

## Evolution of sex ratios in social hymenoptera: consequences of finite brood size

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**Abstract.** Evolutionarily stable sex ratios are determined for social hymenoptera under local mate competition (LMC) and when the brood size is finite. LMC is modelled by the parameter  $d$ . Of the reproductive progeny from a single foundress nest, a fraction  $d$  disperses (outbreeding), while  $(1-d)$  mate amongst themselves (sibmating). When the brood size is finite,  $d$  is taken to be the probability of an offspring dispersing, and similarly,  $r$ , the proportion of male offspring, the probability of a haploid egg being laid. Under the joint influence of these two stochastic processes, there is a nonzero probability that some females remain unmated in the nest. As a result, the optimal proportion of males (corresponding to the evolutionarily stable strategy, ESS) is higher than that obtained when the brood size is infinite. When the queen controls the sex ratio, the ESS becomes more female biased under increased inbreeding (lower  $d$ ). However, the ESS under worker control shows an unexpected pattern, including an *increase* in the proportion of *males* with *increased inbreeding*. This effect is traced to the complex interaction between inbreeding and local mate competition.

**Keywords.** Sex ratios; local mate competition; social hymenoptera; evolutionarily stable strategies; mathematical modelling.

### 1. Introduction

How best—in an evolutionary sense—should sexual organisms allocate their resources between their male and female progeny? Sex ratio theory, which attempts to answer this question, has been a very active area of evolutionary biology (Charnov 1982). Especially interesting are the applications to social insects (Trivers and Hare 1976; Alexander and Sherman 1977), where predictions made on this basis have proved invaluable in testing the various competing theories for the evolution of social behaviour (Craig 1980; for a review, see Gadagkar 1985). Beginning with the classic work of Hamilton (1967), theoretical investigations have encompassed a variety of factors which govern the sex ratio (defined as the proportion of males in the brood)—local mate competition (Taylor and Bulmer 1980), worker control of sex ratio (Trivers and Hare 1976), workers laying male eggs (Benford 1978), multilocus control (Pamilo 1982) and inbreeding (Herre 1985)—either separately, or jointly (Joshi and Gadagkar 1985).

Almost all these studies assume an infinite population and an infinite brood size, and determine the evolutionarily stable sex ratio, i.e. the value of the genetically controlled sex ratio, which, if prevalent in the population, would prohibit the spread of any other sex ratio mutant.

Real life systems, to which these theories have to be applied have, of course, finite populations and finite brood sizes, and it is desirable to investigate the extent to which this would alter the optimal sex ratios. Moreover, even before one applies the sex ratio theory to any specific system, several questions of theoretical interest arise: will the evolutionarily stable strategy (ESS) always be obtained from any arbitrary starting

composition of gene frequencies? If so, how long will it take? To what extent will the sex ratio in a finite population fluctuate in response to stochastic effects? The technique of Monte Carlo simulation is an ideal one for answering these questions. As a prelude to undertaking such an investigation, the present work reports the consequences of finite brood size on the optimal (evolutionarily stable) sex ratio.

Such investigations have been carried out earlier for the special case of highly inbred (though not social) wasps. When there is complete inbreeding, LMC theory predicts the proportion of males to be zero; which implies production of "just enough males (ideally one) to inseminate all the females" (Hamilton 1967). Hartl (1971) was the first to point out that if fertilization of the egg were a binomial process (like the tossing of a highly biased coin), the optimal proportion of males would be higher than that corresponding to only one male. The process of sex determination is more precise than binomial in such highly inbred systems (Green *et al* 1982; Putters and Van der Assem 1985). Green *et al* (1982) have developed an elaborate model for determining optimal sex ratios, which takes into account the effect of such enhanced precision.

The present work extends these studies to cover the entire spectrum from complete inbreeding to complete outbreeding. It also examines the situation where the workers in the nest control the sex ratio. Consequences of polyandry are also explored.

## 2. The model

An outline of the model is presented below. The detailed model, except for the effects of the finite brood size, has been described at length in an earlier publication (Joshi and Gadagkar 1985).

