

## Colony-level sex ratio selection in the eusocial Hymenoptera

J. J. Boomsma<sup>1,2\*</sup> and A. Grafen<sup>2†</sup>

<sup>1</sup>*Department of Population Biology and Evolution, University of Utrecht, Utrecht, The Netherlands.* <sup>2</sup>*Department of Zoology, University of Oxford, Oxford, U.K.*

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### Abstract

We present an inclusive fitness model on worker-controlled sex investments in eusocial Hymenoptera which expands the existing theory for random mating populations as formulated by Trivers and Hare (1976) and Benford (1978). We assume that relatedness asymmetry is variable among colonies – owing to multiple mating, worker reproduction and polygyny – and that workers are able to assess the relatedness asymmetry in their own colony. A simple marginal value argument shows that “assessing” workers maximize their inclusive fitness by specializing on the production of the sex to which they are relatively more related than the average worker in the population is related to that sex. The model confirms our earlier verbal argument on this matter (Boomsma and Grafen, 1990) and gives further quantitative predictions of the optimal sex ratio of relatedness-asymmetry classes for both infinite and finite, random mating populations.

It is shown that in large populations all but one of the relatedness-asymmetry classes should specialize on the production of one sex only. The remaining, balancing class is selected to compensate any bias induced by the other class(es) such that the population sex ratio reflects the relatedness asymmetry of that balancing class. In the absence of worker-reproduction, the sex ratio compensation by the balancing-class is generally close to 100%, unless the population is very small.

In the Discussion we address explicitly the likelihood of our relatedness-assessment hypothesis and other assumptions made in the model. The relationship of our model with previous theory on sex allocation in eusocial Hymenoptera is worked out in the Appendix.

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\* Present address: Institute of Ecology and Genetics, University of Aarhus, DK-8000 Aarhus C, Denmark.

† Present address: Department of Plant Sciences, University of Oxford, Oxford OX1 3RA, U.K.

## Introduction

Trivers and Hare (1976) presented the first formal analysis of the conflict over the sex ratio between mother-queens and daughter-workers in the eusocial Hymenoptera. By combining sex ratio theory (Fisher, 1958), inclusive fitness theory (Hamilton, 1964, 1972) and parent offspring conflict (Trivers, 1974), they predicted that population sex-ratios should represent an overall 3:1 investment ratio in favour of females when full-sib workers control the sex allocation process, whereas no such bias was to be expected if the mother-queens were in control. The Trivers and Hare model considers relatedness asymmetry (henceforth referred to as RA) as effectively constant on an ecological time scale when it focusses on the worker queen conflict over sex allocation and the production of males. This model was extended by Benford (1978) to include further aspects of inter-colony variation in RA in combination with worker reproduction. Empirical data on population-level sex ratios, particularly those of ants, have been extensively reviewed and tend to agree with these theoretical predictions (Trivers and Hare, 1976; Nonacs, 1986a; Boomsma, 1989).

Inclusive fitness aspects of colony-level sex allocation have received much less attention. The early general notion (Kolman, 1960) that – in infinitely large populations – the fitness of an individual (colony) becomes independent of its own sex ratio once the overall population equilibrium is reached has been largely ignored in the theory on social insects. Another general result – that individuals in finite populations maximize their inclusive fitness by producing a sex ratio which is equal to the population equilibrium (Verner, 1965; Taylor and Sauer, 1980; Williams, 1979) – has also not been formally implemented in the theory on worker-controlled sex allocation. The consequence of such notions, however, is obvious. The Trivers and Hare/Benford type of models either predict nothing about the pattern of sex ratio variation between colonies, or predict a unimodal distribution around the single female-biased mean value of the sex ratio which reflects the average RA of the investing agents. This would have been a satisfactory state of affairs, if the empirical observations on colony-level variation in the sex ratio of eusocial Hymenoptera were also characterized by unimodality or an overall lack of pattern. However, the available sex ratio data of ants (Pamilo and Rosengren, 1983; Nonacs, 1986a) usually show a clearly bimodal pattern of variation, i.e. one mode of colonies which produce exclusively or predominantly males and another mode that produces mostly females.

The most obvious explanation for the occurrence of exclusively male producing colonies is that workers reproduce after the queen has died, a situation which is in fact quite common in eusocial Hymenoptera (Bourke, 1988). The consequences of worker reproduction in orphaned colonies were theoretically analysed by Taylor (1981). He concluded that the queenright colonies are selected to compensate for the overall male-bias induced by queenless colonies, but that – in his particular case of worker reproduction – only half of the difference was met. Taylor's argument thus predicts two modes of colony sex ratios to coexist, but still only as a result of population-wide frequency dependent selection on the sex ratio.

It was shown by Grafen (1986) that selection for different sex ratios can occur at the level of the separate colonies, if the cost of producing an individual of either sex differs between colonies, and provided that the workers are able to detect cost-related cues in the environment. Pursuing a similar kind of reasoning, Boomsma and Grafen (1990) argued that colony-level variation in RA itself should also produce bimodal sex ratios if workers can evaluate and capitalize on this intra-colony cue. This verbal argument leads to the general prediction that the extent of bimodality in the colony sex ratios should be positively correlated with the extent of variation in RA across populations. Some comparative evidence on ant sex ratios was provided to show that such trends do indeed occur (Boomsma and Grafen, 1990). For separate populations the (qualitative) prediction is that colonies with relatively low RA should specialize on males, whereas colonies with relatively high RA should specialize on females.

In the sections below we will elaborate on this idea in a formal inclusive fitness model for random mating populations of both infinite and finite size. The model provides quantitative predictions as to how the colony sex ratio in eusocial Hymenoptera with worker control should vary as a function of relatedness asymmetry, reproductive value and colony productivity (in finite populations). We also show that – under our RA-assessment assumption – the equilibrium population sex-ratio is not a simple function of the weighted mean of relatednesses (Benford, 1978) but is usually maintained at or close to a value reflecting the relatedness symmetry of one “balancing” class of colonies.

In the final part we discuss the simplifying assumptions made in our model and also the relationship between our approach and models on sib-competition in subdivided populations. The power of the marginal value approach used in this paper is evaluated in the Appendix, by showing that the existing theory on sex allocation in random mating populations of eusocial Hymenoptera can be rederived relatively easily by applying an inclusive fitness notation.

## The model

### *Worker inclusive fitness*

In the existing theory on sex allocation by hymenopteran workers, the inclusive fitness of the controlling agents is determined by population parameters only, i.e. the mean relatedness of females and males towards the workers, the total numbers of females and males in the mating swarm, and the efficiency of the two sexes for transferring genes. The latter term is usually indicated as “reproductive value” (e.g. Benford, 1978; Oster and Wilson, 1978) and quantifies that – as gene carriers – haploid males are half as valuable as diploid females. The model presented in the sections below is additional to this population-level approach and shows how workers can be selected to adjust their sexual investment both to the mean relatednesses in the population, and to the RA in their own colony.

The inclusive fitness function remains basically the same when we shift our attention from population-level equilibria to colony-level sex ratio optimization. The only difference is that the separate RA-classes in a population are characterized by different values for the same variables and that the classes are hypothesized to maximize the same function simultaneously, but with a different set of values. In such more complex situations, it is useful to denote (regression)-relatedness ( $b_{yx}$ ) and reproductive value ( $V$ ) separately, instead of merging them directly into the life-for-life coefficients of relatedness as used by Hamilton (1972) and Trivers and Hare (1976). This distinction allows us to use the same fitness function to analyse the RA-effects of worker-reproduction, multiple mating and polygyny. Also, it keeps the colony-level effects of worker reproduction (a higher relatedness to males) separate from the population effects (all males in the population increase in reproductive value depending on the overall level of worker reproduction). For a full explanation on these matters we refer to Pamilo and Crozier (1982), Grafen (1986) and Taylor (1988).

