



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

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Received 30 June 2005; received in revised form 3 August 2005

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.

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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

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