### 2.1 The breeding system

The model assumes an infinite population of nests, each founded by an inseminated female (the queen). After reproduction, the queen dies. A fraction  $d$  of the brood (both males and females) disperses from the nest to join the mating pool where the females are inseminated (outbreeding). In the fraction  $1-d$  remaining at the nest, sibmating takes place. The inseminated females emerging from the nest, as well as those from the pool, establish new nests to begin the next generation.

The sex ratio trait is modelled by a one-locus two-allele ( $A$  and  $B$ ) system. When the queen controls the sex ratio, the proportion of males produced by the genotype  $AA$  is  $r_A$  and by  $BB$  is  $r_B$ . The two alleles are assumed to be co-dominant, and the proportion for  $AB$  is  $(r_A + r_B)/2$ . Under worker control, the sex ratio is taken to be the weighted average of the sex ratios specified by the genotypes of the workers.

### 2.2 A probabilistic approach when the brood size is finite

Let  $N$  be the total number of eggs laid in a nest. If  $r$  is the sex ratio for the nest then the probability that a male (haploid, unfertilized) egg is laid is also taken to be  $r$ . Assuming a binomial distribution, the probability that exactly  $K$  fertilized eggs are laid ( $K$  females are produced) is

$$P(K) = [N!/(N-K)!K!](1-r)^K r^{N-K}. \quad (1)$$

Similarly,  $1-d$ , the fraction of offspring which remain at the nest, is also taken to be the probability that an offspring remains at the nest. Under binomial distribution, the probability that  $n$  out of  $K$  females remain at the nest is

$$P(n, K) = [K!/(K-n)!n!] (1-d)^n d^{K-n}. \quad (2)$$

For these females to be inseminated, at least one of the  $N-K$  males produced in the nest should remain at the nest, and the associated probability is  $1-d^{N-K}$ .

Hence, the expected number of inseminated females emerging from the nest is given by

$$\begin{aligned} F_{\text{nest}} &= \sum_{K=0}^N P(K) \sum_{n=0}^K P(n, K) n (1-d^{N-K}) \\ &= \sum_{K=0}^N P(K) (1-d^{N-K}) \left[ \sum_{n=0}^K n P(n, K) \right]. \end{aligned}$$

The term in the square brackets is just  $(1-d)K$ . Thus, using (1)

$$F_{\text{nest}} = (1-d) \sum_{K=0}^N [N!/(N-K)!K!] (1-r)^K r^{N-K} K (1-d^{N-K}).$$

This summation can be evaluated to yield

$$F_{\text{nest}} = N(1-d)(1-r) \{1 - [1-r(1-d)]^{N-1}\}. \quad (3)$$

The term  $[1-r(1-d)]^{N-1}$  thus represents a correction due to the finite brood size, and tends to zero as  $N$  tends to infinity, as expected.

### 2.3 Stability analysis

Each nest is characterized by the genotype of the foundress, and the genotype of the male(s) she has mated with. Social hymenoptera being haplodiploid, the genotype of the male is either  $A$  or  $B$ . Under single insemination, there are six types of females:  $AA.A$ ,  $AA.B$ ,  $AB.A$ ,  $AB.B$ ,  $BB.A$  and  $BB.B$ . If the frequencies  $P_1, \dots, P_6$  of each of these six classes in the  $n$ th generation are known, then for given values of  $d$ ,  $r_A$  and  $r_B$ , the contributions from each of the above classes to the next generation, via inseminated females from the nests, and via the males and females joining the mating pool, can be evaluated, and the frequencies,  $P_1 \dots P_6$  for the next  $(n+1)$ th generation can be determined. When a population consisting entirely of the genotype  $A$  is invaded by a small proportion of the competing allele  $B$ , the dynamics is expressed by

$$[P_1(n+1), \dots, P_5(n+1)]^T = G[P_1(n), \dots, P_5(n)]^T, \quad (4)$$

where  $G$  is a  $5 \times 5$  matrix (since the frequencies add up to 1, only 5 variables need be considered) whose elements are functions of  $r_A$ ,  $r_B$  and  $d$ . If the dominant eigenvalue  $\lambda$  of the matrix is greater than unity, this implies that  $B$  can invade the population of  $A$ ; if it is less than unity,  $A$  is uninvadable. The optimal sex ratio  $\hat{r}$  corresponding to the ESS is obtained from the condition (Maynard Smith 1982),

$$\partial \lambda / \partial r_B = 0 \quad |_{r_A=r_B=\hat{r}}.$$

The calculations were done numerically on the DEC-1090 computer system at the Indian Institute of Science.

