Adaptive production of fighter males: queens of the ant *Cardiocondyla* adjust the sex ratio under local mate competition

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Hamilton's concept of local mate competition (LMC) is the standard model to explain female-biased sex ratios in solitary Hymenoptera. In social Hymenoptera, however, LMC has remained controversial, mainly because manipulation of sex allocation by workers in response to relatedness asymmetries is an additional powerful mechanism of female bias. Furthermore, the predominant mating systems in the social insects are thought to make LMC unlikely. Nevertheless, several species exist in which dispersal of males is limited and mating occurs in the nest. Some of these species, such as the ant *Cardiocondyla obscurior*, have evolved dimorphic males, with one morph being specialized for dispersal and the other for fighting with nest-mate males over access to females. Such life history, combining sociality and alternative reproductive tactics in males, provides a unique opportunity to test the power of LMC as a selective force leading to female-biased sex ratios in social Hymenoptera. We show that, in concordance with LMC predictions, an experimental increase in queen number leads to a shift in sex allocation in favour of non-dispersing males, but does not influence the proportion of disperser males. Furthermore, we can assign this change in sex allocation at the colony level to the queens and rule out worker manipulation.

Keywords: sex ratio; alternative reproductive tactics; male polymorphism; sexual selection; Formicidae

1. INTRODUCTION

Selective allocation of parental investment into male and female offspring has received much attention in evolutionary biology. Despite Fisher's (1930) central dogma of equal fitness returns per investment unit, which under most conditions predicts a numerical sex ratio of 1:1, female-biased sex ratios have been reported in many species of insects, mainly within the Hymenoptera (Hamilton 1979; Waage & Lane 1984; Frank 1985; Van Welzen & Waage 1987; Herre 1987; Bourke & Franks 1995; West & Herre 1998). Two explanations have been developed to explain these deviations from the 1:1 investment: the hypothesis of local mate competition (LMC) reported by Hamilton (1967), and the theory of worker control of the sex ratio in response to relatedness asymmetries described by Trivers & Hare (1976). The latter explanation applies only to the social Hymenoptera, i.e. ants, and social bees and wasps, in which a non-reproducing worker caste exists in addition to the reproducing female (queen). On the contrary, LMC can occur in social and non-social species, but as the hypothesis has been developed for solitary insects, it was hitherto tested mainly within non-social taxa.

Hamilton's concept of LMC postulates that highly female-biased sex ratios are selected when males do not disperse and thus brothers compete for mates in a locally restricted area. Female bias can be relaxed in favour of a more equal investment when the relatedness of the competing males is reduced. This can be due to an increase in the number of mothers contributing non-dispersing males to the pool of sexuals in a patch, or by an increase

in the fraction of males that disperse before mating. Many examples of LMC influencing the sex ratio have been found in Hymenoptera, in which females, due to the haplodiploid sex determination, have the power to determine the sex of their offspring by selective fertilization of their eggs. As predicted, the production of male offspring significantly increases with the number of females per patch in fig wasps (Hamilton 1967, 1979; Frank 1985; Herre 1987; West & Herre 1998) and parasitoid wasps (Waage & Lane 1984; Van Welzen & Waage 1987; Luck *et al.* 2001). Male offspring production is lower in species of fig wasps with locally mating, wingless males than with winged disperser males and intermediate in species with a male dispersal dimorphism (Hamilton 1979; West & Herre 1998; Fellowes *et al.* 1999).

Despite this convincing evidence of the relevance of LMC in solitary Hymenoptera, there has been a long-standing controversy over its role in social Hymenoptera. Whereas Alexander & Sherman (1977) suggested that LMC underlies the common female bias of sex ratios in social Hymenoptera, subsequent studies have shown that for most species the alternative explanation by Trivers and Hare is more plausible (Bourke & Franks 1995). In contrast to solitary Hymenoptera, in which sex allocation is controlled only by the females during the process of oviposition (Waage & Lane 1984; Van Welzen & Waage 1987), in colonies of social Hymenoptera, non-reproducing workers care for the brood after the eggs are laid by the queen. The interests over sex allocation may strongly diverge between these two parties due to the kin relationships in haplodiploid species. Whereas the queen is equally related to her (haploid) male and (diploid) female offspring, workers are three times more related to their sisters than brothers (relatedness asymmetry; Boomsma & Grafen 1991; Pamilo 1991) and, hence, can maximize

