sibs’ and ‘Non-sibs’, respectively). Virgin females were isolated from each family and housed individually for up to 24 h, before being provided with a randomly chosen male and left to mate for 24 h. Once mated, females from the different families were allocated to patches of 10 *V. unguiculata* seeds in Petri dishes. We randomly assigned 12 families to the ‘Sibs’ treatment and allocated one pair of sisters to each patch. This was replicated for three pairs of sisters from each family to minimise intra-treatment variation. We randomly paired the other 24 families in the ‘Non sibs’ treatment and one female from each family was assigned to each patch. We also replicated this three times for each pair of families. Mean values were subsequently calculated per family to avoid pseudoreplication *sensu* Hurlbert (1984). In both treatments, females were given 24 h to oviposit. After this time, females were removed, eggs counted and offspring allowed to develop at 30 °C. Offspring were assigned to a strain, counted, sexed upon emergence, and the elytra length of the first male and female to emerge from each patch was measured.

2.5. Analysis

To retain maximum power when analysing sex ratio (proportion) data, analyses should assume binomial errors and use a logit link function in an analysis of deviance, as proportion data often have non-normally distributed error variance and unequal sample sizes (Crawley, 2002; Wilson and Hardy, 2002). Proportion data can be overdispersed, which can lead to overestimation of significance. If the dispersion parameter (heterogeneity factor; HF) is <4, data can be scaled and F tests used to assess significance (Crawley, 2002). However, if the dispersion parameter is >4, arcsin square root tansformed data should be analysed. Our sex ratio data were substantially overdispersed so all analyses were carried out on transformed proportions. No other response variables showed significant deviation from the normal distribution. We used general linear modelling techniques in S-Plus (Insightful Corporation) with stepwise deletion to assess the significance of main effects and interactions. Non parametric one-sample tests were used to ask if sex ratios deviated from equality.

3. Results

3.1. Experiment 1: varying foundress number

We obtained focal female and patch sex ratios from 100 replicates. Neither our focal female or patch sex ratios were significantly influenced by foundress number (Fig. 1; $F_{4,74} = 0.962$, $P = 0.415$ and $F_{4,74} = 1.512$, $P = 0.218$). In the multiple foundress treatments, focal female sex ratios were closely correlated with patch sex ratios ($r = 0.78$, $P < 0.0001$). Both focal female and patch sex ratios were not significantly different from equality (focal median = 0.52, $P = 0.203$; patch median = 0.50, $P = 0.919$). Focal female sex ratios were not significantly correlated to the number of their offspring that emerged ($F_{1,73} = 0.027$, $P = 0.870$). There was significant variation in sex ratios across foundress numbers (Levenes test statistic: 7.2, $P < 0.0001$), and this was because single foundress sex ratios were significantly more variable than those in the multi foundress treatments (Levenes test statistic: 19.7, $P < 0.0001$; single foundress range: 0.27–0.83; multi foundress range: 0.27–0.67). The number of offspring to emerge from single foundress broods was not significantly different to that from focal female broods in multi-foundress patches ($F_{1,98} = 2.86$, $P = 0.094$).

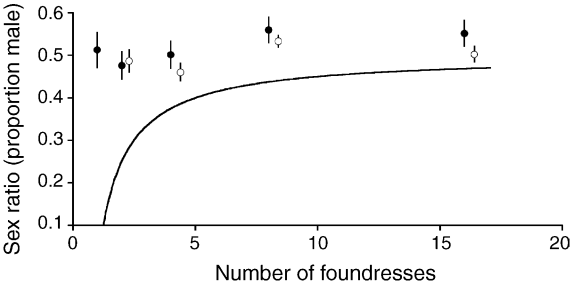

Fig. 1. The mean (±S.E.) sex ratios produced by focal females (filled circles) and from patches (open circles) compared to the sex ratios predicted by LMC theory (solid line). Note that both the focal female and patch data are the same for the single foundress treatment.

3.2. Experiment 2: superparasitism

We obtained sex ratios from 11 focal females in the unparasitised treatment and 19 focal females in the superparasitism treatment. There was no significant difference in focal female sex ratio between the two groups ($F_{1,28} = 1.29$, $P = 0.265$). Both focal female and marker female sex ratios were not significantly different from equality (focal median = 0.55, $P = 0.123$; marker median = 0.59, $P = 0.512$). Within the superparasitism treatment, focal female and marker sex ratios were not significantly different ($F_{1,36} = 1.63$, $P = 0.210$).

3.3. Experiment 3: ovipositing with sisters

We obtained data from 12 families in each treatment. There was no significant effect of relatedness on offspring sex ratios ($F_{1,22} = 0.01$, $P = 0.943$). In contrast, we did find effects of relatedness on female oviposition behaviour. Sibs laid significantly more eggs on patches than non sibs ($F_{1,22} = 10.99$, $P = 0.003$; sibs mean = 73.90 ± 1.97; non sibs mean = 63.44 ± 2.41). In addition, significantly more offspring emerged when sibs oviposited together ($F_{1,22} = 4.67$, $P = 0.042$; sibs mean = 41.2 ± 1.34; non sibs mean = 34.2 ± 2.90). However, relatedness had no significant effect on the proportion of offspring that emerged ($F_{1,22} = 0.34$, $P = 0.565$). Furthermore, there was no significant effect of relatedness on the size of sons ($F_{1,22} = 0.01$, $P = 0.943$) or daughters ($F_{1,22} = 0.24$, $P = 0.652$).