A quantity, which we shall denote  $W$ , is defined to represent the inclusive fitness of an agent. In principle, the agent can either be a mother (queen or worker) or a non-laying worker, but only the latter will be considered in this argument.  $W$  is calculated as the weighted sum of the reproductive values of the gynes and males produced by a colony. Note that throughout this paper we may use the words "females" or "gynes" for offspring females but reserve the word "queens" for colony mothers. Let  $b_{ff}$  and  $b_{mf}$  be the regression-relatednesses of the gynes and the males to the investing workers. Let  $f$  and  $m$  be the investment in females and males made by the colony, and let  $F$  and  $M$  be the total investment in females and males made by the rest of the population. Finally, let  $V_f$  and  $V_m$  be the reproductive values of all females and all males. As derived by Benford (1978), the ratio of these reproductive values depends on the overall rate of worker reproduction in the population, such that  $V_f = (1 + p)V_m$  (see also Appendix), where  $p$  is the proportion of queen-produced males. Then

$$W = b_{ff} \frac{f}{F + f} V_f + b_{mf} \frac{m}{M + m} V_m \quad (1)$$

The idea of this equation is that the investing workers manipulate  $f$  and  $m$  in such a way as to maximise  $W$ , subject to an energetic constraint on the total investment  $t = f + m$  (Oster and Wilson, 1978). The inclusion of  $f$  and  $m$  in the denominators of expression (1) allows one colony's production to be a sizeable fraction of the production of the local population (cf MacArthur, 1965). The ESS aspect of this evolutionary game is seen in the fact that one colony's  $F$  is the sum of every other colony's  $f$ . Relatedness asymmetry (RA) as used throughout this paper is defined as  $b_{ff}V_f/b_{mf}V_m$ , which is the ratio of the sex-specific potentials for transferring the investor's genes to the next generation. Note that the relatednesses may vary from agent to agent and from colony to colony but the values of  $F$  and  $M$  and the reproductive values ( $V$ ) depend on the population and not on the individual. In consequence, the colony-level component  $b_{ff}/b_{mf}$  and the population-level component  $V_f/V_m$  of RA may vary independently.

By the form of the denominators in equation (1), total male fitness is fixed in the same way as total female fitness. This implies the assumption that colonies in a local area form a mating pool of finite or infinite ( $f$  and  $m$  negligible compared to  $F$  and  $M$ ) size, whose offspring all mate together. Mating is thus supposed to be random, i.e. both preferential sib-mating and deliberate incest avoidance are assumed to be absent. Other expression than (1) are required if part of the sexuals should disperse outside the local group and if this dispersal were different for the sexes. A formal treatment of such complications is beyond the scope of this paper, but some remarks on local competition between relatives will be made in the final section.

### *The marginal returns for workers*

Like all organisms, worker ants are selected to specialize on raising that sex for which the marginal fitness-returns per unit of investments are greatest. In order to find the optimal sex ratio strategies for the different classes of RA we thus need to analyse the colony-level marginal returns. These marginal returns are the partial derivatives of the fitness function (1), i.e.

$$\frac{\partial W}{\partial f} = b_{ff} \frac{F}{(F+f)^2} V_f$$

and

$$\frac{\partial W}{\partial m} = b_{mf} \frac{M}{(M+m)^2} V_m \quad (2)$$

respectively. They determine how  $f$  and  $m$  should be chosen to maximise  $W$  (cf MacArthur, 1965).

If the population is infinitely large,  $f$  and  $m$  are effectively zero. The marginal returns then reduce to  $b_{ff}V_f/F$  and  $b_{mf}V_m/M$ , respectively, depending only on population parameters ( $F, M, V_f, V_m$ ) and on the relatednesses of the agent ( $b_{ff}, b_{mf}$ ), but not on the agent's actions ( $f$  and  $m$ ). Therefore, they may be taken as fixed. The population-level equilibrium in the sex ratio is reached when  $\partial W/\partial f = \partial W/\partial m$  for all agents. Accordingly, if RA is the same in all colonies (e.g. the classical Trivers and Hare case of full-sib workers with  $RA_{col} = RA_{pop} = b_{ff}V_f/b_{mf}V_m = 0.75/0.25$ ), the equilibrium sex ratio is reached when the population sex ratio ( $F/M$ ) equals that RA of 3:1.

If RA differs among colonies, but workers have no way of assessing what type of colony they are in, the equilibrium sex ratio of the population will come to reflect the mean RA (Benford, 1978). However, when workers can assess their colony-level RA, they remain under selection to overproduce the sex with the higher marginal returns even after the overall population-level equilibrium sex ratio has been reached. In the following sections we will use these marginal values to derive quantitative predictions as to how workers in different classes of RA should adjust their colony-level sex ratio in order to maximize their inclusive fitness.

*Colony optima in infinite populations*

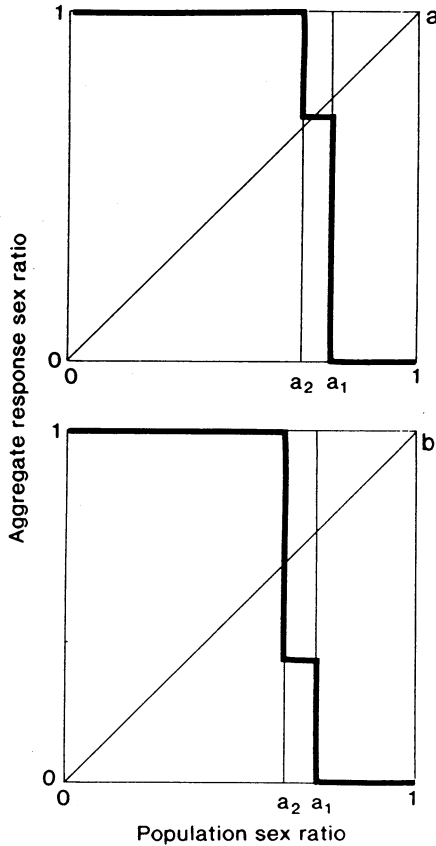
Categorical variation in RA can be induced by multiple matings (Page, 1986), variability in the extent of worker reproduction (Bourke, 1988), and polygyny with variable queen-number and/or variable relatedness among queens. Example cases of RA-variation in several settings are given in Table 1, where RA is expressed both as a ratio and as a proportion. Note that the latter variable,  $a_i$  is also the equilibrium population sex ratio (proportion of females) if a population contains only one particular RA-class of colonies.

If there are two or more RA-classes, both the population-level equilibrium and the colony-level optimum change, but they do so in quite different ways if workers assess the RA in their own colony. An example for 100% accurate RA-assessment is worked out in Fig. 1. The figure illustrates two infinitely large populations in which there are either two or three classes of colonies, each with its own set of relatednesses. In Fig. 1a all males are produced from queen laid eggs ( $p = 1$ ), whereas in Fig. 1b 35% of the males comes from worker laid eggs ( $p = 0.65$ ). Note that Fig. 1b has three classes of colony but only two classes of RA because the relatedness-ratios in two-father colonies and worker-reproductive colonies yield the same value (see Table 1 and below).

The horizontal axis is the population sex ratio, expressed as the proportion of females, and the vertical axis is the cumulative optimal response of the classes differing in RA to the overall population sex ratio. To keep maximizing  $W$  (according to the infinite form of equation (1)), each class has its own critical population sex ratio,  $a_i$  (see Table 1), where it should make its Fisherian switch from making exclusively females (on the left of the graph where the population sex ratio is too male-biased for the RA of the agent) to exclusively males (at the right where the overall frequency of females has become so high that males are the relatively rare sex for the particular class-value of RA).

