

# Lack of conflict during queen production in the social wasp *Vespula maculifrons*

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## Abstract

Social insects display extreme cooperative and helping behaviours. However, social insect colonies are also arenas of intense competitive interactions. One particularly important matter over which colony members may compete centres on the development of sexual offspring. Specifically, colony members may engage in selfish behaviours leading to reproductive competition, whereby individuals either strive to develop as sexuals or assist kin so that close relatives emerge as new reproductives. We investigated whether reproductive competition occurred in the polyandrous social wasp *Vespula maculifrons*. We genotyped *V. maculifrons* workers and new queens at eight polymorphic microsatellite loci to determine if larvae of particular genotypes were reared as gynes more frequently than expected by chance. However, we found no significant evidence of reproductive competition in this species. The proportional contributions of males to workers and new queens did not vary within colonies. Moreover, male reproductive skew did not differ between workers and new queens. Finally, novel statistical techniques uncovered no evidence of patriline reversal, the phenomenon whereby males that contribute little to worker production contribute substantially to new queen production. Consequently, we conclude that individual level selection operating to increase the frequency of selfish behaviours that would lead to reproductive competition has been nullified by colony-level selection acting to maintain colony efficiency and cooperation.

**Keywords:** DNA microsatellite marker, hymenopteran social insect, kin selection, polyandry, reproductive skew, *Vespula*, yellowjacket wasp

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## Introduction

The evolution of highly social groups represented an important and successful innovation in biological history (Wilson 1971; Maynard Smith & Szathmari 1998). The success of highly social groups stems from the helping and cooperative behaviours displayed by group members. Members of social groups work together to complete complex tasks such as food acquisition, colony defence, and the rearing of young (Hölldobler & Wilson 1990; Ross & Matthews 1991).

The evolution of the remarkable behaviours displayed by social individuals originated partly through kin selection.

Under kin selection, helping behaviours directed at relatives increased in frequency in populations, because such acts ultimately augmented the indirect fitness of the helper (Hamilton 1964a, b; Bourke 2005). However, kin selection theory also predicts that individuals within social groups will sometimes come into conflict. Conflict potentially occurs over a variety of issues concerning reproductive behaviours when interacting individuals are related by less than unity (Queller & Strassmann 1998; Bourke 2005; Boomsma & Franks 2006; Ratnieks *et al.* 2006).

Social hymenopteran insects (ants, some bees, and some wasps) represent key taxa for studying the interplay between cooperation and conflict in social systems (reviewed by Foster & Ratnieks 2001a; Tarpay *et al.* 2004; Boomsma & Franks 2006; Ratnieks *et al.* 2006). Many social hymenopteran societies are characterized by variance in relatedness among society members, thereby providing the conditions necessary for conflict among group members.

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Conflict may be particularly likely to occur in colonies composed of multiple subfamilies. Such situations arise if the colony is headed by multiple queens or is headed by a queen mated to multiple males (polyandry) (Keller 1993; Boomsma & Ratnieks 1996).

One particularly important area where conflict among subfamilies may arise is over the rearing of new queens (gynes). In these cases, selection should lead to reproductive competition, defined as competitive interactions leading to differences in reproductive success among subfamilies (modified from Tilley & Oldroyd 1997). Reproductive competition may take the form of individual workers within nests helping their close relatives develop as gynes or harming less related individuals so that they fail to develop as sexual offspring (nepotism). Alternatively, developing larvae derived from particular lineages may be sexualized by workers at high rates because these larvae are more attractive. Finally, reproductive competition may take place through sperm-competition among male mates of polyandrous queens (Franck *et al.* 2002; Boomsma *et al.* 2005).