4. Discussion

We carried out 3 experiments to investigate how interactions between relatives influence sex allocation behaviour in the seed beetle *C. maculatus*. We did not find any evidence that females adjust their offspring sex ratios in response to LMC when given various cues: foundress number; the presence of conspecific eggs; ovipositing with a sister. We were also able to ask more general questions about kin discrimination in *C. maculatus* and found that sisters contribute more eggs to patches than non-sisters.

Why don't female *C. maculatus* respond to LMC? There are several non-mutually exclusive possibilities, which could explain why our data do not support our sex ratio predictions: (1) there may not be strong selection to respond to LMC. Given that founding females may encounter patches that vary from ovipositing alone to very high foundress numbers, this seems unlikely (Cipollini, 1991). An intriguing possibility is that when patch resources become limiting, dispersing morphs are produced which found new populations and respond to LMC (Colegrave, 1997). Dispersal and sex ratio adjustment may be genetically correlated traits and our stock culturing procedure may have selected against dispersing morphs. Furthermore, in *Tribolium casteneum*, dispersal and competitive ability are negatively correlated traits and high population densities select for competitive ability (Zirkle et al., 1988); (2) in *C. maculatus*, females are known to mate multiply and may wish to mate with different males each time (Fox, 1993); (3) LMC models assume that males mate only on their natal patch and do not disperse. It is possible that male *C. maculatus* are capable of dispersing throughout seed stores to locate females. However, when a new population is founded, males would have to disperse to other populations in order to find more mates; (4) there may be significant costs associated with inbreeding and females may wish to avoid mating with kin. However, evidence suggests that no significant costs are associated with inbreeding in *C. maculatus* (Tanaka, 1990; Tran and Credland, 1995); (5) differential mortality may overshadow sex ratio adjustment. Previous studies of *C. maculatus* have reported that males suffer greater mortality than females from competition in late larval stages (Cipollini, 1991; Ishihara and Shimada, 1993). If this was the case, we would expect to observe female biased offspring sex ratios at higher foundress numbers.

There are at least three possible reasons why we did not detect such differential mortality in our data set. First, in multiple foundress treatments, the degree of larval competition may not have been severe enough to induce larval mortality. In the eight and 16 foundress treatments each larvae was, on average, competing with 7 other successful larvae (overall mean offspring emerged per patch was 79.83 ± 2.86). This level of competition has been shown to affect male weight at emergence but not the emergence sex ratio (Giga and Smith, 1991). Second, sex differences in competitive ability may only be detectable when analysing the sex ratios per seed, rather than per patch, and future sex ratio studies may benefit from collecting data in this way. Third, both differential mortality and LMC were occurring and their opposing effects resulted in equal sex ratios.

A type two error (accepting a false null hypothesis) is unlikely as we have > 80% power to detect the predicted difference in sex ratio between single foundresses and 16 foundresses and > 60% power to detect the predicted difference between one and two foundresses. In all experiments, sex ratios were considerably overdispersed, which may be an indicator of sex ratio adjustment (Krackow et al., 2002). Furthermore, in experiment one, focal foundress sex ratios were more variable in the single foundress treatment than the muti-foundress treatments. Sample variance can increase with brood size (Krackow et al., 2002), but the number of offspring to emerge from focal foundress broods did not differ significantly between the single and multi-foundress patches. This may be because females were adjusting their sex ratios, and this was only apparent in the single foundress treatment where larval competition was low. Females could have been adjusting their sex ratios in response to patch quality (e.g. seed mass), or mate quality (Trivers and Willard, 1973).

The results of experiment three, showing that sibs oviposit at a higher rate than unrelated females, indicates that females may have some ability to discriminate kin (Fellowes, 1998). Patches in the sibs treatment yielded more total offspring, but not proportionally more than the non sibs treatment. It is unclear why more eggs were laid in the sibs treatment, because the proportion of offspring to emerge usually decreases with increasing larval density (Credland et al., 1986). Relatives may be able to extract more resources from the seed by increasing production of detoxifying or digestive enzymes. Conversely, we may expect sisters to lay fewer eggs on the patch and show a greater tendency to disperse, in order to reduce competition between related offspring (Frank, 1996). Also, females can reduce or delay oviposition when presented with an unsuitable patch (Credland et al., 1986). Female *C. maculatus* have previously been observed adding more eggs to seeds bearing their own eggs than to equally loaded seeds bearing the eggs of another female (Ofuya and Agele, 1989). It is unclear why this occurs, but it is possible that this was happening in the sibs treatment in our experiment, as pheromone markers used by sisters are likely to be similar.

The results of our three experiments do not provide support for the prediction that female *C. maculatus* respond to LMC, but do provide areas for future studies: the possibility of conditional sex allocation in response to an environmental cue, the possibility of kin discrimination and understanding why females increase their clutch size when ovipositing with a sister.

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