



Extreme reproductive specialization within ant colonies: some queens produce males whereas others produce workers

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A key feature differentiating animal societies is the partitioning of reproduction among breeders. We studied how reproduction is partitioned among nestmate queens of the ant *Formica exsecta* in laboratory colonies. In polygynous (multiple-queen) colonies, queens can increase their reproductive success by laying more eggs or by increasing the proportion of eggs that develop into reproductive individuals instead of workers. We found that reproductive skew among queens for egg production was low, but that 84% of all queens contributed exclusively to one type of brood, either males or workers (no new queens are produced in the laboratory). Furthermore, our data revealed that the degree of reproductive specialization among queens significantly increased during brood development. Contrary to predictions of most reproductive skew models, the extent of reproductive skew was not associated with relatedness among co-breeding queens. We also found no association between the pattern of queen specialization and relatedness between queens and their mates. Such an association would occur if queens mated to related males specialize in male production to avoid the cost of inbreeding. Altogether, our findings show a yet undescribed pattern of reproductive specialization among nestmate queens in ants and emphasizes the need to investigate reproductive contributions of queens for each type of offspring separately.

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One of the major transitions in evolution is the shift from solitary organisms to societies with reproductive division of labour (Maynard Smith & Szathmary 1995; Szathmary & Maynard Smith 1995). A key feature differentiating animal societies is the partitioning of reproduction among individuals (Keller & Reeve 1994), which can range from strictly equitable breeding (referred to as low-reproductive skew) to extreme skew where reproduction is limited to one or a small subset of breeders.

In social Hymenoptera, reproductive skew is generally very high in colonies containing a single queen because queens typically monopolize most of the reproduction (Bourke 1988; Jeon & Choe 2003; Hammond & Keller 2004). In many species, however, colonies may contain two or more fertile queens (Keller 1993b, 1995; Bourke

& Franks 1995), and there is considerable intra- and inter-specific variation in the relative contribution of these queens to reproduction (Reeve & Keller 2001). Most studies conducted to date investigated the extent to which nestmate queens differ in their overall reproductive output (Reeve & Keller 2001). However, even if queens contribute similar number of eggs, they might differ in their reproductive success (Keller 1993a) because the fitness of nestmate queens does not only depend on their fecundity, but also on the type of egg produced (haploid male or diploid female) and their developmental fate (gyne (new queen) or worker development of diploid eggs).

Several studies revealed that queens in multiple-queen (polygynous) ant colonies may, indeed, differ in their relative contribution to the production of different offspring classes (gynes, males and workers) (Ross 1988; Fournier & Keller 2001; Ruppell et al. 2002; Fournier et al. 2004; Hammond et al. 2006, Kümmerli & Keller 2007). Some of these studies also showed trade-offs in the relative contribution of queens to two different classes of offspring (Ross 1988; Fournier & Keller 2001; Fournier et al. 2004). A significant trade-off between a queen's contribution to

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gyne and worker offspring has been found in *Solenopsis invicta* (Ross 1988) and *Pheidole pallidula* (Fournier et al. 2004), while in the Argentine ant *Linepithema humile* the trade-off is between the production of males and gynes (Fournier & Keller 2001).

A recent study of the ant *Formica exsecta* suggested an extreme case of reproductive specialization with an estimate that approximately 79% of queens appear specialized in the production of either males or workers (Kümmerli & Keller 2007). However, the high queen number per colony in the population studied did not allow us to determine brood maternity and the estimated degree of queen specialization was based only on colony kin structure.

The first aim of this study was to test under laboratory conditions whether there is high reproductive specialization among nestmate *F. exsecta* queens. In particular, we wanted to test whether some queens show complete specialization in the production of a single offspring class, a pattern that has not yet been firmly documented in any social insect species. The second aim of the study was to identify the proximate mechanism underlying queen specialization. To do so, we compared the degree of reproductive specialization among queens at the egg and pupal stages to test whether reproductive specialization is mediated by some queens producing exclusively or mostly haploid male eggs while other queens produce only or mostly diploid female eggs. This analysis also permitted to test whether queen specialization changed between the egg and the pupal stage with such a change possibly being caused by differential survival of haploid or diploid eggs or by workers manipulating brood composition.