Previous studies, primarily conducted in *Apis* honeybees, attempted to detect reproductive competition within colonies. However, evidence for reproductive competition in *Apis* has been mixed (reviewed by Tarpy *et al.* 2004). Studies of queenright *A. mellifera* colonies failed to detect reproductive competition (Estoup *et al.* 1994; Franck *et al.* 2002). Unfortunately, these studies were hindered by the fact that *Apis* colonies produce relatively few gynes, thereby decreasing the power to detect the results of competitive interactions. In contrast, evidence of reproductive competition has been uncovered in *Apis* colonies when the queen heading the colony is removed, a situation that results in a relatively large number of gynes being reared by workers (Tilley & Oldroyd 1997; Osborne & Oldroyd 1999; Chaline *et al.* 2003; Schneider *et al.* 2003; Moritz *et al.* 2005). These latter studies provide tantalizing evidence that reproductive competition may occur in normally functioning social insect colonies (Moritz *et al.* 2005).

The purpose of this study is to determine if reproductive competition occurs in natural, unmanipulated colonies of the social wasp *Vespula maculifrons*. *Vespula* wasps are particularly attractive candidates for studying reproductive competition for several reasons. First, wasps hold a place of central importance to the study of social behaviour. The significance of wasps stems partly from the diversity of social systems that they display (Ross & Matthews 1991; Turillazzi & West-Eberhard 1996). *Vespula* wasps are a particularly useful taxon to study because of their known phylogeny, social biology and caste system (Spradbery 1973; Edwards 1980; Greene 1991; Foster & Ratnieks 2001a). *Vespula* thus represents an important taxon in which to test predictions from kin selection theory and investigate the role of reproductive competition.

Second, annual *Vespula* colonies are headed by a single, multiply mated queen (Greene 1991; Spradbery 1991). Consequently, colonies are composed of several subfamilies, thereby providing the genetic variation necessary to set the stage for conflict among colony members. However, the breeding system of *Vespula* ensures that the genetic differences among colonymates is determined solely by the number of times that a queen mates and not the number of queens within colonies. This is important, because studies in *Vespula* can isolate the effects of polyandry without the additional confounding issues that arise from the presence of multiple queens (e.g. Holzer *et al.* 2006).

A third reason for studying reproductive conflict in *Vespula* wasps is that *Vespula* colonies produce large numbers of sexuals. For example, *V. maculifrons* colonies produce hundreds of gynes and males each year (MacDonald & Matthews 1981). This contrasts with *Apis* bees, which produce relatively few gynes per colony (Seeley 1995). The ability to obtain large numbers of reproductives per colony greatly increases the power of tests aimed at detecting reproductive competition.

A final reason for investigating reproductive competition in *Vespula* wasps is that *Vespula* colonies are typically annual (Greene 1991; Spradbery 1991). This differs from many species of ants and bees, where colonies persist for several seasons. The reason for studying an annual species is that the sexuals produced at the end of the season represent the entire reproductive output of the colony. Therefore the lifetime output of sexuals can be readily analysed. This is more difficult in perennial taxa where many years of study may be required to document the lifetime reproductive success of individuals.

This study sought evidence for reproductive competition in *V. maculifrons*. Specifically, we used genetic markers to investigate whether the paternity of males varied with regard to the worker and gyne castes, as would be expected if reproductive competition occurred within colonies. We also determined the extent that male reproductive skew differed between workers and gynes within colonies. Finally, we investigated if males that contributed substantially to the production of one caste necessarily contributed little to the production of the other. Overall, our results provide a more thorough understanding of the prevalence of reproductive competition in highly social organisms.

## Materials and methods

We sampled workers and gynes from 11 *V. maculifrons* colonies collected in and around Atlanta, Georgia, USA in 2004–05. The genotypes of all sampled workers were determined at the eight polymorphic microsatellite loci: LIST2003, LIST2004, LIST2013, LIST2019, LIST2020, Rufa5, VMA-3, and VMA-6 (Foster *et al.* 2001; Daly *et al.* 2002; Hasegawa & Takahashi 2002). The gene diversities at these