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their inclusive fitness by investing three times more into female than male sexuals. Relatedness asymmetry (RA) is reduced when queens are multiply mated or when several related queens contribute to the brood of a colony. Therefore, as under LMC, the highest deviation from the 1:1 investment is expected for single-queen colonies (monogyny). If, however, several unrelated queens reproduce in a colony, the value of RA does not change for the workers and sex allocation under worker control is expected to be the same as that in monogynous colonies (Bourke & Franks 1995).

The two hypotheses are not mutually exclusive and the underlying mechanisms may act simultaneously within a colony of social insects (Krebs & Davies 1993). Empirical testing of LMC, however, is difficult because the sexuals of most species mate randomly in nuptial flights (Hölldobler & Wilson 1990). But numerous taxa have evolved alternative mating tactics, such as intra-nest copulation, and dispersing and non-dispersing males may coexist within a single species (Heinze & Tsuji 1995). The ant *Cardiocondyla obscurior* shows such a male dimorphism, with winged males specialized in dispersal and wingless 'ergatoid' males specialized in competing with nest-mate males for access to female sexuals (Kugler 1983). Ergatoid males do not leave the nest and engage in mortal combat with their rivals to obtain matings with the virgin queens produced in their natal colony (Kinomura & Yamauchi 1987; Stuart *et al.* 1987). By contrast, winged males behave peacefully and emigrate a few days after eclosion to mate outside the nest (Heinze *et al.* 1998). Intra-nest copulations of winged males do occur but seem negligible compared to the behaviourally and physiologically specialized ergatoid males (Heinze & Hölldobler 1993; Heinze *et al.* 1998; in the five studies mentioned above, *C. obscurior* has been referred to as its close relative *C. wroughtonii*). Both male morphs are capable of multiple inseminations, which is an important prerequisite for a selective advantage of female bias under LMC (Nonacs 1986), although it is not required to lead to a female bias due to RA. Furthermore, because of a non-genetic morph determination (S. Cremer and J. Heinze, unpublished data), flexible investment into the two male morphs is possible.

In addition to the occurrence of alternative dispersal tactics in males, *C. obscurior* also contains a variable number of reproducing females per nest (from one to several queens per colony), hence both factors that influence the degree of LMC are combined within a single species. Due to this peculiar life history it is possible to test the significance of LMC as a selective force for sex allocation in social insect species. We first conducted experiments to determine whether the investment of colonies of *C. obscurior* in female sexuals and the two male morphs is in concordance with expectations based on LMC or on RA. Second, we determined whether queens or workers are in control of the sex allocation and which are the likely cues that they use to detect the colony structure. To our knowledge, this is the first attempt to simultaneously study the investment of colonies with changing queen number into two male morphs differing in dispersal tactics within a single species. Even though male-dimorphic species have been included in cross-species comparisons in fig wasps (Fellowes *et al.* 1999), data on the exact allocation of the

distinct male morphs are lacking so far. Furthermore, by testing within a single species, we avoid all the problems inevitably arising in cross-species comparisons, such as phylogenetic dependency of data points (Hardy & Mayhew 1998; West & Herre 1998; West *et al.* 2001).

