

# Split Sex Ratios in Perennial Social Hymenoptera: A Mixed Evolutionary Stable Strategy from the Queens' Perspective?

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**ABSTRACT:** In social Hymenoptera, relatedness asymmetries due to haplodiploidy often generate conflicts of genetic interest between queens and workers. Split sex ratios are common in ant populations and may result from such conflicts, with workers favoring the production of males in some colonies and of gynes in others. Such intercolonial differences may result from variations in relatedness asymmetries among colony members, but several examples are now known in which this hypothesis does not hold. We develop here a simple model assuming monogynous, monoandrous, worker-sterile, perennial colonies without dispersal restrictions. Workers may eliminate eggs of either sex and determine the caste of the female brood, but the queen controls the number of eggs of each sex she lays. In such conditions, we demonstrate that split sex ratios can result from queens adopting a mixed evolutionary stable strategy (ESS), with one option being to put a strict limit to the number of diploid eggs available and the alternative one to provide diploid eggs ad lib. In the former situation, workers should raise all diploid eggs as workers and release only male sexuals. In the latter, workers should adjust the caste ratio so as to reach the maximum sexual productivity for the colony, which is entirely invested into gynes. For a particular relative investment in gynes at the population level, between 0.5 (ESS under full queen control) and 0.75 (ESS under full worker control), an equilibrium is reached at which both strategies yield an equal genetic payoff to the queen. Male-specialized colonies are predicted to be equally abundant but less populous and less productive than gyne-specialized ones. Available data on the monogyne form of the fire ant, *Solenopsis invicta*, suggest that this model may apply in this

case, although more specific studies are required to test these predictions.

**Keywords:** Hymenoptera, ants, kin selection, sex allocation, queen-worker conflict.

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Over the past decades, the study of sex ratio in eusocial Hymenoptera (ants, bees, wasps) has provided some of the best quantitative evidence for the importance of kin selection and inclusive fitness theory (Hamilton 1964; Bourke and Franks 1995; Crozier and Pamilo 1996; Chapuisat and Keller 1999). This is largely due to the haplodiploid sex determination system, which results in queens being equally related to their sons and daughters, whereas workers are more closely related to their sisters than to their brothers. These asymmetrical values of relatedness may generate a conflict of genetic interest between the queen and her workers over sex allocation. For instance, in a monogynous, monoandrous, and worker-sterile colony, workers are three times more closely related to their sisters than to their brothers. They may therefore maximize their inclusive fitness by favoring a female-biased sex investment ratio. By contrast, the queen is symmetrically related to both sexes of her progeny and is selected to favor an equal investment in males and gynes. A critical issue concerning the sex ratio of reproductive offspring in eusocial Hymenoptera is therefore to what extent each caste manages to control the allocation of resources into dispersers of either sex. Haplodiploidy allows queens to control the primary sex ratio (i.e., the relative abundance of male and female embryos) by fertilizing or not fertilizing the eggs they lay. However, because workers rear the brood, they can potentially control the secondary sex ratio (i.e., the relative abundance of males and gynes among sexuals) by selective elimination of male larvae (Aron et al. 1994, 1995, 1999; Passera and Aron 1996; Sundström et al. 1996) or by altering the proportion of female larvae developing into workers or gynes (Hammond et al. 2002). Thus, as formulated by Trivers and Hare (1976), when all

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colony members are the offspring of a single once-mated queen and in the absence of dispersal restrictions, the population-wide sex allocation is predicted to be 3 : 1 in favor of gynes under full worker control and to stabilize near 1 : 1 under full queen control. Under mixed control, intermediate sex allocation ratios are predicted. In such a case, workers should attempt to favor the production of gynes, whereas the queen should favor males.

Whether conflicts over sex allocation imply conflicts over resource allocation between castes (reproductives vs. workers) has been a controversial issue (Pamilo 1991; Bourke and Chan 1999; Herbers et al. 2001; Reuter and Keller 2001). A crucial point is the relationship between the present sex allocation pattern and that expected in the future. In annual colonies, with an explosive strategy, the condition is trivial: there is no cost for the queen in limiting the number of diploid eggs laid toward the end of the colony's life because no workers are needed for the future. The queen can therefore impose an upper limit to the amount of gynes that can be raised, thereby forcing workers to invest the surplus of resources into males. However, a conflict may arise in perennial colonies because diploid eggs are needed to maintain a worker population, but workers could choose to direct them to gynes rather than to new workers.

Colony sex ratios have been analyzed across a broad range of eusocial Hymenoptera. In many instances, most colonies in a population produce almost exclusively dispersers of a single sex (Bourke and Franks 1995; Crozier and Pamilo 1996). To explain such patterns, the relatedness asymmetry hypothesis (Boomsma and Grafen 1990, 1991) assumes that colony kin structure and therefore relatedness asymmetry (i.e., the relative value of gyne-worker and male-worker relatedness) may vary between colonies within populations. The theory predicts that if workers are in control of sex allocation and can assess relatedness asymmetry in their own colony, they should favor gynes wherever the relatedness asymmetry is higher than the population average and males wherever it is lower (Boomsma and Grafen 1990, 1991). A strong point of this theory is that it unequivocally predicts strongly bimodal or split sex ratios. It has received ample support from ants, bees, and wasps (reviews in Queller and Strassmann 1998; Chapuisat and Keller 1999).