The extent to which the population sex ratio is affected at each critical point depends on the relative abundances of the classes. In the example case of Fig. 1a both classes are selected to produce only females if the population sex ratio (horizontal axis) is to the left of the lowest critical value  $a_2$ , i.e. the aggregate response on the vertical axis takes a value of one. When the population sex ratio is in between the two critical values, the one-father class should go on producing females, but the two-father class should now switch to producing only males. Assuming that the mean productivity per colony is equal in the classes, the aggregate response sex ratio is then 0.7 ( $0.7 \times 1 + 0.3 \times 0$ ). If the population sex ratio on the horizontal axis should become higher than the critical value  $a_1$ , both classes are selected to produce males only and the aggregate response sex ratio is zero.

Fig. 1b illustrates the situation where half of the one-father colonies of Fig. 1a has shifted to producing males from worker laid eggs ( $p = 0.65$ ). If we assume that all subsequent investments are made by non-laying workers both the two-father colonies and the worker-reproductive colonies have a 1.65:1 relatedness asymmetry –  $0.5(1+p)/0.5$  and  $0.75(1+p)/0.75$ , respectively – and thus share the same



**Fig. 1.** A population is illustrated which consists of colonies belonging to two classes of RA. The best response of each class to the population sex ratio  $F/(F + M)$  is to produce all females if the population sex ratio is below a critical value and to produce all males if it is above that critical value. If the classes differ in RA, their critical switch-values are also different (Table 1). Fig. 1a is illustrative for the case where variation in RA is due to a certain proportion (30%) of double matings in a monogynous species with sterile workers. The critical values are  $a_1 = 0.75$  and  $a_2 = 0.667$  for the one-father and two-father colonies, respectively (Table 1). The aggregate response of the two classes is the sex ratio  $F/(F + M)$  they would produce together if each produced its own best response to the population sex ratio shown on the horizontal axis. The aggregate response curve always travels down on the critical value lines, but the position at which it travels horizontally to the next critical value line depends on the relative frequencies of the two classes. The ESS sex ratio is found at the intersection of the aggregate response curve and the  $45^\circ$  line, for only there can each class be behaving optimally at the current population sex ratio. Fig. 1b illustrates the situation where half of the one-father colonies of Fig. 1a has shifted to producing males from worker-laid eggs. If we assume that all investments are done by non-laying workers, it appears that the two-father colonies and the worker-reproductive colonies share the same critical value ( $a_2$ ) of 0.623. This is because the ratio  $b_{ff}/b_{mf}$  equals 1 for both classes (0.5/0.5 and 0.75/0.75, respectively), and because the population-wide reproductive-value ratio  $V_f/V_m$  is also the same (1.65 instead of 2, because 35% of the males is now produced from worker laid eggs). The remaining 35% of one-father colonies with sterile workers keep a higher critical value ( $a_1$ ). Their  $b_{ff}/b_{mf}$  ratio equals 1.5, which multiplied with 1.65 produces an RA of 2.475, i.e. a critical value of 0.712.

**Table 1.** Examples of colony-level variation in relatedness asymmetry (RA) owing to multiple mating, worker reproduction and/or polygyny. The critical switch value  $a_i = RA/(RA + 1)$ .  $p$  is the overall proportion of queen produced males

Colony-type	$RA = b_{ff}V_f/b_{mf}V_m$ $= b_{ff}(1 + p)/b_{mf}$	$a_i$
<i>monogyny, variable mating and sterile workers</i>		
1 father	3	0.75
2 fathers	2	0.67
3 fathers	1.67	0.63
<i>monogyny, single mating and 20% worker reproduction (<math>p = 0.8</math>)</i>		
males from queen	2.70	0.73
males from laying workers	1.80	0.64
<i>monogyny, single mating and 60% worker reproduction (<math>p = 0.4</math>)</i>		
males from queen	2.10	0.68
males from laying workers	1.40	0.58
<i>monogyny, partial double mating and 30% worker-reproduction (<math>p = 0.7</math>)</i>		
1 father, males from queen	2.55	0.72
1 father, males from laying workers	1.70	0.63
2 fathers, males from queen	1.70	0.63
<i>variable polygyny, single mating and sterile workers</i>		
1 mother	3	0.75
$n$ unrelated mothers	3	0.75
2 half-sister mothers	2.60	0.72
3 half-sister mothers	2.33	0.70
2 full-sister mothers	2.14	0.68
3 full-sister mothers	1.80	0.64

Notes: Colonies are assumed to have either all males produced by the queen or to have exclusive male production from worker-laid eggs. In worker-reproductive colonies, laying workers are assumed to be rare and thus only the RA for non-laying workers is relevant. Colony-production is assumed to be equal for colonies with sterile and reproductive workers and polygynous mothers and multiple fathers are assumed to contribute equally to the offspring of the colony.

critical value  $a_2 (= 0.623)$ , whereas the remaining 35% of one-father colonies with sterile workers now have a RA of  $0.75(1 + p)/0.5 = 2.475$  ( $a_1 = 0.712$ ).

The forty-five degree line intersects with the response line at the only point where the aggregate (cumulative) response of all classes is equal to the population sex ratio. This intersection represents the ESS sex ratio, for only there can each subpopulation be behaving optimally at the current population sex ratio. Any class whose critical value is to the left of the ESS is selected to make all males, and still has its marginal value for males greater than its marginal value for females. Equally, any class with a critical point to the right of the ESS should favour



females. If the ESS occurs at a horizontal part of the response curve (Fig. 1a), then every class falls into one of these two categories, i.e. should produce either exclusively males or exclusively females. If the ESS occurs at a vertical part of the response curve (e.g. Fig. 1b), then the ESS coincides with the critical value of the intersected class. For the colonies in such a class there is a (mixed) class sex-ratio that makes the marginal values for females and males equal. Accordingly, this “balancing” class should produce both sexes, in a ratio that maintains the equilibrium sex ratio of that class as the population sex ratio. The balancing class’ contribution is thus complementary to the single sex batch of offspring produced by the other class(es). To achieve this compensation, the sex ratio of a balancing class may take any value between 0 and 1.

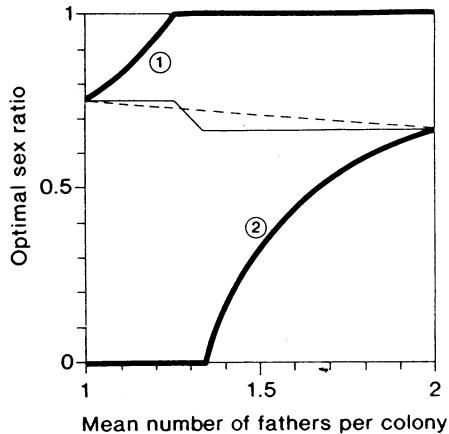
The above implies that the larger a class is, the more likely it is to be the balancing class, i.e. the more likely the population sex ratio is to be equal to its critical value. This can be inferred from Fig. 1 by imagining one of the vertical parts of the response curve to elongate at the expense of the other. It thus follows that workers are not selected to produce exclusively one sex in all circumstances, but that the optimal colony-level sex-investment is more extreme than the average RA in the population or even the RA in the colony itself. The only exception are the colonies in the balancing class at one particular frequency distribution of RA-classes (see below).

If more than two critical values occur in a population (see Table 1), the number of steps in the aggregate response curve increases likewise (always one less than the number of critical values), but there is never more than one intersection of the aggregate response curve with the 45° line and never more than one balancing class (and there may well be none). The level of the step in the aggregate response curve of Fig. 1 equals the frequency of the class that remains exclusively gyne-producing at that horizontal trajectory, i.e. 0.70 in Fig. 1a and 0.35 in Fig. 1b. In analogy, when there are more than two RA-classes, the level of each additional step equals the cumulative frequency of the exclusively gyne-producing classes.