2. MATERIAL AND METHODS

(a) *Colony-level sex allocation in single- and multiple-queen associations*

Colonies of *C. obscurior* were collected from their nests in aborted coconuts in an experimental dwarf coconut plantation on the territory of Comissão Executiva do Plano da Lavoura Cacaueira of the Brazilian Ministry of Agriculture in Una, Bahia, Brazil, in March 1998 and cultivated in the laboratory under standard conditions (Heinze *et al.* 1998). Natural nests contained one or several queens (median, 3; maximum, 45 queens; $n = 27$ colonies, four of which contained a single queen). Individual field colonies comprising multiple queens were used to experimentally produce one colony fragment containing a single queen (monogyny) and another fragment containing several queens (polygyny: 2, 5 or 10 queens, $n = 6, 6, 6$ colonies), with an initial number of 20 workers per colony fragment. As young queens mate in the nest and then either disperse or reproduce in the maternal colony, queens of natural colonies are likely to be related. However, adoption of alien queens seems to be possible, as discrimination against non-nest-mates is not very strong. Therefore, we produced a second set of polygynous colonies, in which we combined 10 queens, each stemming from a different field colony, with 20 workers from one of these nests ($n = 6$ colonies). Whereas the first 18 polygynous colonies are assumed to reflect the case of 'polygyny with related queens', the latter represent the case of 'polygyny with unrelated queens'. Unfortunately, a lack of variable genetic markers as yet prevents the verification of relatedness values. All colonies were checked every other day and new sexuals were removed immediately after emergence. We determined how many of the three types of sexuals (females, ergatoid males and winged males) were produced among the first 20 hatching sexuals per colony. Only 10 out of 18 monogynous colony fragments produced 20 sexuals during the course of the experiment (duration eight months).

(b) *Manipulation of brood composition to detect the controlling party and informative cues for colony composition*

In a second experiment, we set up another 12 monogynous colonies as described above. Subsequently, the brood composition of these colonies was altered by adding eggs from 'donor' colonies that were either monogynous (treatment A, $n = 6$ colonies) or polygynous (treatment B, $n = 6$ colonies). Workers of the manipulated nests, which were referred to as 'focal' nests, readily accepted alien eggs. Twenty eggs were added per colony once a week, representing roughly the equivalent of eggs produced in each of the focal colonies themselves, hence leading to a mixture of alien to own eggs at a ratio of approximately 1:1. This manipulation leads to colonies hosting a single queen and brood originating from several queens (increased brood heterogeneity). Whereas in treatment B one polygynous colony was used as the egg donor for each focal colony, several donor colonies were used to provide the 20 eggs per week for each focal colony of treatment A, to establish a brood heterogeneity of similar extent in treatments A and B. Worker heterogeneity was presumably similarly high in all, manipulated and

unmanipulated, colonies, as these represent fragments of originally polygynous colonies. Even though worker heterogeneity correlates with queen number in natural colonies that are stable over a long period of time, this does not hold for our experimental colonies (given an expected survival of workers of several months).

(c) Statistical analysis

Our experimental set-up, i.e. using each field colony only once within each group of colonies, assures independence of data. All data were tested to be normally distributed and to show equal variance and hence fulfil the assumptions for one-way analyses of variance. As the monogynous colonies were statistically compared with the polygynous colonies (first experiment), and also with the experimentally manipulated colonies A and B (second experiment), we used Bonferroni correction for multiple testing and adjusted the significance level α to 0.025.

As the LMC hypothesis is formulated for numerical sex allocation, we presented our results as the pure numerical values of sexuals. These data can be transformed into the investment sex ratio given the dry weight of females (5.7×10^{-5} g), ergatoid males (4.2×10^{-5} g) and winged males (6.7×10^{-5} g; each value represents the mean of 10 individuals that had been dried for 48 h at 60 °C). For a comparison between groups it was irrelevant whether numerical or investment sex ratios were used.

3. RESULTS AND DISCUSSION

(a) Sex allocation under monogyny and polygyny

The first experiment comprises a comparison of the sex allocation in monogynous colonies and four types of polygynous colonies, which differed in queen number and queen relatedness: we produced colonies with an increasing number of related queens (2, 5 or 10 queens) and with 10 unrelated queens (see § 2a).

(i) Expected sex allocation under LMC or RA

Applying Hamilton's theory to the dimorphic males in *C. obscurior*, we predicted a reduction in ergatoid male production in single- versus multiple-queen colonies, but an equal abundance of disperser males independent of colony queen number. The LMC hypothesis does not make distinctive statements on queen relatedness, but as competition between queens should become more intense with decreasing relatedness, we predicted a rise in locally mating males of the same or even higher magnitude under polygyny with unrelated than related queens. By contrast, the RA between female and male sexuals is only reduced if queens in a colony are related, but remains unchanged from 3:1 when queens are unrelated. Increased male production is therefore only expected under polygyny with related queens, whereas under polygyny with unrelated queens investment into males should be equally low, as under monogyny. The hypothesis reported by Trivers and Hare does not make definite statements about allocation into dispersing and non-dispersing males, but as the RA between female sexuals and winged males should be the same as the RA between female sexuals and wingless males, there is no reason to assume that the interest of workers to invest in either male morph is different based on their relatedness. As our experimental colonies all contained the same level of worker heterogeneity (see § 2) these predictions only hold true if ant workers use either