Furthermore, we tested whether the extent of reproductive skew among queens is associated with the relatedness among co-breeders and colony productivity as predicted by reproductive skew models (reviewed in Keller & Reeve 1994; Johnstone 2000; Reeve & Keller 2001). There are three different types of reproductive skew models that can be distinguished according to their assumption about who is controlling the allocation of reproduction. The different models assume that the allocation of reproduction is either controlled by the dominant (concession models), the subordinate (restraint models) or by none of the two group members (tug-of-war models). Concession models predict that the dominant should yield just enough reproduction to a subordinate to make it favourable for the latter to stay in the group (Emlen 1982; Vehrencamp 1983; Reeve & Ratnieks 1993), hence leading to a positive association between relatedness among breeders and skew. Alternatively, restraint models predict that the subordinate should capture the largest share of reproduction that the dominant will tolerate before ejecting the subordinate (Johnstone & Cant 1999), which is predicted to result in a negative association between relatedness among breeders and skew. Finally, tug-of-war models assume that the conflict over reproductive allocation takes place at the expense of total group productivity (Reeve et al. 1998) and they predict no or a weakly negative correlation between relatedness among breeders and skew but a positive association between relatedness and overall group productivity.

Finally, we investigated whether the pattern of queen specialization was associated with the relatedness between queens and their mate(s). Previous studies showed that a high proportion of *F. exsecta* queens mate with related males (Sundström et al. 2003; C. Haag-Liautard, J. S. Pedersen, O. Ovaskainen & L. Keller, unpublished data), which may translate in the production of less fit diploid (female) offspring (Charlesworth & Charlesworth 1987) and a higher probability of producing diploid nonfertile males (Cook & Crozier 1995; Crozier & Pamilo 1996). Hence, queens mated with a related male should be more specialized in male production than queens mated with an unrelated male. This might be either due to reduced survival rate of diploid brood produced by queens mated with a related male or because these queens actively choose to produce mostly males to avoid the cost of inbreeding.

METHODS

Sampling Procedure

To establish laboratory colonies, we collected 3.0 ± 0.5 (mean \pm SD) queens and approximately 300 workers from each of 20 field colonies on 29 April 2003 when queens were about to start egg laying. Ants were collected at 'les Chenevières', a cattle pasture at 1220 m altitude in the Swiss Jura Mountains. In this population, colonies are known to contain many queens (Cherix et al. 1980; Brown & Keller 2000; Liautard & Keller 2001). Sex ratio is bimodally distributed (Brown & Keller 2000) and highly male biased with about 90% of all colonies producing only male sexuals (along with workers). We created artificial colonies in plastic compartments (26 \times 41 cm and 15 cm) by providing peat as nest material and a tile as nesting site. Colonies were kept at 22–24°C and regularly fed with honey water and a mixture of agar, egg, honey and water.

Queens started egg laying shortly after colonies were established in the laboratory. After two weeks, we carefully opened 10 randomly chosen colonies out of the 20 colonies to collect eggs for genetic analyses. We collected all queens and pupae and a random sample of workers from the 20 experimental colonies 4 weeks after the egg sampling. To check whether queens were inseminated, we dissected all queens and determined the presence or absence of sperm in their spermathecae.

Laboratory Methods

All experimental colonies produced males and/or workers (Table 1). We determined the sex and caste of all pupae produced by moistening them in ethanol and observing their size, eye shape and genitalia (Brown & Keller 2000; Liautard et al. 2003). All queens, the sperm in their spermathecae and eight workers per colony were genotyped at seven microsatellite loci (FL21, Chapuisat 1996 and FE13, FE17, FE19, FE21, FE37, and FE51, Gyllenstrand et al. 2002). The mean number of alleles per locus was high (mean \pm SD: 9.8 ± 6.8). We also genotyped 17 ± 10 (mean \pm SD) male and 22 ± 12 worker pupae per colony at the four most variable loci (FL21, FE13, FE17 and

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