In populations consisting of two classes of colony with different RA (Fig. 1), the optimal sex ratio for the upper RA-class can be simply inferred from the ratio of the critical value  $a_1$  and the numerical frequency of that class  $q_1$  (assuming that all colonies contribute equally). This ratio either quantifies the exact optimum of a balancing class (if in between 0 and 1) or indicates the unisexual optimum for a non-balancing class (if  $\geq 1$  or  $\leq 0$ ). More generally, for  $n$  ( $\geq 2$ ) classes of RA, numbered in decreasing order of their class-specific critical values  $a_i$  (e.g.  $a_1 = 0.75$ ,  $a_2 = 0.67$ ,  $a_3 = 0.63$ , etc), the optimal class sex-ratio  $\mu_n$  can be worked out as:

$$\mu_n = \left( a_n - \sum_{i=1}^{n-1} q_i \right) / q_n \quad (3)$$

Expression (3) – in which the summation term is the cumulative frequency of the exclusively gyne-producing classes – takes again a value  $\geq 1$  for all non-balancing classes which produce exclusively gynes and a value  $\leq 0$  for all non-balancing classes producing only males. Any class for which we find  $0 < \mu_n < 1$  is a balancing class. Note that there is only one ratio of  $q_n$  and the cumulative frequency of  $q_1$



**Fig. 2.** Optimal sex ratio for a one-father and two-father class of colony (bold lines, marked 1 and 2 respectively) and for the population as a whole (thin line), both as a function of the arithmetic mean number of fathers per colony, assuming that higher mating frequencies, worker-reproduction and polygyny are all absent. For comparison, the equilibrium population sex ratio according to Benford (1978) is given as a dashed line. Note that Fig. 1a refers to the vertical cross section through this figure at 1.3 fathers per colony.

through  $q_{n-1}$  at which a balancing class should produce a sex ratio that corresponds to its own RA. An example of how these optimal class sex ratios can be worked out graphically is given in Fig. 2.

Finally, we should stress that the predicted optimal sex ratio ( $\mu$ ) concerns the colony-level in the non-balancing class, because all colonies are equally selected to produce the same one sex. Accordingly, for colonies in a non-balancing class the marginal value of the favoured sex is and remains higher than the marginal value of the other sex. For the balancing class, however, the theory does predict the optimal sex ratio for all colonies in that class together, but not for the separate colonies in that class. In contrast to the non-balancing class(es), the marginal values of males and gynes in the balancing class are equal when the equilibrium according to (3) is reached. From then on, all colony sex ratios within the balancing class are equally fit, as were all sex ratios in the entire population according to the original approach by Trivers and Hare and Benford.

#### *Complications in finite populations*

In finite populations, the sex ratio produced by individual colonies does affect the composition of the entire mating swarm and hence the  $f$  and  $m$  in the denominators of (2) can no longer be neglected. The next question to be addressed is, therefore, how the production of "your own" sexuals ( $f$  and  $m$ ) alters the marginal returns in finite populations.

The most obvious consequence is that the marginal values can now only equalize if the sex ratio of the deciding colony is the same as the cumulative sex ratio of all other colonies ( $f/m = F/M$ ). Accordingly, a deciding colony will always be under some selection (very weak in large populations and stronger in small populations) to produce a sex ratio reflecting its own RA, which should lead to a unimodal distribution of colony sex ratios in populations with constant RA (cf Verner, 1965; Williams, 1979). If there is more than one RA-class, however, workers in any deciding colony are under additional selection to bias their investments towards the sex to which they are relatively most related. These two selection forces work in opposite direction and it is less obvious than in the infinite case of Fig. 2 what the equilibrium sex ratio will be for each class and for the population as a whole.

When  $f$  and  $m$  are small compared to  $F$  and  $M$ , it alters the marginal returns very little. So if the making of exclusively one sex is advantageous at  $(f + m)/(F + M) = 0$ , it will remain advantageous until the colony makes some appreciable fraction of the local population's production of that sex. If  $f$  and/or  $m$  are such appreciable fraction, the outcome depends on the size of the average local population and also on the variability in sexual output between the colonies.

First we will deal with the effect of small population size itself and assume colony-productivity to be a constant. We will analyse how unconstrained selection should shape the sex ratio of any "deciding" colony, again under the explicit assumption that workers can assess the colony-level variables ( $b, f, m$ ) but not the population-level variables ( $F, M, V$ ), set by the other colonies. However, the latter variables are likely to have fixed probability distributions – at least on an ecological time-scale – for each species or meta-population. Thus, even though workers in a deciding colony do not know how many other colonies belong to their local population or how these neighbours will contribute to the local mating swarm, they can be supposed to "treat"  $F, M$  and  $V$  as random variables each with its own probability distribution among local populations and to respond to the mean value of these variables across those local populations. This use of (constant) means for  $F, M$  and  $V$  instead of probability distributions represents a simplifying assumption, but should not affect the qualitative nature of the results, as long as these frequency distributions are fixed, thus being statistically predictable on an ecological time-scale (see also Discussion). The advantage of this simple approach is, however, that the frequency dependent response of both balancing- and non-balancing classes can be quantified relatively easily. We will illustrate this case by analysing two examples where the number of "other" colonies is fixed but still relatively high (either 40 or 10).

Secondly, we will illustrate what may happen when the numerical output of colonies is variable and when workers also assess their own colony's productivity ( $t = f + m$ ) relative to some overall average for their species. Then, the optimal allocation between  $f$  and  $m$  in a deciding colony becomes also a function of the colony's own  $t$ , but the cumulative sex ratio of "the other" colonies ( $F/M$ ) still remains independent of the sex ratio optimization in the one deciding colony. This is because colonies are assumed – as before – to be unable to assess each others output, i.e. workers in a deciding colony are assumed to assess whether their

productivity is below or above some species-specific average value, but they can only act as if “the other” colonies do indeed produce that average.

### *The sib-competition effect*

If all colonies invest equally in reproduction (no variation in  $t = f + m$ ), the total output of a particular class of RA still depends – as in the infinite case – only on the proportion of colonies belonging to that class. The complication with finite size is that every deviation which takes the sex ratio of a “deciding” colony away from an investment ratio reflecting its own RA, induces a quadratic decrease in the marginal returns to the overproduced sex (see expression 2). This is because the deviating colony sex ratio not only increases the share of one sex in the mating swarm, but also increases the competition between that colony’s own related offspring of that sex. This implies that, unlike the infinite case illustrated in Fig. 1, small deviations of the population sex ratio from the critical value of a class may not solicit the extreme “one sex only” response.

In the infinite case there is one particular critical value ( $a_i$ ) where the marginal returns are equal. If the population sex ratio passes that value, every colony in the appropriate class should switch from making exclusively one sex to making exclusively the other. In finite populations, however, the particular class-specific values broaden into zones and we can quantify these zones by comparing the (finite population) marginal values (2).

Let  $F/M$  be the equilibrium sex ratio in a meta-population reflecting the RA of workers in the balancing-class colonies across the local populations and let the sexual output of every single colony in a local non-balancing class be  $t$  ( $=f + m$ ). If we define the colony sex ratio as  $\mu = f/t$ , we can replace  $f$  by  $\mu t$  and  $m$  by  $\mu(1 - t)$ . Setting the marginal returns (2) equal and rearranging thus produces after some algebra the colony sex ratio that makes the marginal returns equal, i.e.

$$\mu = \frac{S}{1 + S} + \frac{1}{t} \cdot \frac{MS - F}{1 + S} \quad (4)$$

or, using  $\tau = t/(F + M)$ ,

$$\mu = \frac{S + (1/\tau)(MS - F)/(F + M)}{1 + S} \quad (4a)$$

where  $S = \sqrt{(b_{ff}FV_t/b_{mf}MV_m)}$  and where  $(MS - F)/(F + M)$  is a dimensionless measure of the discrepancy between the colony’s limiting sex ratio and the sex ratio produced by the rest of the population.