Figure 1. Production of ergatoid (dark hatched bars) and winged (light hatched bars) males of *Cardiocondyla obscurior* in colonies with 1 queen (Q) (monogyny), 2, 5 and 10 related (rel) queens and 10 unrelated (unrel) queens (mean $\pm$ s.d.).

Figure 2. Sex allocation into female sexuals (squares), ergatoid males (triangles) and winged males (diamonds) under monogyny and polygyny (with related and unrelated queens; mean $\pm$ s.d.).

brood heterogeneity or queen number, but not adult-worker relatedness, to assess RA. The latter would lead to equal sex allocation in all types of colonies.

(ii) Colony-level sex-allocation data are in agreement only with predictions of LMC

Data on male production for the five groups of colonies are given in figure 1. The production of ergatoid males was significantly lower in monogynous (M) than in all groups of polygynous (P) colonies (mean number of ergatoid males in 20 sexuals: M, 5.3, $P_{\text{rel-2Q}}$, 9.8, $P_{\text{rel-5Q}}$, 10.0, $P_{\text{rel-10Q}}$, 10.2, $P_{\text{unrel-10Q}}$, 10.8 where rel, related; unrel, unrelated; Q, queen; one-way analysis of variance: $F_{4,29} = 3.32$, $p = 0.02$; post-hoc least significant difference test: each comparison of P colonies with M colonies, $p < 0.02$; between P colonies, $p > 0.6$). For the winged males, by contrast, no significant difference could be detected between all groups (M, 1.7, $P_{\text{rel-2Q}}$, 1.5, $P_{\text{rel-5Q}}$, 3.3, $P_{\text{rel-10Q}}$, 2.5, $P_{\text{unrel-10Q}}$, 0.5; one-way analysis of variance: $F_{4,29} = 1.56$, $p = 0.21$). Figure 2 presents the difference between monogynous and polygynous colonies in sex

allocation for all three types of sexuals (female sexuals, ergatoid and winged males). Here, all four groups of polygynous colonies are pooled ($n = 24$ colonies) as they do not differ in sex allocation. Sex allocation is female biased only under monogyny (numerical: 65% female sexuals, 26.5% ergatoid males, 8.5% winged males; investment: 69% female sexuals, 21% ergatoid males, 11% winged males), not under polygyny (numerical: 38% female sexuals, 50% ergatoid males, 12% winged males; investment: 43% female sexuals, 41% ergatoid males, 16% winged males). Overall, ergatoid male production under polygyny is increased by 92%, whereas winged male production is increased by only 12%. Even though the power of the ANOVA for winged males is low (< 0.8) and our sample size is quite small, an increase in winged male production of the same order as that in the ergatoid males would have been detected.

Our data reveal that with polygyny, the proportion of ergatoid males increases rapidly and at the expense of the number of female sexuals, whereas there is no such increase in the winged males. This result is in accordance only with the predictions of the LMC hypothesis. The hypothesis reported by Trivers and Hare, by contrast, fails to explain the different investment into the two male morphs (indirect expectation) and, more importantly, the difference in sex allocation between monogynous colonies and polygynous colonies with unrelated queens (direct prediction). All three investigated colony structures (M , $P_{\text{rel } Q}$ and $P_{\text{unrel } Q}$) are likely to occur frequently in nature, as queen number rises by the adoption of daughters or alien queens and decreases by colony splitting (budding). Therefore, the members of a colony may often experience, and should therefore be adapted to, a quick change in queen number, including shifts from monogynous to polygynous conditions and changes in queen relatedness. For that reason, the observed investment in sexuals is probably a true effect and not an artefact of our laboratory experiment. Generally, the best fit of theory to data is expected when natural conditions are the same as the tested ones, so that a response of the animals could have been selected (Herre 1987), which seems to be valid in our study system.