However, in several ant species, workers do not bias colony sex ratios as predicted by the relatedness asymmetry theory. This suggests either that queens are in control of the sex ratio or that factors other than relatedness asymmetry are predominant. For instance, split sex ratios occur in the monogyne form of the fire ant *Solenopsis invicta*, which is monoandrous and worker sterile and is therefore not expected to display intercolonial differences in relatedness asymmetry (Fletcher and Ross 1985; Ross and

Fletcher 1985; Ross 1993; Vargo 1996). In *Pheidole pallidula*, sex ratio specialization is not associated with relatedness asymmetry but with the number of queens and probably with the level of available resources (Aron et al. 1999; Fournier et al. 2003). In the polygyne form of *Formica exsecta*, the need for replacement queens seems to be the main factor favoring gyne-biased sex ratios independently of relatedness asymmetry (Brown and Keller 2000, 2002). Another possible explanation is that the controlling party itself differs among colonies (Bourke and Franks 1995): for instance, if the queen controls sex allocation in small colonies whereas workers control it in large colonies, the former should specialize in males and the latter in gynes. A positive association between colony size and relative investment in gynes has been reported in several ant species (review in Crozier and Pamilo 1996), but whether this is due to the queen's ability to control sex allocation in smaller colonies is hard to demonstrate. In particular, the queen's ability to direct the development of the female castes in her own interest is often questionable (Keller and Nonacs 1993). Other hypotheses have been put forward, such as the constant male hypothesis (Frank 1987) and multifaceted parental investment (Rosenheim et al. 1996), but neither of them satisfactorily accounts for extreme sex ratio specialization.

The first experimental evidence for queen control on sex allocation in ants recently came from the monogyne form of the fire ant *S. invicta*, in which the relative amount of haploid eggs laid by the queen determines whether the colony will be male or gyne specialized (Aron et al. 1995; Passera et al. 2001). The queen thus exerts some control over colony sex allocation, although actual sex investment ratios are female biased at the population level, suggesting some extent of worker control as well (Aron et al. 1995; Vargo 1996). It has long been suggested that the queen may attempt to manipulate the sex allocation ratio by limiting the amount of diploid eggs available, thereby forcing workers to raise males: according to the theoretical approaches of Bulmer (1981) and Bulmer and Taylor (1981), this strategy could allow the queen to achieve a substantial degree of control over sex allocation, especially if the relative cost of a gyne is low compared with that of a worker. This hypothesis was recently revived by Reuter and Keller (2001). However, none of these models predicted the occurrence of split sex ratios. In this article, we reexamine the hypothesis of diploid egg limitation on slightly different bases. We show with the help of a very simple model that under basic assumptions, split sex ratios can evolve as a mixed evolutionary stable strategy (ESS; Maynard Smith 1982) from the queens' point of view.

### The Model

We consider the most straightforward case of a population of monogynous, monoandrous, and worker-sterile hymenopteran colonies, which release dispersing males and gynes. Local mate competition (Hamilton 1967), local resource competition (Clark 1978), and inbreeding are assumed not to occur. The overall colony's productivity is a function of the resources brought in by the workers. We consider that these resources depend solely on the colony's worker force ( $w$ ), which comes to assume that all colonies live in a similar, equally favorable environment. Colony productivity  $p(w)$  is deemed to increase with  $w$  at the beginning, but because additional workers yield a decreasing return as  $w$  rises, this function levels off.

We suppose that colonies are perennial and that their constituting individuals will adjust their pattern of resource investment so as to maximize their genetic payoff over a potentially infinite series of similar reproductive cycles. That is, we do not consider colonies in an ergonomic phase of growth, nor do we consider colonies displaying an explosive production of winged sexuals after which they would collapse. Instead, colonies are in a stable phase of maturity during which they maintain their worker population under a constant renewal rate while investing the surplus of production into sexuals. Therefore, the following equation describes the distribution of the colony's total productivity at each reproductive cycle:

$$p(w) = c_w w + c_f f + c_m m,$$

where  $c_w$ ,  $c_f$ , and  $c_m$  are the costs of production of a worker, of a gyne, and of a male, respectively, and  $w$ ,  $f$ , and  $m$  are the number of workers replaced and the number of gynes and males released. The costs of production are assumed to be equal for all individuals of a caste. The colony's total sexual productivity is given by

$$s(w) = c_f f + c_m m = p(w) - c_w w.$$

It is necessary for our model to split the investment values for each caste between their constituents, that is, the number of individuals and their cost of production. This will allow us to express the workers' and queen's genetic payoffs as functions of the number of individuals of each sex raised by the colony ( $f$  and  $m$ ). We will also distinguish between the numerical proportion of gynes among sexuals in the whole population ( $F$ ) and the proportional investment in gynes relative to the total investment in sexuals ( $X$ ; as in Pamilo 1991). Thus, for  $F$  gynes, there are  $1 - F$  males, and for an investment of  $c_f F$  in gynes, the investment in males equals  $c_m(1 - F)$ . Therefore,

$$X = \frac{c_f F}{c_f F + c_m(1 - F)}.$$

The population of colonies is allegedly large so that sex allocation decisions taken in a single focal colony do not immediately affect sex allocation at the population level. According to classical sex allocation theory (eq. [4] of Bulmer and Taylor 1981; eq. [5.7] of Crozier and Pamilo 1996), the workers' and queen's genetic payoffs are proportional to, respectively,

$$V_w = \frac{0.75f}{F} + \frac{0.25m}{1 - F},$$

$$V_Q = \frac{0.5f}{F} + \frac{0.5m}{1 - F}.$$

These functions describe the genetic payoffs obtained during one reproductive cycle, but because the colony is allegedly in a phase of stability, equal payoffs can be expected for each of the following cycles. Maximizing these functions thus also maximizes the lifetime genetic payoffs.