**Table 1** Variability of eight microsatellite loci in *V. maculifrons*. The number of alleles sampled ( $N$ ) were obtained from the inferred genotypes of diploid females and haploid males that produced workers sampled in a larger study of this species. The total number of alleles ( $A$ ) and gene diversities ( $h$ ) illustrate that the loci are highly variable in *V. maculifrons*

| Locus    | $N$ | $A$ | $h$   |
|----------|-----|-----|-------|
| LIST2003 | 259 | 21  | 0.916 |
| LIST2004 | 273 | 12  | 0.853 |
| LIST2013 | 275 | 15  | 0.808 |
| LIST2019 | 240 | 12  | 0.740 |
| LIST2020 | 277 | 17  | 0.864 |
| Rufa5    | 242 | 2   | 0.152 |
| VMA-3    | 235 | 19  | 0.896 |
| VMA-6    | 275 | 39  | 0.943 |

loci are sufficiently high (Table 1) that the probability of two males having the same genotype (nondetection error; Boomsma & Ratnieks 1996) is low ( $<< 0.0001$ ). The genotypes of the workers within colonies were used to reconstruct the genotype of the queen and her male mates. Subsequently, the genotypes of the gynes from each colony were determined at a subset of loci (LIST2004, LIST2013, LIST2019, LIST2020, and VMA-6) that displayed sufficient variation to distinguish all patrilines within colonies.

We calculated the effective paternity ( $k_{e3}$ ) for workers and gynes using the sample size correction proposed by Nielsen *et al.* (2003). The metric  $k_{e3}$  combines information on the number of times a queen mates and the unequal contributions of a queen's male mates to offspring (Boomsma & Ratnieks 1996).  $k_{e3}$  describes the amount of genetic variability of diploid individuals within colonies and will be less than the actual mate number of queens if males display reproductive skew. We tested if the paired estimates of  $k_{e3}$  obtained for workers and gynes within colonies differed using a Wilcoxon signed rank test.

We also calculated the magnitude of reproductive skew of males mated to queens using the measure  $B$  of Nonacs (2003). The 95% confidence intervals for each estimate of  $B$  were also estimated to determine the significance of skew. Values of  $B$  were considered to be significant if the 95% confidence intervals failed to overlap 0. Both the skew and significance of skew were calculated using the program `SKREW CALCULATOR`. As was the case with our estimates of  $k_{e3}$ , we tested if the paired estimates of  $B$  obtained for workers and gynes differed via a Wilcoxon signed rank test.

We next determined if the contributions of males to workers and gynes within colonies differed. To conduct this test, we used the program `STRUC` contained within the `GENEPOP` package of programs (Raymond & Rousset 1995). The algorithm implemented by `STRUC` calculates an approximation of an exact  $P$ -value for a probability test on

a contingency table. Significant estimates of  $P$  indicate that male mates of queens contribute unequally to workers and gynes within colonies.

Finally, we investigated if males that were particularly successful in siring workers tended to be unsuccessful in siring gynes and if males that were mostly unsuccessful in siring workers were successful in siring gynes (i.e. patriline reversal, Moritz *et al.* 2005). To test for patriline reversal, we determined the proportional contribution of each male to workers and gynes for each colony. We then examined the linear relationship between the proportional contribution to gynes and the proportional contribution to workers for males within colonies. If no patriline reversal occurred, then the slope of the line describing this association (if male contribution to workers is taken as the independent variable), hereafter referred to as the worker-gyne linear relationship, should be close to 1.0. However, if patriline reversal did occur, then the slope of the worker-gyne linear relationship would tend to be less than 1.0.

To determine if slopes obtained from our data were less than unity more often than expected by chance, we conducted computer simulations. Specifically, we simulated a population composed of queens that mated with multiple males. We then assumed that the male mates of queens sired equal fractions of workers and gynes; the actual distribution of male contributions was chosen from a uniform distribution. Then, the estimated contribution of males to workers and gynes was simulated by sampling a particular number of individuals of each caste from the true distribution. Finally, the worker-gyne linear relationship was estimated using standard least-square regression (Ott 1988).