The equations for  $\mu$  give the optimal proportional investment in gynes if  $\mu$  is between zero and one. Otherwise, the colony should produce all males (when  $\mu \leq 0$ ) or all females (when  $\mu \geq 1$ ). The marginal production levels at which the unisexual optimum changes into one including the production of some quantity of both sexes follows from setting  $\mu = 0$  and 1 in equation (4). If  $S_1$  and  $S_h$  refer to categories of

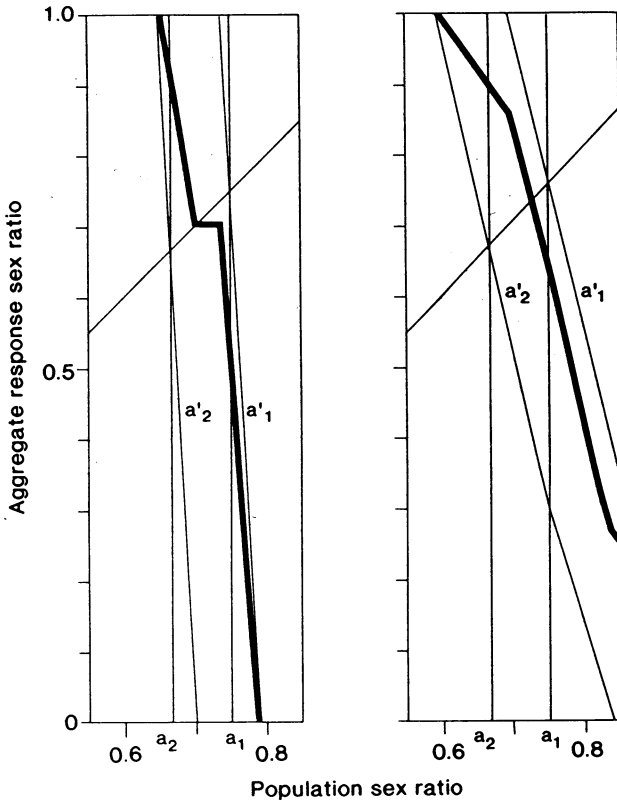
colonies with lower and higher RA, respectively, exclusive male production is optimal for

$$t < (F - MS_1)/S_1 \tag{5}$$

whereas specialization on females is optimal for

$$t < MS_0 - F \tag{5a}$$

If  $t$  has a fixed value and no variance, we can substitute that value into equation (4) and work out how  $\mu$  should respond to the population sex ratio  $F/M$ . Two such cases are illustrated in Fig. 3, taking again the case of partial double mating as example. Fig. 3a refers to a moderately finite population of 41 colonies with equal sexual production (i.e.  $t/(F + M) = 0.025$ ). The former vertical critical-value lines



**Fig. 3.** As in Fig. 1a, the aggregate response curve is illustrated for a population with 70% one father colonies and 30% two-father colonies. The difference with Fig. 1 is that the populations are now finite, i.e. 41 equally productive colonies in Fig. 3a ( $t/(F + M) = 0.025$ ) and 11 colonies in Fig. 3b ( $t/(F + M) = 0.10$ ). Since with these two RA-classes, the population sex ratio will always equilibrate between 0.67 and 0.75, only this part of the horizontal axis is given. The critical value lines for the respective population sizes are indicated as  $a'_1$  and  $a'_2$ . The other lines are the same as in Fig. 1a.

(at  $a_1$  and  $a_2$  in Fig. 1) have now shifted into slightly oblique lines and there is a narrow zone of population sex ratios around the former critical values where a non-balancing colony can make the marginal returns equal by producing some quantity of both sexes. The intersections of the critical-value lines with the  $45^\circ$  line have remained the same, but the aggregate response sex ratio – i.e. the sex ratio which the RA-classes would produce together if each produced its own best response to the population sex ratio shown on the horizontal axis – no longer simply travels down along the critical-value lines. The intersection of the response curve and the  $45^\circ$  line has become dependent on the frequencies of the RA-classes also when it occurs at a non-horizontal part of the response curve. The consequence is that – in the moderately small population of Fig. 3a – the horizontal part of the response curve has decreased, which implies that – compared to the infinite example – it has become less likely to find two non-balancing classes producing opposite single-sex batches of colony-offspring.

The population size of the example case in Fig. 3a is still large enough to make sure that, whatever the frequencies, always one of the classes is selected to produce one sex only (i.e. to be non-balancing) and the other is selected to respond (i.e. be balancing). This changes when population size is reduced further. Fig. 3b illustrates what happens if the population of Fig. 3a is reduced to 11 colonies ( $t/(F + M) = 0.10$ ). Now the critical lines have become so skewed that the one to the left intersects the vertical  $a_1$ . This implies that even if the one-father colonies should be able to maintain the population sex ratio at  $a_1$  ( $=0.75$ ), the two-father colonies should no longer produce only males, but a mixed sex ratio which is, however, still more male-biased than their own RA.

In Fig. 3b, there is a considerable trajectory of population sex ratios, where both classes are selected to produce a mixed sex ratio and where part of the aggregate response curve – instead of being horizontal – follows the slopes of the critical value lines. In such cases, the equilibrium situation is that both RA-classes produce a mixed but different sex ratio.

We can conclude that non-balancing classes in finite populations remain under selection to overproduce the sex towards they are relatively most related, but that the magnitude of the predicted response goes down with decreasing population size. From this perspective, we thus expect to see a similar but less extreme pattern of bimodal sex ratios as predicted for infinite populations. We note, however, that finite distributions of colony sex ratios are still expected to show significant deviations from a unimodal pattern in all species of eusocial Hymenoptera which fit to our assumptions of variable RA and assessing and controlling workers.

The next question to be asked is, whether colonies in a balancing class will indeed be able to compensate completely for the excess productions of non-balancing classes as was the case in infinite populations. As it turns out, colonies in the balancing class face the problem that also their acts of counter-biasing the sex ratio increases competition between their offspring of the overproduced sex. The magnitude of this effect depends in a rather complex way on the number of RA-classes, their frequencies, and the population size (i.e.  $t$  relative to  $F + M$ ). As long as the balancing is done by a reasonably large number of colonies, the sib-competition

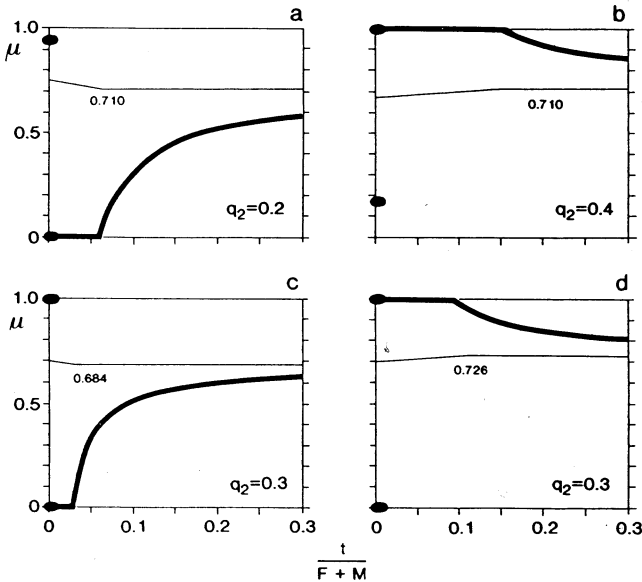
disadvantage is negligible for each separate colony and the population sex ratio should still equilibrate at a value close to the RA of the balancing class.