The extent of control each caste (queen or workers) exerts on the amount of sexuals of each sex raised in the colony is of paramount importance. Here, both castes are given extensive freedom: the queen is in control of the absolute quantities of haploid (male) and diploid (female) eggs she lays, whereas workers are given full control of the number of eggs of each sex that are raised to maturity as well as of the caste identity (gynes or workers) of the diploid individuals. We assume that the population-wide sex allocation is comprised between 1 : 1 and 3 : 1 female biased ( $0.5 < X < 0.75$ ). Within these limits, queen-worker conflict over sex allocation is expected: the queen may attempt to limit the number of diploid eggs in order to favor the production of males, whereas workers may both eliminate haploid eggs (or male larvae) and direct as many diploid larvae as they wish toward either female caste as long as resources are sufficient. If the population-wide sex allocation lies outside of these limits, the queen and workers should agree to raise the less frequent sex, thereby returning the population-wide figures toward this conflict window.

Let  $N$  be the number of diploid eggs laid by the queen. Since there is no point for the queen to limit the number of haploid eggs, we suppose that such eggs are available ad lib. Let us now examine how the payoff functions vary according to  $N$ . Our notation is summarized in table 1.

As long as  $N$  is small, the amount of diploid eggs will be a limiting factor. A fraction of these diploid eggs will necessarily be raised as workers to perpetuate the colony. Because gynes constitute a better investment than males from the workers' viewpoint, the workers should then as-

Table 1: Notation used

Notation	Definition
Population parameters:	
$c_w, c_f, c_m$	Cost of production of one worker, gyne, male
$X$	Proportional investment in gynes at the population level
$F$	Numerical proportion of gynes (relative to the total number of sexuals) at the population level
Parameters of the reproductive cycle:	
$N$	Number of diploid eggs laid
$w, f, m$	Number of workers, of gynes, of males produced
$V_w, V_Q$	Genetic payoff to workers, to the queen
$p(w)$	Total colony productivity (invested in sexuals and workers)
$s(w)$	Colony productivity invested in sexuals (gynes and males)
$w^*$	Value of $N$ for which function (1) presents a maximum; intuitively: value of $N$ below which workers should raise all diploid eggs as workers (giving $w = N$ and $f = 0$ )
$N^\circ$	Value of $N$ for which $w^*$ workers can produce exactly $w^*$ workers and raise all remaining $(N - w^*)$ diploid eggs as gynes; intuitively: threshold value of $N$ above which workers should not raise any males
$s_{\max}$	Highest possible value of $s(w)$
$w_{\max}$	Value of $w$ corresponding to $s_{\max}$
$N_{\max}$	Value of $N$ corresponding to $s_{\max}$ and $w_{\max}$ ; intuitively: value of $N$ above which additional diploid eggs become superfluous
Productivity function constants:	
$K$	Maximum colony productivity (asymptote for $w \rightarrow \infty$ )
$\mu$	Slope of the productivity function at origin ( $w = 0$ ); intuitively: growth rate of incipient colony

sign the remaining resources by priority to the remaining diploid brood to raise gynes. Any surplus of resources will then be invested into males. For a given value of  $N$ , we thus have

$$\begin{aligned}
 f &= N - w, \\
 m &= \frac{p(w) - c_f(N - w) - c_w w}{c_m}, \\
 V_w &= \frac{0.75(N - w)}{F} + \frac{0.25[p(w) + (c_f - c_w)w - c_f N]}{c_m(1 - F)}.
 \end{aligned} \tag{1}$$

Let us call  $w^*$  the maximum of function (1), calculated by derivation:

$$\frac{dV_w}{dw} = -\frac{0.75}{F} + \frac{0.25[dp(w)/dw + c_f - c_w]}{c_m(1 - F)},$$

and for  $dV_w/dw = 0$ ,

$$\left[ \frac{dp(w)}{dw} \right]_{w^*} - c_w = \frac{3c_m(1 - F)}{F - c_f}. \tag{2}$$

At this point, the left-hand side of this equation should

be positive:  $[dp(w)/dw]_{w^*} > c_w$ . This inequality just means that an additional worker collects more resources than the amount just necessary to replace itself. Now, what about the right-hand side? The expression  $3c_m(1 - F)/F - c_f > 0$  means that the population-wide investment in gynes is less than three times the population-wide investment in males, which is the necessary condition for workers to favor gynes over males. Let  $w^*$  be the positive value of the worker force satisfying equation (2). Note that  $w^*$  depends on  $F$  but is independent of  $N$ . Since the derivative  $dp(w)/dw$  itself decreases as  $w$  increases,  $w^*$  will increase with  $F$ . Three cases must be considered.

*Case 1:  $N \leq w^*$*

Since  $w$  may never exceed  $N$ , the condition  $N < w^*$  implies that  $w^*$  is an out-of-reach maximum. The genetic payoff-maximizing rule is thus, from the workers' viewpoint, to channel all diploid eggs into workers ( $w = N$ ) and use the remaining resources to raise males. We have then

$$V_w = \frac{0.25[p(N) - Nc_w]}{c_m(1 - F)},$$

$$V_Q = \frac{0.5[p(N) - Nc_w]}{c_m(1 - F)}.$$

These functions will both rise with  $N$  up to their limit of applicability ( $N = w^*$ ). At this point,

$$\begin{aligned} V_w &= \frac{0.25[p(w^*) - w^*c_w]}{c_m(1 - F)}, \\ V_Q &= \frac{0.5[p(w^*) - w^*c_w]}{c_m(1 - F)}. \end{aligned} \tag{3}$$