Generalization of the above procedure to cases where a female mates with more than one male is straightforward.

## 2.4 Optimal sex ratios using the Hamiltonian approximation

The contribution of a female to the next generation (fitness) is given by the sum of the number of daughters produced by her and the number of inseminations which her sons have performed (Hamilton 1967). If the sons and daughters are not equally related to the mother, the corresponding terms should be weighted by the appropriate coefficients of relatedness. Hence, in the present model, the fitness  $f_2$  of a mutant female (sex ratio  $r_2$ ) in a population with sex ratio  $r_1$  is given by

$$f_2 = (1 - r_2) \cdot R_f + (1 - r_2) \cdot (1 - d) \cdot R_m + [d(1 - r_1)r_2/r_1] \cdot R_m, \quad (5)$$

where  $R_f$  and  $R_m$  denote her relatedness to the daughter and the son, respectively. The second term corresponds to the inseminations by the sons at the nest, while the third one to those in the mating pool. The ESS  $\hat{r}$  is obtained from the conditions  $\partial f_2 / \partial r_2 = 0$ ,  $r_1 = r_2$ , and is seen to be

$$\hat{r} = d R_m / (R_m + R_f). \quad (6)$$

A slight departure from outbreeding ( $d = 1 - \varepsilon$ ) leads to the expression (neglecting terms in  $\varepsilon^2$  and beyond)

$$\hat{r} = [(1 - \varepsilon) R_m] / (R_m + R_f). \quad (7)$$

On the other hand, when the brood size is finite ( $N$ ), the fitness is given by

$$f_2 = (1 - r_2) [1 - (1 - d)(1 - r_2(1 - d))^{N-1}] R_f \\ + (1 - r_2)(1 - d) \{1 - [1 - r_2(1 - d)]^{N-1}\} R_m + [d(1 - r_1)r_2/r_1] R_m.$$

The expression for  $\hat{r}$  turns out to be too involved to be expressed as a convenient formula. However, under a slight departure from outbreeding ( $d = 1 - \varepsilon$ ), it can be shown that

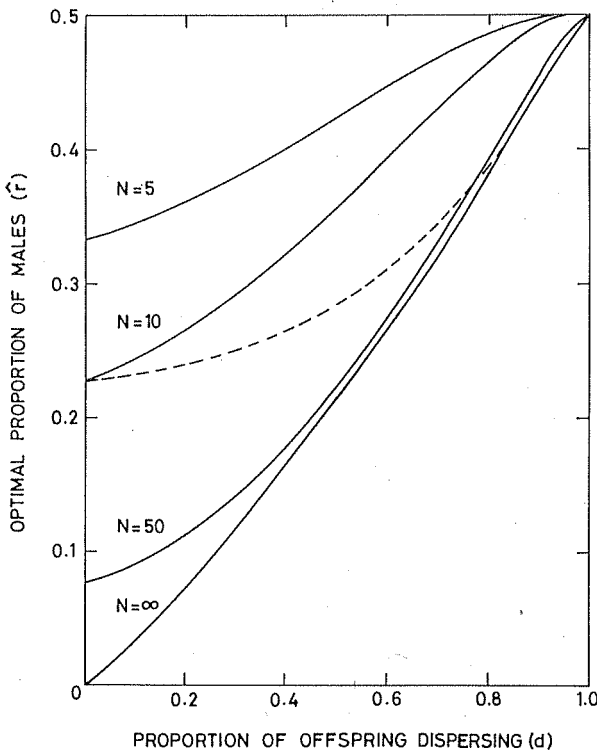
$$\hat{r} = R_m / (R_m + R_f). \quad (8)$$

When workers control the sex ratio,  $R_m$  and  $R_f$  denote the relatedness with brother and sister respectively. As will be discussed in the last section, the differences in (7) and (8) have an important bearing on the differences in the optimal sex ratios under queen control and worker control.