In very small populations like the example case of Fig. 3b, however, the sib-competition effect becomes noticeable. For instance, if two out of ten colonies are two-father colonies producing only males, this brings the (unbalanced) population sex ratio down from 0.75 to 0.60. However, if we calculate the marginal values for the eight balancing (one-father) colonies when their output gets increasingly female-biased, it appears that the marginal values become equal already at an overall sex ratio of 0.73, i.e. when all one-father colonies produce a sex ratio of 0.91. So, even in this rather extreme case, 75% of the difference between the RA's of the two classes (0.75 and 0.67) is being met. We conclude, therefore, that selection on the balancing class will be such as to maintain the overall population sex ratio close to the value that reflects its own RA, even if the population is very small.

### *Effects of variable colony productivity*

An interestingly different situation arises if there is substantial variation in the colony-level reproductive effort ( $t$ ) – e.g. in correlation with age and/or patch quality – and workers also assess this variable prior to making their allocation decisions. The following argument will make this clear. We assume, as before, that the average reproductive investment of colonies is the same for each class of RA and that the population is large enough that the sex ratio of the balancing class has equilibrated at a level that compensates for virtually all of the single-sex production(s) of the non-balancing class(es). The workers in the colonies of the non-balancing class(es) are then selected to let their sex ratio depend on the contribution they make to the mating swarm. If a colony in the non-balancing class produces much less than average it decreases the total unisexual production of its class. The non-balancing status of its class, however, remains unchanged and the exclusive production of the same one sex still is the optimal sex ratio for workers. On the other hand, if an individual colony produces much more sexual offspring than the average colony, it may reach a point where it is no longer optimal to produce only one sex.

Returning to the marginal values (2) shows what happens if a colony grows and starts by itself to produce an appreciable fraction of all the sexuals in the local population. Suppose it is initially advantageous for a colony to make only males. As it produces males, and  $m$  increases, the marginal returns (2) to males for that colony decreases quadratically, and will continue to decrease until the marginal returns for males equal that for females. From that point, the colony is selected to make both females and males and the two marginal values further decline in unison. In the limit, as the colony should become larger, the local population becomes dominated by the output of this single colony. Then, the local sex ratio would increasingly come to reflect the RA of this large colony, in the same way as it may reflect the RA of a large balancing class of colonies.



**Fig. 4.** Optimal sex ratio  $\mu$  ( $=f/t$ ) for a non-balancing colony (bold line) and the concurrent population equilibrium (thin line), both as function of the colony's sexual production ( $t$ ) relative to the cumulative sexual production of all other colonies in the breeding population ( $F + M$ ). The deciding colony is imagined to belong to a population of monogynous ants, where all workers are sterile, queens are singly or doubly mated and in which all other colonies are small. The fraction of doubly inseminated mothers among the other colonies ( $q_2$ ) is 0.2 in Fig. 1a, 0.4 in Fig. 1b and 0.3 in Fig. 1c and Fig. 1d. The big dots on the vertical axis represent the optimal sex ratios of balancing and non-balancing classes of colonies when all colony outputs are small, e.g.  $<0.01$  ( $F + M$ ), as approximated from equations (3).

The predicted sex ratio optima for workers in a “growing” colony of the non-balancing class are graphically summarized in Fig. 4. The examples in the Figure refer again to a monogynous species where variation in RA is due to a certain frequency ( $q_2$ ) of double mating, but the actual values of  $q_2$  are chosen such as to illustrate also how this type of sex ratio adjustment should depend quantitatively on the frequency of the classes of colonies with different RA. To keep the example cases simple, workers are assumed to be sterile.

The figure presents the relationship between the relative amount of energy available to a non-balancing colony for producing sexuals,  $t/(F + M)$ , and the sex-investment ratio ( $\mu$ ) it should produce to maximize worker inclusive fitness according to equation (4) (after filling in the appropriate RA and the values for  $F$  and  $M$  at  $t = 0$ ). The dots on the left vertical axis are the optimal class sex-ratios for infinite populations ( $t/(F + M) = 0$ ) according to equation (3), which – as argued above – hold approximately for large finite populations. Fig. 4a and 4b depict cases where the frequencies of the two classes of colony are such ( $q_2 = 0.2$  and 0.4, respectively) that one class is balancing and the other is not. However, when  $q_2 = 0.3$  (Fig. 4c and 4d) both classes are non-balancing and the two



responses can occur simultaneously. The population sex ratio at increasing values of  $t$  is calculated by combining the sex ratio at  $t = 0$  with the additional production of the deciding colony (i.e. no additional compensation by the balancing class occurs). It is assumed throughout that the average sexual production in "the other" colonies is the same for both classes and that fathers contribute equal amounts of sperm which mixes completely in the queen's spermatheca.

At  $t/(F + M) = 0$ , the equilibrium population sex ratio (proportion of females) either reflects the critical value (RA) of the balancing class (Fig. 4a,b) or the frequency  $(1 - q_2)$  of the female specialist class (Fig. 4c,d). Note that the increasing unisexual production of the deciding colony will shift the population sex ratio, but that the population sex ratio remains constant (assuming no additional action of the balancing class) after the colony starts to produce both sexes. The shift is smaller, however, than the shift which a balancing class is selected to achieve and the population sex ratio will now not come to reflect the critical value of the non-balancing class. This is again due to the fact that the marginal value of the initially favored sex decreases quadratically until it equals the marginal value of the other sex. When the colony's  $t$  increases above the appropriate upper threshold for unisexual output, as given in equations (5), the marginal values start to decline in unison, and from then on the additional effect of increasing sib-competition has become equal for the two sexes.

Also colonies in the balancing class are expected to show some additional response to variation in their colony output  $t$ . Together, these colonies should produce a sex ratio which keeps the marginal values equal. However, as larger colonies suffer more from the sib-competition effect than smaller colonies, we should expect to see effects in both directions, i.e. more compensating-bias in the smaller colonies and less in the larger ones. The magnitude of these effects should again depend on the mean value of  $t$ .

The conclusion about colony-level sex ratio patterns under variable RA and variable colony productivity is therefore that as colonies increase in sexual output (e.g. in correlation with colony-size), their sex ratios should become less extreme and tend towards the value a population would have if all its colonies had the relatednesses of the large colony. However, as single colonies that "suddenly" grow to produce more than say 5% of the local population's reproductives (Fig. 4) are likely to be a rare phenomenon in most natural populations, we may reasonably expect that our prediction of bimodality of the sex ratio derived for infinite populations, will remain approximately valid unless local populations are typically very small.

## Discussion

In this paper we have mainly followed through the simple case where RA-variation is due to some frequency of double mating. But, as indicated by Table 1, more complex patterns of RA-variation involving polygyny and/or worker reproduction (affecting the reproductive value ratio of females-to-males), can also be

tackled by the same equations, after making the proper substitutions in the variables  $b$  and  $V$ . This makes our model both general and fully compatible as an addition to the existing theory on worker-controlled sex allocation in eusocial Hymenoptera (e.g. Trivers and Hare, 1976; Benford, 1978; Taylor, 1981; Nonacs, 1986a). It is shown in the Appendix that all previous results for random mating populations can be rederived by using our marginal value approach. An important general conclusion from those comparisons is that sex ratio compensation in infinite populations amounts to 50% in the case of male bias through worker-oviposition (Taylor, 1981), but to 100% for any sex ratio bias where only completely sterile workers are involved.