*Case 2:  $N > w^*$  and  $N < [p(w^*) + (c_f - c_w)w^*]/c_f$*

In this case, workers should raise  $w^*$  diploid eggs as workers and the remaining  $N - w^*$  diploid eggs as gynes. The second inequality implies that some resources are left to be invested into males. Therefore,

$$m = \frac{p(w^*) - c_f(N - w^*) - c_w w^*}{c_m}.$$

Genetic payoff functions then become

$$\begin{aligned} V_w &= \frac{0.75(N - w^*)}{F} + \frac{0.25[p(w^*) - c_f(N - w^*) - c_w w^*]}{c_m(1 - F)}, \\ V_Q &= \frac{0.5(N - w^*)}{F} + \frac{0.5[p(w^*) - c_f(N - w^*) - c_w w^*]}{c_m(1 - F)}. \end{aligned}$$

How do these functions vary if the queen manipulates  $N$ ?

$$\frac{dV_w}{dN} = \frac{0.75}{F} - \frac{0.25c_f}{(1 - F)c_m}, \tag{4}$$

$$\frac{dV_Q}{dN} = \frac{0.5}{F} - \frac{0.5c_f}{(1 - F)c_m}. \tag{5}$$

Equation (4) shows that  $dV_w/dN$  is constant and positive as long as  $c_m(1 - F) > c_f F/3$ . This is just the general condition on population-wide sex allocation for which workers should favor the production of gynes ( $X < 0.75$ ). In a similar yet opposite way, equation (5) shows that  $dV_Q/dN$  is constant and negative as long as  $c_m(1 - F) < c_f F$ , which is the general condition on population-wide sex allocation for which queens should favor the production of males ( $X > 0.5$ ). Under an increase of  $N$  within the limits defined for this case, the favored option for workers would thus be to maintain  $w$  at  $w^*$ , keeping the total productivity of the colony stable, while using the increasing surplus of diploid eggs to raise gynes at the expense of males. This would be advantageous for the workers but detrimental to the queen.

*Case 3:  $N \geq [p(w^*) + (c_f - c_w)w^*]/c_f$*

If  $N$  rises and workers invest more and more in gynes, they will ultimately be constrained by the amount of resources rather than by the number of diploid eggs available. At a critical point (let  $N^\circ$  be this limit value of  $N$ ), the resources remaining available after raising  $w^*$  workers will exactly permit to raise the remaining  $N^\circ - w^*$  diploid eggs as gynes:

$$p(w^*) - w^*c_w = (N^\circ - w^*)c_f,$$

thus,

$$N^\circ = \frac{p(w^*) + (c_f - c_w)w^*}{c_f}.$$

No males are raised anymore ( $m = 0$ ). The workers' and queen's genetic payoffs are given by

$$\begin{aligned} V_w &= \frac{0.75[p(w^*) - c_w w^*]}{c_f F}, \\ V_Q &= \frac{0.5[p(w^*) - c_w w^*]}{c_f F}. \end{aligned} \tag{6}$$

If  $N$  rises beyond  $N^\circ$ , workers cannot improve their genetic payoff anymore by sacrificing males to raise gynes. However, they can still improve it by increasing the total productivity of the colony. Since no males are raised, we obtain

$$\begin{aligned} V_w &= \frac{0.75[p(w) - c_w w]}{c_f F}, \\ V_Q &= \frac{0.5[p(w) - c_w w]}{c_f F}. \end{aligned}$$

Both functions now increase with  $w$  and  $N$  and reach their maximum value for  $dV_w/dw = 0$ . Since  $dV_w/dw = 0.75[dp(w)/dw - c_w]/c_f F$ , we obtain  $dV_w/dw = 0$  for

$$\frac{dp(w)}{dw} = c_w.$$

This expression means that  $w$  has reached its limit value over which the return provided by any additional worker does not exceed its own cost. This corresponds to the maximum value of the sexual productivity  $s(w)$ , hereafter called  $s_{\max}$ , all of which is invested into gynes. Let us call  $w_{\max}$  the value of  $w$  satisfying this condition and  $N_{\max}$  the corresponding value of  $N$  given by  $N_{\max} = w_{\max} + s_{\max}/c_f$ .

There is no advantage in raising  $N$  any further beyond  $N_{\max}$ , because at this point the availability of diploid eggs

does not restrain colony productivity anymore. Unnecessary eggs should be destroyed and recycled. Genetic payoff functions then reach

$$\begin{aligned} V_w &= \frac{0.75[p(w_{\max}) - c_w w_{\max}]}{c_f F}, \\ V_Q &= \frac{0.5[p(w_{\max}) - c_w w_{\max}]}{c_f F}. \end{aligned} \quad (7)$$

This value of  $V_w$  is an absolute maximum. As to the value of  $V_Q$ , it is higher than that corresponding to  $N^\circ$  (eq. [6]) by a factor  $s_{\max}/s(w^*)$ . But this latter value of  $V_Q$  is also lower than that corresponding to  $N = w^*$ , since  $V_Q$  decreases linearly as  $N$  increases from  $w^*$  to  $N^\circ$ . As workers manipulate eggs according to their own genetic interests, the queen's payoff function thus presents a minimum for  $N = N^\circ$  and two maxima: one for  $N = w^*$  and one for  $N \geq N_{\max}$  (plateau). In the former case, the colony produces only male sexuals, while in the latter, it produces only gynes. How do these extrema compare with each other? The first maximum (for  $N = w^*$ , all-male sexuals) is given by equation (3), which is equivalent to

$$V_Q = \frac{0.5s(w^*)}{c_m(1-F)}. \quad (8)$$

Because  $w^*$  and hence  $s(w^*)$  increase with  $F$  (see deductions from eq. [2] above), this expression increases with  $F$  as well. The minimum of  $V_Q$  reached for  $N = N^\circ$  is given by equation (6). Its value is lower than that corresponding to  $N = w^*$  by a factor  $(1-F)c_m/Fc_r$ , or  $(1-X)/X$ , which shows that the cost to the queen of having gynes raised instead of males increases with the female bias  $X$  in the population. In the absence of bias ( $X = 0.5$ ), this cost is, logically, nil. The second maximum (for  $N \geq N_{\max}$ , all-female sexuals) is given by equation (7), which is equivalent to