## 3. Results

### 3.1 Queen control of the sex ratio

Optimal sex ratios (OSR) under queen control were determined for the entire range of  $d$  ( $d = 0$ , complete inbreeding, to  $d = 1$ , complete outbreeding), for brood sizes ranging from 5 to infinity. The results are summarized in figure 1. The OSR is always female biased for  $d < 1$ . As expected, for a fixed value of  $d$ , an increase in the brood size leads to a decrease in the proportion of males. For moderate to high values of  $d$ , and



**Figure 1.** Optimal proportion of males ( $\hat{f}$ ) is plotted as a function of  $d$ , the proportion of offspring dispersing when the queen controls the sex ratio. The brood size is denoted by  $N$ . The broken line corresponds to  $\hat{f}$  for  $N = 10$  under the density dependent dispersal model.

brood sizes beyond 50, the OSR for finite and infinite broods are almost indistinguishable. However, for low  $d$  (high inbreeding) there are marked differences between the two.

For the special case of complete inbreeding ( $d = 0$ ), the OSR is the one which maximizes the number of inseminated females emerging from the nest (Hartl 1971; Green *et al* 1982). This can be readily obtained from (3) to be

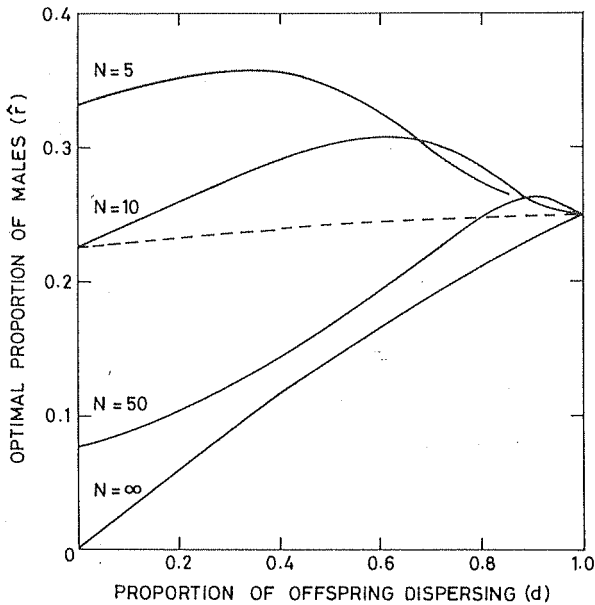
$$\hat{f} = 1 - (1/N)^{1/(N-1)}, \quad (9)$$

which agrees very well with the results shown in figure 1, obtained from stability analysis described in §2.3.

When the queen mates with more than one male, the OSR are, as expected, indistinguishable from those under single insemination.

### 3.2 Worker control of the sex ratio

The variation of OSR with the extent of inbreeding under worker control of the sex ratio is shown in figure 2 for various brood sizes. The pattern is qualitatively different from that under queen control. For a fixed brood size, the optimal proportion of males first increases with  $d$ , attains a maximum, and then decreases with increasing  $d$ . In particular,



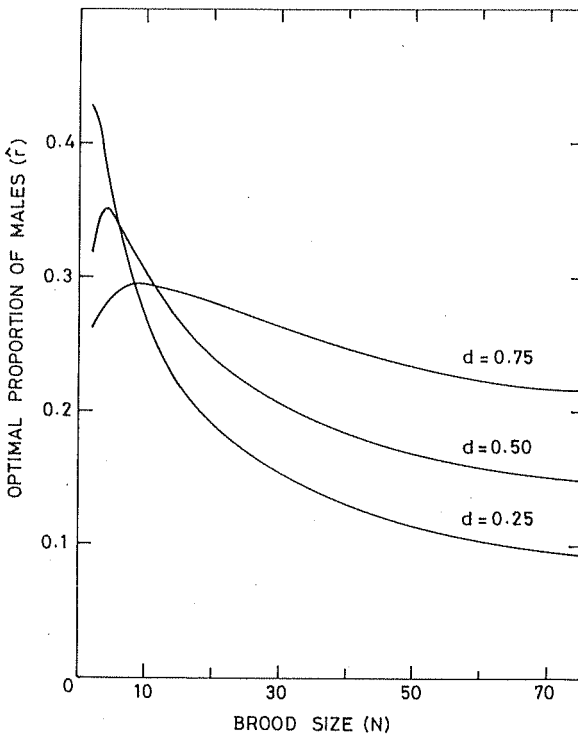
**Figure 2.** Optimal proportion of males ( $\hat{f}$ ) is plotted as a function of  $d$ , the proportion of offspring dispersing, when workers control the sex ratio and the queen is singly inseminated. The brood size is denoted by  $N$ . The broken line corresponds to  $\hat{f}$  for  $N = 10$  under the density dependent dispersal model.