The simulations were conducted 1000 times for varying ranges in mate number and sample sizes. The proportion of the 1000 slopes for the worker-gyne linear relationship that fell below 1.0 for our sample size was used as the probability of a slope falling below 1.0 in our test. We then used a binomial test to determine if the number of slopes describing the worker-gyne linear relationship in our study that fell below 1.0 differed significantly from that expected by chance.

## Results

We obtained the genotypes of  $52.82 \pm 36.94$  workers ( $\bar{x} \pm \text{SD}$ ) and  $36.09 \pm 2.88$  gynes from 11 colonies (Table 2). We found that all queens mated multiply. The number of males responsible for the production of workers and gynes within colonies were usually similar (Table 2). The sole exception was colony 36, where four more males sired gynes than workers. However, more than twice as many gynes as workers were sampled in this colony, thereby permitting for detection of rare male patrilines among gynes.

The estimates of effective paternity ( $k_{e3}$ ) for workers and gynes within nests fell below the observed number of

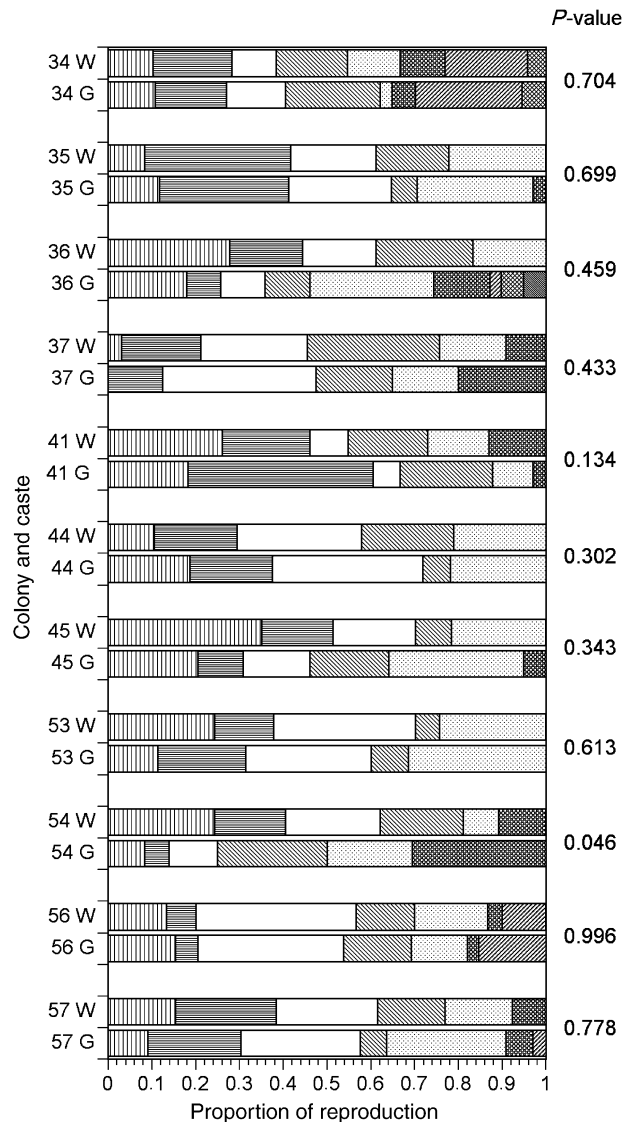
**Table 2** The observed ( $k$ ) and effective ( $k_{e3}$ ) number of male mates of polyandrous queens contributing to workers (W) and gynes (G) in 11 *V. maculifrons* colonies ( $N$  = sample size). The estimates of reproductive skew ( $B$ ) indicate if males contributed unequally to each caste; significant estimates of  $B$  are denoted by an asterisk