(b) Identification of the party adjusting sex allocation and of the cues used to detect the colony structure

Even though our data documented that the observed sex allocation at the colony level reflects a reaction to LMC and not to RA, this does not yet reveal which party adjusts sex ratios in response to changes in the intensity of LMC. As the interests of queens and workers are approaching each other under LMC (Bourke & Franks 1995), sex allocation might be modified by different egg fertilization by the queens (primary sex ratio), brood manipulation by the workers, or a combination of both. To unravel how the observed shift in sex allocation in *C. obscurior* is achieved, we conducted a second experiment in which we manipulated monogynous colonies by adding eggs from alien 'donor' colonies (see § 2b). We thus confronted the ants with an unnatural colony composition of a single queen but brood from different queens (increased brood heterogeneity). By this procedure we attempted to obtain information not only on the party

Figure 3. Expected relative production of ergatoid males under four alternative scenarios of sex allocation in *Cardiocondyla obscurior* for the experimentally manipulated colonies (A and B) and controls (co). The scenarios differ in the assumption of the party ((i) queens, (ii) workers) adjusting the sex ratio in response to different levels of LMC and of the cues potentially used by the ants to detect colony structure ((a) direct measurement of queen number, (b) indirect measurement of brood heterogeneity). In the case of worker control (a(ii), b(ii)), only the focal nest (black bars) has to be considered, whereas in situations a(i) and b(i) the eggs from the focal (black bars) and donor (white bars) nests are mixed, leading to the average expected production of ergatoid males in the recipient colonies (grey bars).

adjusting the sex allocation, but also on likely cues that the ants use to estimate the number of reproducing queens in their colony and thus the strength of LMC. In principle, ants could 'count' the number of queens actually present in the nest or they could detect the degree of genetic heterogeneity of the brood (Evans 1995) or the adult workers in the colony. As in our experiments, worker heterogeneity was invariably high in all types of colonies (see § 2), we can exclude worker-derived cues as a source of information in our experiment. Hence, we assume that only the first two cues might be relevant in our experimental situation.

(i) Predictions on ergatoid male production in manipulated colonies

Combining the two potentially controlling parties and the two potentially informative cues, four possible scenarios of sex allocation arise in colonies of *C. obscurior*. Following the results of the first experiment, we derived a theoretical framework (figure 3), which includes the four scenarios and the expectations on ergatoid male production in manipulated colonies (A, monogynous donor colonies; B, polygynous donors) compared with unmanipulated monogynous control colonies. Under queen adjustment (figure 3a(i), b(i)), we expect queens to produce a more male-biased primary sex ratio under polygyny than monogyny (different egg laying of queens). Hence, the eggs added to colonies of treatment B should already contain a higher proportion of haploid male-destined eggs than the eggs added to colonies of treatment A. If the queens derive information on the colony compo-

Figure 4. Observed ergatoid (dark hatched bars) and winged (light hatched bars) male production (mean + s.d.) in the controls and the experimental colonies A and B, supporting figure 3*a*(i), under which queens are assumed to adjust sex allocation and to use queen number as a direct measure of colony structure.

sition from the actual queen number present in the nest (figure 3*a*(i)), an increased male production is only expected in the truly polygynous donor colonies, but not in the monogynous manipulated colonies. However, if queens estimate colony structure from the degree of brood heterogeneity (figure 3*b*(i)), in both A and B, queens should increase male production as the addition of donor brood indicates polygyny. As the manipulated nests contain a mixture of own eggs and added eggs from donor colonies, this would lead to a higher male production only in treatment B (figure 3*a*(i)), or to a continuous increase from control colonies over A to B (figure 3*b*(i)). By contrast, if workers modify sex ratios (figure 3*a*(ii), *b*(ii)), we expect the increased proportion of males under polygyny in the first experiment to result from more males being reared to adulthood, independently of the primary sex ratio (different brood rearing by workers). In this case, only the colony structure of focal nests and not of donor nests is relevant to predict ergatoid male production. Under figure 3*a*(ii), sex allocation should not differ among the three nest types as queen number always equals one, whereas under figure 3*b*(ii), male production should be increased in treatments A and B, as both contain brood that derives from more than a single queen (see § 2 and figure 1).