near  $d = 1$ , for a small increase in inbreeding (small decrease in  $d$ ), there is an *increase* in the proportion of males. The variation of OSR with brood size (figure 3) for a fixed value of  $d$  is also not monotonic, unlike that under queen control. The pattern of variation also seems to depend on the value of  $d$ . The anomalous increase in the proportion of males with brood size is very small in magnitude, however, and is restricted to low values of brood size. The OSR for  $d = 0$  are identical to those under queen control, as expected, since under conditions of complete inbreeding, the females are equally related to their sisters and daughters and to their brothers and sons.

Optimal sex ratios obtained when a female mates with two males are shown in figure 4. The pattern is similar to that in figure 2. The differences between the patterns under queen control and worker control are seen to diminish with polyandry, as expected.

#### 4. Discussion

A major impetus for sex ratio theory was provided by the observation (Trivers and Hare 1976) that its predictions could be useful in evaluating the competing theories for the evolution of sociality on the basis of field data. Subsequent rigorous analyses (Oster *et al* 1977; Taylor and Bulmer 1980; Uyenoyama and Bengtsson 1981; for a review, see Charnov 1982) have highlighted the influence of factors like local mate competition, queen-worker conflict etc. on the OSR. The present work demonstrates that the brood size is also likely to affect the OSR to a significant extent, and for empirical tests of sex ratio theory, data on brood size should also be taken into account. For most of the species of ants, the reproductive brood sizes are of the order of several hundreds and the



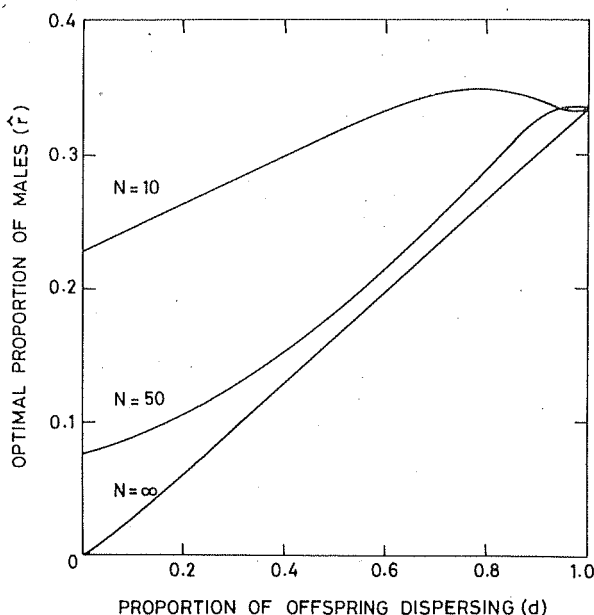
**Figure 3.** Optimal proportion of males ( $\hat{F}$ ) is plotted as a function of  $N$ , the brood size, for different values of  $d$ , the proportion of offspring dispersing.

infinite brood size approximation is adequate. However, individual nests of some primitively eusocial wasps (e.g. *Polistes*, *Vespula*) produce 5–50 reproductives and the results presented here would be relevant to these (see Brian 1965).

The two stochastic processes which influence OSR, when the brood size is finite, are sex determination and dispersal. Unlike the binomial distribution assumed here, brood sex ratios (at least in highly inbred species) are known to be determined with a better than binomial precision (Green *et al* 1982; Putters and van der Assem 1985). Even if it were so for less inbred species, the random component due to dispersal would still maintain the differences between the OSR under finite and infinite brood sizes. Yet another factor, not considered in the present work, is brood mortality (Green *et al* 1982); if all the offspring do not survive to adulthood, some females in the nest may remain unmated due to the absence of males, and shifts in the OSR similar to the present model would be expected.