| Colony | Caste | $N$ | $k$ | $k_{e3}$ | $B$     |
|--------|-------|-----|-----|----------|---------|
| 34     | W     | 117 | 8   | 7.4419   | 0.0092  |
|        | G     | 37  | 8   | 6.806    | 0.0201  |
| 35     | W     | 36  | 5   | 4.7089   | 0.0432* |
|        | G     | 34  | 6   | 4.8034   | 0.0389* |
| 36     | W     | 18  | 5   | 5.9218   | 0.0494  |
|        | G     | 39  | 9   | 7.1345   | 0.0272* |
| 37     | W     | 33  | 6   | 5.1862   | 0.0239  |
|        | G     | 40  | 5   | 4.7048   | 0.0437* |
| 41     | W     | 115 | 6   | 5.6082   | 0.0114* |
|        | G     | 33  | 6   | 4.0075   | 0.079*  |
| 44     | W     | 95  | 5   | 4.8021   | 0.008   |
|        | G     | 32  | 5   | 4.6018   | 0.0152  |
| 45     | W     | 37  | 5   | 4.5685   | 0.0497* |
|        | G     | 39  | 6   | 5.3768   | 0.0178  |
| 53     | W     | 37  | 5   | 4.4466   | 0.0231  |
|        | G     | 35  | 5   | 4.5496   | 0.018   |
| 54     | W     | 37  | 6   | 6.0636   | -0.003  |
|        | G     | 36  | 6   | 5.13     | 0.0262  |
| 56     | W     | 30  | 7   | 5.317    | 0.0419* |
|        | G     | 39  | 7   | 5.4963   | 0.037*  |
| 57     | W     | 26  | 6   | 6.5197   | 0.0076  |
|        | G     | 33  | 7   | 5.3434   | 0.0415* |

mates ( $k$ ) in most colonies (Table 2). However, there were a few cases where  $k_{e3}$  was greater than  $k$  (e.g. workers in colonies 36, 54, and 57). These instances may reflect situations where our sample size did not enable us to accurately estimate the number of mates or where the distribution of male contributions were overly uniform relative to expectations (Nielsen *et al.* 2003). Regardless, the values of  $k_{e3}$  were seldom far from the observed number of mates suggesting that magnitude of reproductive skew in this species is fairly low (Table 2).

We next used a Wilcoxon signed rank test to determine if the effective paternity of queens differed between workers and gynes within colonies. Such a result might be expected if fewer males tended to contribute to gynes than workers. However, we found no evidence that the effective paternity for workers and gynes within colonies differed in a consistent fashion ( $T = 10.0$ ;  $P = 0.413$ ).

We investigated the magnitude of reproductive skew displayed by males. Estimates of skew ( $B$ ) tended to be small, although a few values differed significantly from zero (Table 2). We tested if there were consistent differences in male skew between workers and gynes, as would occur if some males monopolized gyne production. However, as with the case of effective paternity, we found no



**Fig. 1** Proportional contribution of males to workers (W) and gynes (G) in 11 *V. maculifrons* colonies. Note that the same patterns are used to distinguish contributions of different males in distinct colonies. The  $P$ -values provided result from probability tests used to determine if the proportions of contributions by males to workers and gynes differed. Overall, we found little evidence that males sired different proportions of workers and gynes within colonies.

evidence that skew was consistently greater or smaller in workers than in gynes ( $T = -11.0$ ;  $P = 0.817$ ).

We next turned our attention to the question of whether males contributed differentially to workers and gynes within colonies. In general, there was little evidence that the male mates of polyandrous queens contributed differentially to the production of workers and gynes. Indeed, our tests generally failed to uncover differences in the proportional contribution of males to the two castes (Fig. 1). Colony 54 showed marginally significant variation in