However, our simplified approach also has its weaknesses. The first is that the quantitative predictions rely on additional assumptions of accurate assessment of various within-colony cues by the investing workers. These assumptions are likely to be only partly justified in most natural populations and the degree to which such complications might affect the applicability of our model will be discussed in some detail below. Secondly, the model is too simple because it ignores natural variation with regard to population subdivision and assumes differential dispersal of the sexes to be absent. The implication of these omissions and some tentative ideas as to how the sib-competition effects in our model may relate to results derived earlier for structured populations with non-random mating will also be discussed.

### *The assumptions of the model*

In our earlier paper (Boomsma and Grafen, 1990), we have argued that the kind of RA-assessment by workers required for our model is likely to be based on cumulative information and may thus be much more accurate than individual recognition of differently related nestmates. Two complications in this reasoning have since then received more formal analysis, both referring to a similar example case of partial double mating.

It was shown by Ratnieks (1990) that assessment errors will also occur with cumulative information, because the genetic odor information obtained from each additional nestmate will not be independent. In fact, several recognition-loci with considerable allelic diversity appeared to be needed to reduce the average rate of erroneous-RA assessment to less than 5%. In another paper, Ratnieks (1991) showed that, if workers have complete control over the sex allocation, a facultative strategy of biasing the colony sex ratio in response to relative RA can easily evolve. This is because only marginal abilities for both RA-assessment and effective colony-level sex ratio adjustment suffice to give a consistent inclusive fitness increase for an assessing worker-mutant. If the population sex ratio is less female biased than the Benford equilibrium (e.g. because queens exert some control), the invasion conditions become less lenient and depend on a more accurate RA assessment and on the frequency of one- and two-father colonies. Overall, the boundary-conditions explored by Ratnieks (1991) do not seem to be too restrictive for our model-predictions to apply at least qualitatively in many natural

populations of eusocial insects, but it is also obvious that – apart from effective worker control – a reasonably large diversity of genetic odor cues is a general requisite.

How constrained are Hymenopteran workers in practice in making the RA-assessments hypothesized in this paper? It is clear that a perfect individual kin-recognition may well be rather costly. We note, however, that such skills – if they are at all possible – are beyond the scope of our model, as full-sib and/or “own son” nepotism tend to destroy our model predictions (see Boomsma and Grafen, 1990). As argued by Ratnieks (1991), qualitative RA-assessment by workers, as needed for our model, may well be negligible in cost as the information can be picked up during normal colony activity and does not require additional sensory capacities beyond those functioning in the (obviously adaptive) discrimination between nestmates and non-nestmates. So, even in cases where individual kin-recognition is just a non-selected artifact of nestmate recognition (Carlin, 1989; Grafen, 1990), such (limited) abilities may be adaptive when used to capitalize on relative RA.

Are workers really able to assess relative RA and relative colony-productivity ( $t$ ) with enough accuracy to achieve a consistent inclusive fitness advantage of colony-level sex ratio biasing in natural populations? We have only worked out example cases with specific classes of RA where the values of  $F$ ,  $M$ , and  $V$  (and  $t$  in Fig. 3) were kept constant. The earlier introductory statement that such simplified illustration may still be roughly correct for real populations where these variables follow their own species-specific frequency distributions can in fact be made somewhat more precise. As long as variables like  $F$ ,  $M$  and  $V$  have defined species- (or meta-population-) specific frequency distributions (e.g. Poisson or Normal with a variance that is fixed per species on an ecological time scale), it will pay individual workers in local populations to act as if these variables or certain functions of them (e.g.  $F/(F + M)$ ) were fixed at their means. However, if the variance around such means is substantial, workers will be more and more selected to “hedge their bets” (Seger and Brockmann, 1987), and the optimal colony-level strategies will become less extreme. In the ultimate but unlikely case of complete unpredictability of the local variables, the optimal colony strategy may effectively converge on a “no-assessment” Benford (1978) type of strategy, but even then the question remains to what extent the frequency dependent sex ratio selection occurs at the level of the local population or the meta-population.

### *Subdivided populations and differential dispersal*

A formal treatment of differential migration of the sexes in the context of our model is beyond the scope of this paper. Such differences in dispersal either result in Local Mate Competition (LMC; if males disperse less than females) (Hamilton, 1967), or in Local Resource Competition (LRC; if males are the better dispersers) (Clark, 1978). It seems likely, however, that such inclusion would primarily affect the theoretically expected values for the equilibrium sex ratios of the local popula-

tions, but not the expectation that the optimal sex ratios for separate classes of RA are different and more extreme than those expected for constant RA. The effect of extreme LMC on the population sex ratio was mathematically worked out by Bulmer (1986b) using a fitness formula like our equation (1), but with a female component without a denominator, as all females were assumed to disperse outside the local area.

Without differential dispersal of the sexes, our results for single finite populations are likely to be a reasonable approximation for what can be expected in a system of interacting local populations, i.e. in cases where Hamilton's (1967) concept of population viscosity applies. Recent models by Bulmer (1986a,b) and Frank (1986) imply that only minor effects on the overall population sex ratio are to be expected as long as both sexes disperse at equal rates (resulting in equivalent rates of density-dependent competition) and local populations are not very small. Accordingly, the selection forces inducing bimodal colony sex ratios should also be reasonably consistent across local populations, provided that the variables characterizing the local populations are distributed as indicated above. An issue related to this discussion is that our approach makes yet another simplifying assumption. This is that the relative fitnesses in finite populations are equivalent to the absolute fitnesses in infinite populations. Again, a formal treatment of this complication is not given here and the extent to which our simplification will remain valid in models that address population subdivision explicitly remains to be seen.

Apart from influencing the equilibrium population sex ratio, local competition between sibs has recently also been argued to affect the colony sex ratio. A model by Frank (1987) showed that even a relatively small imbalance between LMC and LRC is expected to have an influence on the colony-level proportional investment in males and gynes. The rationale of his model is that colonies producing many sexuals lose more inclusive fitness due to competition between related offspring than do small colonies. Therefore, the larger colonies should invest less in the more competing sex than the average colony in the population, whereas the smaller colonies should do the opposite.

Our model implies that such sib-competition effects in finite populations can be understood from the fact that the denominators of the marginal values change quadratically with a colony's production of gynes and males. The marginal values decline in unison for a colony that produces both sexes, but this changes if one of the sexes should partly disperse outside the local population, whereas the other sex does not. Then the rate of decline with increasing  $t$  will be lower for the better dispersing sex. At equilibrium the marginal values should be equal for the average of colony productivity ( $t$ ). Within that overall equilibrium, however, the better dispersing (less competing) sex has higher marginal returns at higher values of  $t$ , but the other sex has higher marginal returns at lower values of  $t$ . If gynes disperse better than males (the LMC scenario) Frank's (1987) model predicts that the average colony sex ratio should become more female-biased at increasing colony productivity ( $t$ ).

Accordingly, Frank's (1987) model assumes constant or non-assessable RA and predicts population-wide adjustment of colony sex ratios following within-colony

assessment of relative productivity. Our model predicts varying degrees of sex ratio specialization for classes of colony with different RA, following within-colony assessment of relative RA and relative  $t$  by the workers. We note that Frank's prediction of changing degrees of female-bias as a function of colony productivity and our prediction of bimodal sex ratio variation could apply simultaneously, and in fact the same comparative data show some evidence for both trends (Nonacs, 1986a,b; Boomsma and Grafen, 1990).

### *Conclusion*

In retrospect, Trivers and Hare (1976) proposed that the major selective forces in ant sex ratios were relatedness asymmetry and worker control over sexual investments. However, one of the most puzzling features of ant sex ratios has been the strong colony-to-colony variation within species, which has led subsequent authors to suggest additional resource correlated explanations (Grafen, 1986; Nonacs, 1986a) and additional evolutionary scenarios (Frank, 1987; Nonacs, 1986a; Boomsma and Grafen, 1990). In this paper we have elaborated on the general concept of relative RA to show that – under the assumption that workers are able to assess their colony relatednesses – our earlier predictions of extreme colony sex ratios as a function of colony-level RA (Boomsma and Grafen, 1990) are theoretically robust and quantifiable and that they could in principle apply to all random mating hymenopteran societies where RA is variable and workers are in control of the sex allocation process.