One of the important consequences of finite brood size is the possible dependence of OSR on the dispersing characteristics of the males, which may be different from those of the females (Hamilton 1979). When the brood size is infinite, as long as the proportion of males dispersing is different from zero or unity, the OSR is determined exclusively by the  $d$  corresponding to the females. An examination of (3) shows that if the proportions of males and females dispersing from the nest are  $d_m$  and  $d_f$ , respectively, then the number of inseminated females leaving the nest would be given by

$$F_{\text{nest}} = N(1 - d_f)(1 - r) \{1 - [1 - r(1 - d_m)]^{N-1}\},$$



**Figure 4.** Optimal proportion of males ( $\hat{F}$ ) is plotted as a function of  $d$ , the proportion of offspring dispersing when workers control the sex ratio, and the queen is doubly inseminated. The brood size is denoted by  $N$ .

indicating an explicit dependence on  $d_f$  and  $d_m$ . The consequences of the differential dispersal of male and female offspring on OSR are being investigated.

Another possibility to be examined is the density dependent dispersal of males. The probability of a male dispersing may be a function of the number of males present in the nest; the lower the number, the lower the probability of dispersal. This would lead to a decrease in the number of uninseminated females and consequently a reduction in the optimal proportion of males. In a simplified version of this model, it is assumed that at least one male remains in the nest. In this case, only an all-female brood leads to some of the females remaining uninseminated. The optimal sex ratios obtained for such a model are shown by the broken lines in figures 1 and 2. When there is complete inbreeding ( $d = 0$ ), none of the males disperse; under complete outbreeding ( $d = 1$ ) all of them disperse and the two models lead to identical values of  $\hat{F}$ . For intermediate values of  $d$ , the density dependent dispersal model leads to a reduction in the proportion of males (figures 1 and 2).

The higher proportion of males, predicted under worker control in an almost outbreeding population compared to the completely outbreeding one, is intriguing at first sight. This effect can be understood when one looks at the two factors determining the OSR which are often compounded—local mate competition and inbreeding. Herre (1985) has emphasized the distinction between the two, and has very elegantly demonstrated how their effects can be separately examined. It can be seen from (7) that the optimal sex ratio is determined by the product of  $d$  which denotes the extent of local mate competition, and  $R_m/(R_m + R_f)$  which reflects the effect of inbreeding. A decrease in  $d$ , implies more local mate competition, and hence a reduction in the proportion of males.



Under complete outbreeding, the queen is related to both her sons and daughters by  $1/2$ , while under complete inbreeding, these values change to  $1/2$  and  $1$  respectively, and the ratio  $R_m/(R_m + R_f)$  decreases from  $1/2$  to  $1/3$ . Thus, inbreeding also leads to a reduction in the proportion of males.

On the other hand, under complete outbreeding, a worker is related to her brother by  $1/4$  and sister by  $3/4$ ; and under complete inbreeding, by  $1/2$  and  $1$  respectively. The ratio  $R_m/(R_m + R_f)$  thus increases from  $1/4$  to  $1/3$ . Since the increase (and consequently, the rate of increase) is small, the term corresponding to  $LMC(1 - \varepsilon)$  dominates in (7), and for infinite brood size, near  $d = 1$ , a reduction in the proportion of males with  $d$  is observed. When the brood size is finite, however, as seen from (8), near  $d = 1$ , only the inbreeding term influences the sex ratio, and an increase in the proportion of males is expected, as seen in figure 2. In fact, even under queen control, when the brood size is finite, near  $d = 1$ , only the inbreeding term contributes to the OSR, and the decrease in the proportion of males (figure 1) is slower than when the brood size is infinite.

In fact, a more general prediction can be made in the light of this analysis. If, in an experimental situation, the effects of LMC and inbreeding are separately examined (see Herre 1985), then when the workers control the sex ratio, an increase in the proportion of males with increasing inbreeding would be observed.

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