**Table 3** Slopes of the worker-gyne linear relationship for simulated data. The median slope value (and associated 95% confidence interval) is given for varying numbers of male mates and differing number of workers (W) and gynes (G) sampled. The proportions of slopes that are less than 1.0 ( $P_{unity}$ ) in 1000 simulations are provided. Note that  $P_{unity}$  is frequently greater than the random expectation of 0.5

| W    | G    | 3–5 mates             |             | 5–10 mates            |             | 10–20 mates           |             |
|------|------|-----------------------|-------------|-----------------------|-------------|-----------------------|-------------|
|      |      | Median slope (95% CI) | $P_{unity}$ | Median slope (95% CI) | $P_{unity}$ | Median slope (95% CI) | $P_{unity}$ |
| 10   | 10   | 0.563 (–0.833, 2.000) | 0.753       | 0.175 (–0.731, 1.350) | 0.915       | N/A                   | N/A         |
| 100  | 10   | 0.966 (–0.480, 2.152) | 0.528       | 0.915 (0.050, 1.776)  | 0.572       | 0.814 (–0.187, 1.742) | 0.643       |
| 1000 | 10   | 1.003 (–0.181, 2.001) | 0.497       | 1.022 (0.022, 1.815)  | 0.480       | 0.977 (0.164, 1.774)  | 0.519       |
| 10   | 100  | 0.700 (–0.260, 1.500) | 0.816       | 0.518 (–0.024, 1.113) | 0.948       | 0.327 (–0.033, 0.735) | 0.999       |
| 100  | 100  | 0.962 (0.497, 1.434)  | 0.576       | 0.924 (0.537, 1.294)  | 0.694       | 0.845 (0.478, 1.229)  | 0.794       |
| 1000 | 100  | 1.003 (0.665, 1.341)  | 0.496       | 0.987 (0.688, 1.282)  | 0.536       | 0.984 (0.720, 1.245)  | 0.545       |
| 10   | 1000 | 0.744 (–0.155, 1.581) | 0.810       | 0.577 (0.060, 1.089)  | 0.961       | 0.381 (0.073, 0.760)  | 0.999       |
| 100  | 1000 | 0.962 (0.552, 1.315)  | 0.642       | 0.928 (0.668, 1.184)  | 0.701       | 0.862 (0.631, 1.116)  | 0.870       |
| 1000 | 1000 | 0.996 (0.833, 1.147)  | 0.531       | 0.994 (0.879, 1.106)  | 0.544       | 0.984 (0.877, 1.108)  | 0.620       |

N/A: Simulations could not be conducted for this sample size.

male paternity between workers and gynes. However, this result was ultimately considered not significant after Bonferroni corrections. Moreover, when the  $P$ -values from all colonies were combined using Fisher's method (Sokal & Rohlf 1995), we found no evidence of significant variation in male contribution to workers and gynes in *V. maculifrons* colonies ( $P = 0.529$ ).

Finally, we investigated if patriline reversal occurred within colonies. We calculated the slopes of the worker-gyne linear relationship for each colony. In total, nine of the slopes were less than 1.0 and two of the slopes were greater than 1.0. If the probability of a slope falling below 1.0 is (incorrectly) set at 0.5, then our data provide evidence of patriline reversal (binomial test;  $P = 0.0269$ ). However, the results of our simulations indicated that the probability of the slope of the worker-gyne linear relationship falling below 1.0 generally was higher than 0.5.

Table 3 demonstrates this point by providing the results of simulations of data sets for various combinations of queen mate number and sample size. When few workers or gynes are sampled from a colony, then estimates for real paternity fractions are poor, which leads to a large proportion of slopes describing the worker-gyne linear relationship falling below 1.0. This pattern arises because of the incomplete sampling of patrilines and the nature of linear regression.

We specifically calculated the probability of the slope of the worker-gyne linear relationship falling below 1.0 for situations where queens mated with 5–9 males (our observed range in mate number) and for which 53 workers and 36 gynes (our mean sample sizes) were sampled per colony. We found that the slope fell below 1.0 in 69.7% of such cases. Consequently, the probability of nine (or more) of 11 slopes falling below 1.0 given that there is a 69.7% chance of such an event occurring is  $P = 0.305$ . In conclusion, our data do not provide significant evidence of patriline reversal.