(ii) *Data suggest that queens adjust sex allocation in response to the number of queens present in the nest*

The results of our manipulation experiment are shown in figure 4. The production of ergatoid males differs significantly among the three groups (mean number of ergatoid males in 20 sexuals: control, 5.3, A, 5.8, B, 10.0; one-way analysis of variance: $F_{2,19} = 6.20$, $p = 0.008$), even after adjusting the significance level for multiple testing of the monogynous controls. Ergatoid male production in treatment B is increased significantly compared with both the control colonies (post-hoc LSD test: $p = 0.003$) and treatment A ($p = 0.015$), whereas treatment A does not differ from the control ($p = 0.71$). Again in this experiment, no significant differences in the relative production of winged males were found in the three nest types

(control, 1.7, A, 2.0, B, 2.5; one-way analysis of variance: $F_{2,19} = 0.22$, $p = 0.81$). On the basis of these data, we reject figure 3*a*(ii), *b*(i) and *b*(ii), and support figure 3*a*(i) as the likely explanation for the observed sex allocation. We therefore conclude that queens of *C. obscurior* are in charge of the observed shift in sex allocation between monogynous and polygynous conditions, and that they use queen number as a direct measurement of colony structure. Even if our data strongly suggest that workers in manipulated colonies do not interfere with the primary sex ratio laid by the queen, we cannot exclude that workers in the donor colonies had already manipulated the embryonated eggs before transfer, as their manipulation would have led to the same tendency as adjustment by the queens themselves. Still, it seems unlikely that workers only in the donor colonies and not in the focal colonies should have manipulated the primary sex ratio.

4. CONCLUSIONS

Taken together, our studies suggest that queens of the ant *C. obscurior* lay more male-destined haploid eggs under polygyny than monogyny. These additional male eggs then develop predominantly into ergatoid fighter males, whereas the allocation into disperser males stays constant. As the morph-determination mechanism and the timing of the developmental switch point are not yet completely known, we cannot make any statement about whether the queens determine the male morph already in the egg stage (blastogenic morph determination; see Bier (1954) for blastogenic caste determination) or whether male development may be influenced by workers or queens at a later stage.

Our data document not only adaptive sex investment in colonies of *C. obscurior*, but also a facultative change in sex allocation by the queens in response to the presence of other reproducing females. Whereas several studies have previously demonstrated adaptive changes in sex ratio (Waage & Lane 1984; Van Welzen & Waage 1987; West & Herre 1998; Luck *et al.* 2001; but see Fellowes *et al.* 1999), this typically does not result from facultative changes in egg fertilization (Waage & Lane 1984). We showed that *Cardiocondyla* queens seem to directly estimate queen number, but a better knowledge of the proximate mechanisms of how the colony, and hence relatedness structure, can be detected would be of great value for other studies on kin selection. So far, in ants, evidence for the potential of queens to adaptively adjust the sex ratio has been found only in a workerless social parasite (Aron *et al.* 1999) and another species, in which workers further manipulated the sex ratio (Keller *et al.* 1996). In *C. obscurior*, workers are present but do not seem to interfere with the sex ratio during larval development. LMC probably reduces the conflict between queens and workers by approaching their optima of sex allocation (Bourke & Franks 1995). Even if workers have been shown to possess the power to win an existing conflict between the two female castes, it is most efficient for the colony that queens adjust sex allocation in the case of an agreement. The broad acceptance of the hypothesis reported by Trivers and Hare (1976) should not lead to an *a priori* rejection of LMC as a powerful selective force for female-biased sex ratios in social insects. The two prin-

ciples underlying sex allocation are not mutually exclusive, and a unified theory on sex allocation might be helpful. Even though typical LMC situations seem to be comparatively rare in social insects, LMC is the most important factor for predicting sex ratios when it occurs (Bourke 1989; Tsuji & Yamauchi 1994). Moreover, recent genetic studies have revealed that LMC may also occur in species with a typical mating behaviour (Hasegawa & Yamaguchi 1995; Pedersen & Boomsma 1998), showing that the influence of LMC on sex allocation of social insects might have been grossly underestimated.

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