$$V_Q = \frac{0.5s_{\max}}{c_f F}. \quad (9)$$

Since  $s_{\max}$  represents the maximum colony productivity with nonlimiting eggs,  $s_{\max}$  is independent of  $F$ . This expression thus decreases as  $F$  increases. The equilibrium value of  $F$  for which both maxima, given by equations (8) and (9), correspond to an equal genetic payoff to the queen is given by

$$\frac{s(w^*)}{c_m(1-F)} = \frac{s_{\max}}{c_f F},$$

thus,

$$\frac{s_{\max}}{s(w^*)} = \frac{c_f F}{c_m(1-F)}. \quad (10)$$

At this equilibrium, any queen has two equally valuable options. She can limit the number of diploid eggs to  $w^*$ —which would drive the workers, acting in their own interest, to channel all these eggs to workers and raise only male sexuals—or, alternatively, the queen can supply nonlimiting amounts of diploid eggs, from which the workers should raise the number of workers needed to achieve the maximum production of sexuals, and invest this production exclusively into gynes. Equation (10) also shows that at this equilibrium, the ratio of sexual productivity between gyne- and male-producing colonies is equal to the total gyne : male investment ratio in the population. Consequently, at equilibrium, gyne- and male-producing colonies should be present in equal numbers.

### Simulation

The purpose of this simulation is to illustrate by a numerical example the qualitative conclusions drawn from the analytical study. We attempted to set the values of the model's parameters within a realistic range, although too many parameters are too variable or imperfectly known to allow quantitative predictions. Our focal organism will be the monogyne form of the fire ant, *Solenopsis invicta* Buren, for the following reasons: first, this species has simple monogynous, monoandrous, worker-sterile colonies that display split sex ratios without inequalities in relatedness asymmetries (Fletcher and Ross 1985; Ross and Fletcher 1985; Ross and Keller 1995; Vargo 1996); second, the proportion of diploid eggs laid by the queen has been shown to determine the colony's secondary sex ratio (Passera et al. 2001); and third, extensive studies on this species allow plausible estimations of life-history parameters (e.g., Porter and Tschinkel 1985; Calabi and Porter 1989; Tschinkel 1993; Vargo 1996).

Vargo (1996) estimated the average dry weight of a gyne at 8.12 mg and the relative cost of production of gynes and males, after Boomsma's (1989) correction for metabolic rates, as  $c_f/c_m = 2.22$ . The average cost of a worker is more difficult to evaluate, since *S. invicta* workers are highly polymorphic: within a single colony, a 15-fold variation in worker weight may occur, and worker polymorphism increases with colony size (Porter and Tschinkel 1985; Tschinkel 1993). Porter and Tschinkel (1985) estimated the average dry weight of a worker at 0.495 mg. Therefore, the average gyne : worker dry weight ratio is 16.4 : 1. We shall use this value to approximate the energetic cost ratio, although gynes are richer in fat and thus probably more costly by unit weight (Tschinkel 1993). Ar-

bitrarily setting  $c_w = 1$ , we thus have  $c_f = 16.4$  and  $c_m = 7.4$ . Note that  $c_w$  represents only the cost of production of a worker. We consider that once at the adult stage, each worker assumes its own metabolic costs, which are not negligible (Tschinkel 1993; Vogt and Appel 1999). It is the productivity function  $p(w)$  that incorporates such costs. It should also be noted that  $w$  represents the number of workers replaced during one (annual) reproductive cycle, not the actual number present in the colony. If the average worker longevity is about 4 mo (Calabi and Porter 1989), worker turnover per annual reproductive cycle should therefore be three times the actual colony population.

In most social insects, constraints on foraging efficiency reduce the productivity per individual worker as colony size increases past the incipient stages (Oster and Wilson 1978). Various productivity functions  $p(w)$  satisfying this requirement can be considered. We tested several classes of curves, which yielded qualitatively similar results. For the present simulation, we selected the function proposed by Bulmer and Taylor (1981) because it allows direct comparisons with their work, it features two constants of straightforward biological significance, and it is reasonably easy to manipulate analytically:

$$p(w) = K \left[ 1 - \exp\left(\frac{-\mu w}{K}\right) \right],$$

in which  $\mu$  and  $K$  are constants. By derivation,

$$\frac{dp(w)}{dw} = \mu \exp\left(\frac{-\mu w}{K}\right).$$

The constant  $\mu$  thus corresponds to the slope of the productivity function at the origin ( $w = 0$ ), which represents the colony's growth rate during its early ergonomic phase. As  $w$  increases, colony productivity approaches  $K$ . The asymptotic nature of this function suggests that for large colony sizes, additional workers are just able to cover their own metabolic expenses but are unable to bring any supplementary resources back to the nest, which is expressed by  $dp(w)/dw \rightarrow 0$  for  $w \rightarrow \infty$ . Critical values of  $w$  are as follows:

$$w^* = -\frac{K}{\mu} \ln \left[ \frac{c_w - c_f + 3c_m(1 - F)/F}{\mu} \right],$$