The model presented here obviously awaits detailed experimental testing and rigorous data collecting in natural populations, as outlined by Boomsma and Grafen (1990) and Ratnieks (1991). Ants will probably again be the most obvious group to test these ideas. Some good recent examples of the kind of field-data required have been provided by Elmes (1987a,b) and Herbers (1984, 1990), who both have demonstrated correlations between queen-number and colony sex ratio that might prove to be consistent with our predictions. We would expect similar trends to occur in other eusocial Hymenoptera provided that RA is variable among colonies. We note, however, that annual life cycles (bumblebees, vespids) and colony-swarming (honeybees) are likely to impose additional constraints both in the formulation of the exact expectations (Bulmer, 1981) and for the setup of tests in field or laboratory populations.

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## Appendix

In this section we show that our colony-level sex-allocation approach is a consistent extension of the existing population-level theory on sex allocation in eusocial insects. For that purpose we rederive the main results of Trivers and Hare (1976), Taylor (1981) and Nonacs (1986a) in the simple terms of our marginal value notation.

Equation (4) can be checked against the standard case (Trivers and Hare, 1976; Oster and Wilson, 1978), which concerns either queen control with overall symmetry in relatedness or worker control with constant asymmetry of relatedness. This implies that there are no RA-classes and that equation (4) should be valid for all colonies (assuming that  $t$  is both constant and  $>0$  but very small compared to  $F + M$ ). It appears that equation (4) will always yield overproduction of the relatively rare sex, until the population reaches its equilibrium reflecting the overall relatednesses. Then, however, the numerator of the second term of equation (4) equals zero. Accordingly, the optimal sex ratio for a colony ( $\mu$ ) coincides with the overall population optimum, because  $S$  has the same value for all colonies in the population. The only exception occurs if the population is infinitely large. As  $t/(F + M)$  is then equal to zero as well, the second term of equation (4) becomes indeterminate and all colony sex ratios are equally advantageous as long as the population sex ratio remains at its equilibrium. Accordingly, exclusive queen-control world yield a population sex ratio of 1:1 at equilibrium and the same 1:1 optimum would apply to individual queens when  $t > 0$ . Worker control under monogyny, single mating and no worker reproduction results in a constant RA of 3:1, which fixes  $\mu$  at 0.75 for every colony as long as  $t > 0$ . Exclusive production of males from worker-laid eggs results in  $\mu = 0.5$  for both queen and workers, as  $b_{ff}V_f = b_{mf}V_m$  for both parties in every colony.

The outcome of expression (4) for worker control can also be compared with Benford's (1978) analysis of populations whose colonies vary in RA, but where workers cannot use any information about which kind of colony they belong to. His results can be rederived from expression (4) by using the mean values of  $b$  and  $V$ , which will again make  $MS - F$  equal to zero at equilibrium. Thus, equation (4)

gives the same results as the previous theory if RA is constant, non-assessable or irrelevant (as hypothesized for slave making ants), and produces in addition the extreme colony-level optima (for non-balancing colonies) in those cases where – owing to variation in RA – the colony optima do not coincide with the ESS population sex ratio.

The population-wide effect of worker-reproduction on the reproductive value ( $V$ ) of males (Trivers and Hare, 1976; Benford, 1978) can also be understood in these very simple terms. Let  $V_f$  and  $V_m$  be the reproductive values of females and males and let  $V'_f$  and  $V'_m$  be the reproductive values for the next generation. If  $p$  is – as before – the proportion of queen produced males, then  $V_m$  equals half of the reproductive value of the next generation females ( $V'_f/2$ ) plus half of the reproductive value of those males in the next generation produced by workers (i.e.  $(1-p)V'_m/2$ ), because worker reproduction makes male genes in one generation get into males in the next generation. Similarly,  $V_f$  equals  $V'_f/2$  (direct gyne production) plus  $pV'_m$  (direct male production) plus  $(1-p)V'_m/2$  (indirect male production by workers). At equilibrium,  $V_f = V'_f$  and  $V_m = V'_m$  and we can thus work out that  $V_f/V_m = 1 + p$ , which is equal to the Benford (1978) result.

The results of earlier models for population-wide sex ratio compensation (Taylor, 1981; Nonacs, 1986a) can be rederived as follows: As the regression relatedness of mother-queens to their own offspring is 0.5 ( $b_{ff}$ ) and 1 ( $b_{mf}$ ), respectively, the relatedness-ratio of queens is 0.5 ( $1 + p$ ). Thus, if the overall proportion of queen-produced males ( $p$ ) should drop from 1 to 0.8 (e.g. because 20% of the males is produced by workers in orphaned nests), the relatedness ratio for queen's goes down only from 1 to 0.9. Expressed as proportions ( $a_i$  in Table 1) this means that a sex ratio shift from  $F/(F + M) = 0.5$  to 0.455 (1/2.2) makes the critical value for queens in queenright colonies change from 0.5 to 0.474 (0.9/1.9). Thus, the (balancing) queenright colonies are selected to overproduce the relatively rare sex only until half of the bias induced by orphaned colonies is being met (cf. Taylor, 1981).

The sex ratio compensation equilibrium for the case when full-sib workers control the allocation process was derived earlier by Nonacs (1986a). The equivalent of his equations emerge from our notation in the following way: If we consider an infinite population and assume that the queenright colonies are the balancing class, the RA for sterile workers is  $(b_{ff}/0.5)(1 + p)$  if all males in these colonies are produced by the mother-queen (see also Table 1). The equilibrium sex ratio for the population as a whole comes to reflect the RA of the balancing class. Thus,  $F/M$  equals  $2b_{ff} + 2pb_{ff}$  and it is again obvious that only half of the bias induced by orphaned colonies will be compensated for. If all workers are full-sibs the proportionate sex ratio follows as:

$$F/(F + M) = (3 + 3p)/(5 + 3p) \quad (6)$$

or, the other way around,

$$M/(F + M) = 2/(5 + 3p) \quad (6a)$$

where, as before,  $M$  is the sum of all queen-produced males ( $M_q$ ) and all worker-produced males ( $M_w$ ).



If we define the share of worker produced males relative to the total sexual production from queen eggs, i.e. use  $\beta = M_w/(M_q + F)$  as done by Taylor (1981) and Nonacs (1986a), it follows directly from the respective definitions of  $p$  and  $\beta$  that  $M_q + M_w = M_w/(1 - p)$  and that  $M_q + M_w + F = M_w + M_w/\beta$ . Hence, expression 6a also equals  $\{1/(1 - p)\}/(1 + 1/\beta)$ , which yields the general relationship that

$$p = (2 - 3\beta)/(2 + 5\beta) \quad (7)$$

where  $\beta$  does not exceed  $2/3$  and which in turn gives Nonacs' population equilibrium for sex ratio compensation under full-sib worker control as

$$M/(F + M) = (2 + 5\beta)/(8 + 8\beta) \quad (8)$$

or alternatively,

$$F/(F + M) = (6 + 3\beta)/(8 + 8\beta) \quad (8a)$$

The general result is, therefore, that for all increases in male production by a non-balancing class which do not affect the status of the balancing class, compensation for worker-produced males will only be 50%. As derived in the paper, however, compensation for queen-produced males (which do not effect  $p$ ) is normally 100%. The examples show that this result is exact if the RA's are expressed as ratios and when populations are infinite but only approximate for proportional sex investments and finite populations.