## Discussion

Members of social insect societies display extreme cooperative behaviours. However, selfish behaviours resulting from conflict among group members also exist (Beekman *et al.* 2003; Bourke 2005; Ratnieks *et al.* 2006). One potential area of conflict among group members concerns the rearing of new sexuals within colonies (Tarpay *et al.* 2004; Ratnieks *et al.* 2006). Colony members may be involved in reproductive competition surrounding new queen (gyne) production. Selection should operate on individuals so that they or their close kin develop as gynes. This study sought evidence for such reproductive competition in the highly social wasp *V. maculifrons*.

The main result from our study is that we failed to detect reproductive competition within *V. maculifrons* colonies. Even though we had sufficient sample sizes to detect competition if it occurred (Table 2), we found no significant evidence that the frequencies of patrilines were different in adult workers and gynes within colonies. Nor did we find that the effective number of male mates contributing to the two castes differed in a consistent fashion. Furthermore, we found no evidence of patriline reversal, whereby patrilines represented highly among workers were represented infrequently among gynes. Thus, we conclude that reproductive competition concerning gyne production is absent in *V. maculifrons*.

Our data suggest that *V. maculifrons* queens use sperm from their male mates consistently throughout their lifetime. This finding supports previous observations in hymenopteran social insect taxa that found that sperm use by polyandrous queens does not vary substantially over time (Ross 1986; Estoup *et al.* 1994; Tilley & Oldroyd 1997; Franck *et al.* 2002). Such findings indicate that sperm competition occurring within the queen's spermatheca after

mating is likely to be rare in highly social insects (Birkhead & Moller 1998).

We also found that estimates of the effective paternity of males mated to reproductive queens (Table 2) tended to be rather close to the actual mate number of queens. This suggests that reproductive skew among male mates is low in *V. maculifrons*. The close match between actual and effective mate number further indicates that male contributions to offspring do not differ from even contributions and that male mates of queens achieve more or less equal reproductive success.

Previous studies have investigated reproductive skew among male mates in other *Vespula* species. For example, male skew in *V. vulgaris* was found to be relatively low (Foster & Ratnieks 2001b). In contrast, skew in *V. germanica* and *V. rufa* reached high and often significant levels, reflecting the fact that males frequently contributed unequally to offspring production (Goodisman *et al.* 2001, 2002; Wenseleers *et al.* 2005). The variation in male skew among distinct taxa may reflect varying selection pressures related to reproductive competition or sexual selection (e.g. Boomsma & Sundström 1998). Regardless, further investigation of the causes and consequences of reproductive skew in this genus is warranted.

The lack of finding of reproductive competition in natural, unmanipulated *V. maculifrons* colonies differs from previous studies that have documented reproductive competition in *Apis* colonies undergoing emergency queen rearing (Tilley & Oldroyd 1997; Osborne & Oldroyd 1999; Chaline *et al.* 2003; Schneider *et al.* 2003; Moritz *et al.* 2005). Nonetheless, our results are not necessarily at odds with these prior reports. The dynamics within normally functioning social insect colonies, such as those studied in this investigation, and colonies that have become queenless likely differ. Indeed, it is possible that selection operating to suppress reproductive competition in normally functioning social insect colonies is absent in potentially deteriorating colonies such as those that become queenless, because colony organization and efficiency are already disrupted in failing nests (Tilley & Oldroyd 1997; Moritz *et al.* 2005).

Overall, our results support the prediction that selection operating on individuals to behave selfishly within social insect colonies through reproductive competition should be overridden by selection operating at the colony level (Wilson & Hölldobler 2005). This prediction stems from the hypothesis that behaviours associated with reproductive competition may be costly within colonies. Indeed, strong evidence of nepotism is generally lacking in social insects (Keller 1997; Queller & Strassmann 1998; Tarpay *et al.* 2004; Ratnieks *et al.* 2006). Thus conflict over the production of gynes within social insect colonies may be quashed due to selection operating at the level of the colony, which requires efficiency and cooperative behaviour for optimal function within the nest (Keller 1997; Queller & Strassmann 1998; Boomsma & Franks 2006; Ratnieks *et al.* 2006).

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