$$w_{\max} = -\frac{K}{\mu} \ln \left( \frac{c_w}{\mu} \right).$$

Therefore,

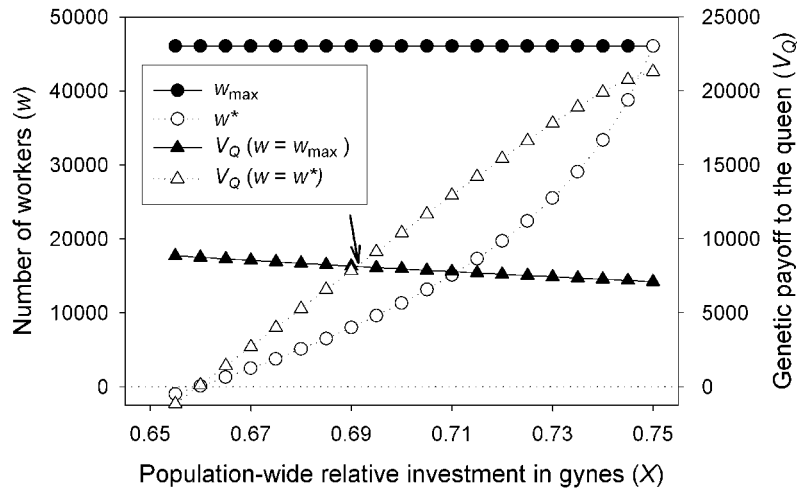
$$p(w^*) = K \left[ 1 - \frac{c_w - c_f + 3c_m(1 - F)/F}{\mu} \right],$$

$$p(w_{\max}) = K \left( 1 - \frac{c_w}{\mu} \right).$$

Bulmer and Taylor (1981) set  $\mu = 10$ . This means that a colony in its early stages of development can decuplate its worker force in 1 yr. For *S. invicta* colonies, Markin et al. (1973) recorded even higher growth rates, near 50 at the end of the first year, but these rates were obtained in a field that had been previously cleared of all ants and therefore offered very favorable conditions for colony development, including the possibility of accelerated growth by absorption of neighboring colonies. In the basic simulation, we will therefore adopt  $\mu = 10$ , which might be a plausible estimate of the average growth rate of a young *S. invicta* colony (Tschinkel 1993) and will facilitate comparisons with Bulmer and Taylor's (1981) results. The actual value of  $K$  is not as important, because  $K$  does not affect the shape of the productivity curve. We set  $K = 200,000$ , yielding values of  $w_{\max}$  near the population figures given by Markin et al. (1973).

With this function and the parameters  $\mu$ ,  $K$ ,  $c_w$ ,  $c_f$ , and  $c_m$  fixed as above, it was possible, as predicted, to vary  $X$  (or  $F$ ) to find an equilibrium at which the genetic payoff to the queen ( $V_Q$ ) presents two maxima of equal height (fig. 1). Equilibrium values are as follows:  $X = 0.6911$  (or  $F = 0.5024$ ),  $w^* = 8,342$ ,  $N^\circ = 11,993$ , and  $w_{\max} = 46,052$  for  $N_{\max} = 54,220$ . This means that for  $X > 0.6911$ , workers will be less reluctant to raise males; the queen can therefore lay more diploid eggs before workers start turning them into gynes. Adopting the male-forcing strategy thus becomes advantageous for the queen. Conversely, for  $X < 0.6911$ , the male-forcing strategy becomes more costly. Note that as  $X$  increases, the genetic payoff of the gyne-producing strategy decreases slowly because the reproductive success of gynes decreases while their total production remains constant (fig. 1). Meanwhile, the payoff of the egg limitation strategy increases rapidly because the reproductive success of males increases, but the production of males increases as well since  $w^*$ , the number of diploid eggs above which workers should start producing gynes at the expense of males, also rises. For  $X \geq 0.75$ ,  $w^*$  reaches  $w_{\max}$ , which confirms that workers should then stop producing gynes.

Figure 2 shows that the equilibrium value of  $X$  is positively affected by the ratio  $c_f/c_w$  and that the equilibrium value of  $w^*$  departs more from  $w_{\max}$  as this ratio rises. This indicates that the male-forcing strategy is harder to enforce if workers can realize a high investment into gynes by influencing the fate of only a few eggs. It can easily be



**Figure 1:** *Solenopsis*-based simulation. Number of workers raised (left-hand scale; circles) and genetic payoff to the queen (right-hand scale; triangles) as a function of  $X$  (the relative investment in gynes at the population level) if the queen either adjusts her egg production to obtain the highest genetic payoff through males (open symbols;  $N = w^*$ ) or lays an excess of female eggs (solid symbols;  $N \geq N_{\max}$ ,  $w = w_{\max}$ ). It is assumed that workers obtain the highest genetic payoff for themselves by controlling the caste of female larvae and eliminating supernumerary eggs of either sex if necessary. Arrow designates point of equilibrium, at which both strategies yield an equal payoff to the queen. For  $X$  below the equilibrium value, the gyne-producing strategy (nonlimiting female eggs) is favored. For  $X$  above the equilibrium value, limitation of female eggs to  $w^*$  (forcing workers to raise males) is favored. Fixed parameters:  $\mu = 10$ ,  $K = 200,000$ ,  $c_i/c_w = 16.4$ .

verified that the cost of males ( $c_m$ ) influences numerical sex ratios but not sex allocation ratios.

The equilibrium value of  $X$  is negatively dependent on the colony growth rate  $\mu$  (fig. 3). This occurs because a higher value of  $\mu$  implies that the relative productivity of workers in small (egg-limited) colonies is higher than in full-sized (non-egg-limited) ones. A higher value of  $\mu$  means that colonies should reach a higher worker population before starting to turn diploid larvae into gynes, as shown by the increase of the ratio  $w^*/w_{\max}$  (fig. 3). Consequently, male-specialized colonies are relatively more productive, and  $X$  decreases.

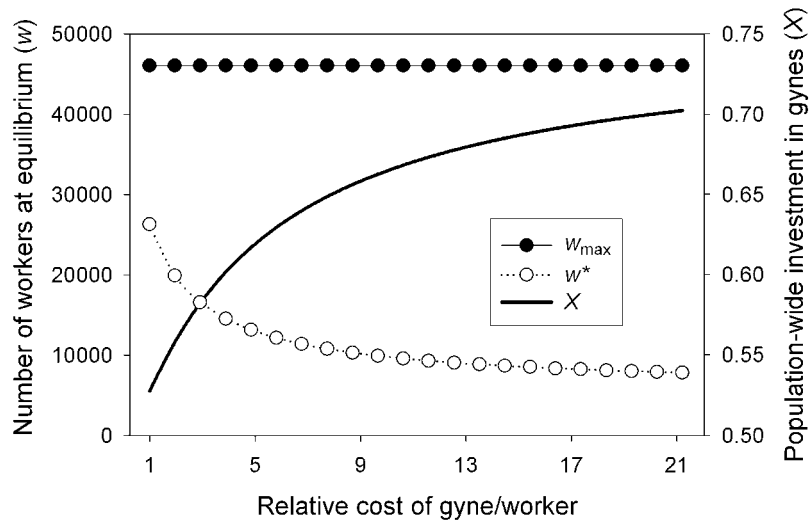
Assuming  $X$  to be at its equilibrium value of 0.6911 with  $c_i/c_w = 16.4$  and  $\mu = 10$ , variations of genetic payoff with  $N$  (number of diploid eggs) for the queen and workers can be visualized (fig. 4). For  $N < w^*$  (8,342 eggs; fig. 4, region A), workers should raise all the diploid eggs as workers and produce only male sexuals. A maximum of genetic payoff to the queen ( $V_Q$ ) is reached for  $N = 8,342$  eggs (fig. 4, thin black arrows). For  $w^* < N < N^\circ$  (8,342 <  $N$  < 11,993), workers should raise 8,342 workers, raise the remaining diploid eggs as gynes, and invest the surplus of resources into males. The queen's genetic payoff decreases as gynes replace males while  $N$  rises in this zone (fig. 4, region B), and it reaches a minimum for  $N = N^\circ = 11,993$  and  $m = 0$  (fig. 4, white arrows). For  $N > N^\circ$ , workers should raise only workers and gynes. The genetic payoff for both queen and workers will rise with

$N$  (fig. 4, region C) up to  $N = N_{\max} = 54,220$  eggs, of which 46,052 ( $= w_{\max}$ ) should be raised as workers and 8,168 as gynes (fig. 4, thick black arrows). Above this value (fig. 4, region D), both  $V_Q$  and  $V_w$  are on a plateau and supernumerary eggs should be eliminated.

## Discussion

Our model fits the simplest colony structure for a perennial social Hymenoptera: monogyny, monoandry, worker sterility, and absence of dispersal restrictions. It shows that split sex ratios can evolve without differences in genetic structure across colonies as a mixed ESS from the queens' perspective. This model rests on two extremely simple assumptions. First, it requires the queen to be in control of the number of diploid (and haploid) eggs she lays. This could allow her to influence the sex allocation in her favor by limiting the number of diploid eggs. Second, workers can eliminate as many male (and female) eggs and larvae as they wish and determine into which caste (worker or gyne) female larvae will develop. In short, workers are allowed to do what is best for themselves with the eggs provided by the queen. On the basis of these assumptions, our model shows that as workers manipulate sex allocation toward their own genetic interest, the queen's payoff function presents two maxima: one corresponding to a strict limitation of the diploid eggs laid and the other to their unlimited supply. Which of these maxima is higher de-



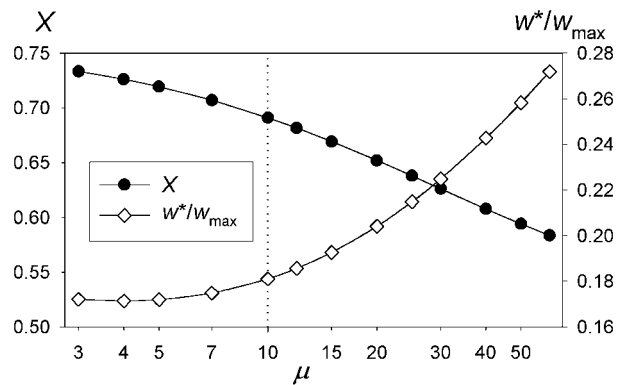


**Figure 2:** *Solenopsis*-based simulation. Number of workers corresponding to either queen strategy (left-hand scale; circles) and population-wide investment in gynes ( $X$ ; right-hand scale; thick line) when both queen strategies are at equilibrium under different values of the gyne : worker cost ratio. Solid circles, nonlimiting diploid eggs,  $w = w_{\max}$ , gyne production. Open circles, diploid eggs limited to  $w^*$ ,  $w = w^*$ , male production. Fixed parameters:  $\mu = 10$ ,  $K = 200,000$ .

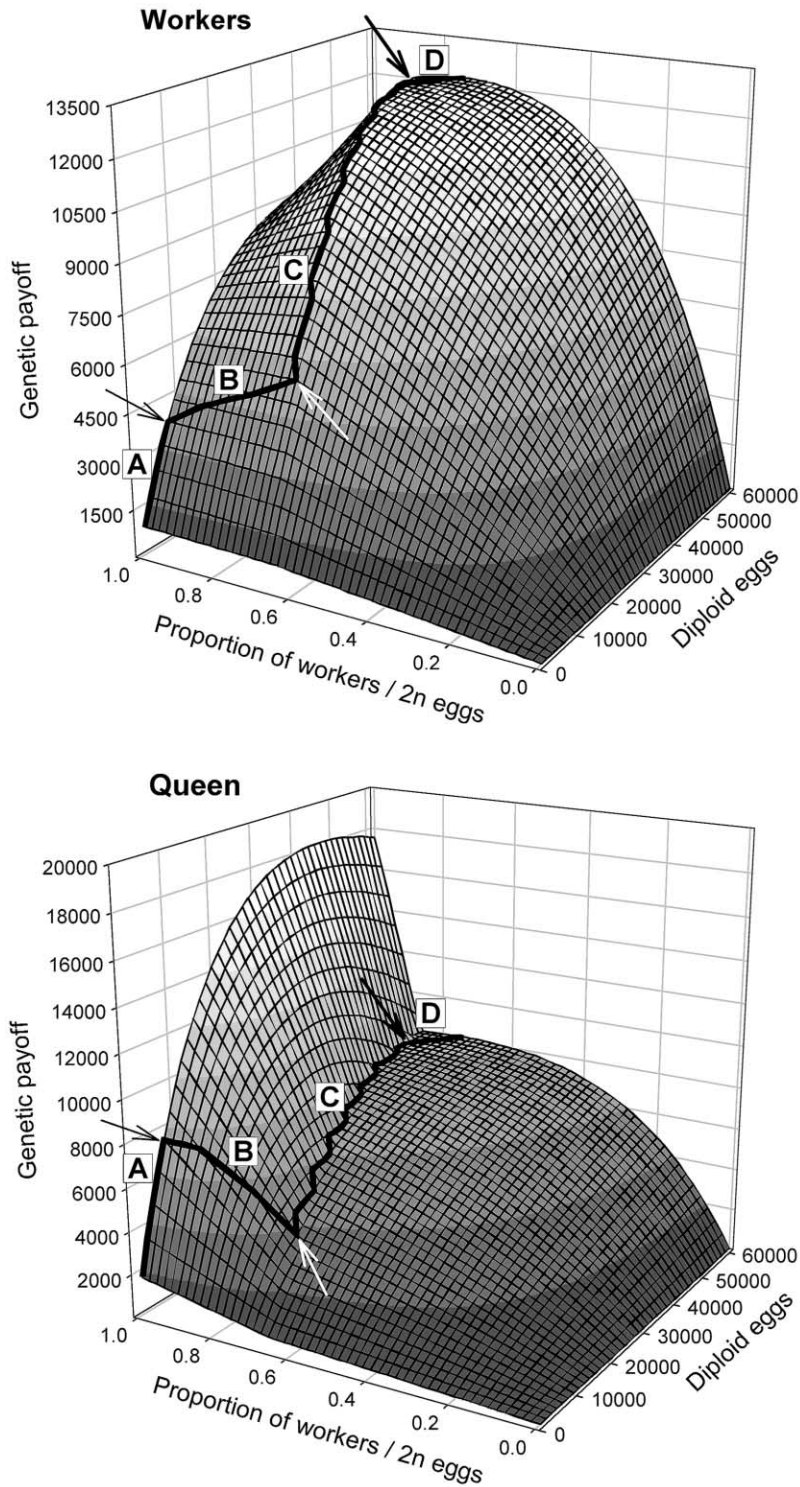
depends on the population-wide sex allocation ratio. Frequency-dependent selection should drive the population of queens toward an equilibrium at which egg-limited (male-producing) and non-egg-limited (gyne-producing) colonies are present in equal numbers. Because male-producing colonies are smaller and can invest less into sexuals than gyne-producing colonies, the overall sex allocation ratio is female biased.

The basic conditions of this model are similar to those of Bulmer and Taylor (1981). Reuter and Keller (2001) also modeled the possibility for the queen to limit the number of diploid eggs but with different assumptions. Why did the models of Bulmer and Taylor (1981) and of Reuter and Keller (2001) not predict split sex ratios? Bulmer and Taylor (1981) did not treat the model analytically but realized a computer simulation, starting by fixing an arbitrary set of worker and queen strategies for an unlikely colony age (1,000 yr) and proceeding backwards. They supposed that the colony had only a limited probability (0.8) of surviving from one season to the next. For each year, they determined the set of strategies maximizing the queen's payoff, assuming that the workers would also maximize theirs. By repeating the operation until the values of  $N$ ,  $f$ ,  $m$ , and  $w$  stabilized, they obtained the equilibrium sex allocation ratio for the modeled colony. This equilibrium sex allocation ratio at the colony level  $\sigma$  depended on the population sex allocation ratio  $s$  (Bulmer and Taylor designated as  $\sigma$  and  $s$  the fraction of the reproductive investment devoted to males, so that their  $s$  is equal to

$1 - X$  according to our notation). When the colony's equilibrium  $\sigma$  coincided with  $s$ , they assumed the population ESS had been reached. The ESS sex allocation was almost unbiased if gynes and workers had equal costs but became more female biased as the cost of a gyne increased relative to that of a worker. This tendency was the same as that observed in this study (fig. 2), although the absolute values differed. What are the sources of discrepancies between their model and ours? Although Bulmer and Taylor (1981) did not provide details as to the procedure followed to



**Figure 3:** *Solenopsis*-based simulation. Influence of the colony's initial productivity per worker  $\mu$  on the relative investment in gynes ( $X$ ) and on the worker force ratio ( $w^*/w_{\max}$ ) at equilibrium. Fixed parameters:  $K = 200,000$ ,  $c_i/c_w = 16.4$ .



**Figure 4:** *Solenopsis*-based simulation. Genetic payoff to workers (*top*) and to queens (*bottom*) as functions of the number of diploid eggs laid and of the proportion of these eggs that are raised as workers. On both graphs, thick curves correspond to the maximum payoff to workers for a given number of diploid eggs. Selection on workers (*top*) should drive them to adjust the sex allocation and caste ratios so as to reach this crest line. Selection on queens (*bottom*) should drive them to adjust their number of diploid eggs so that the sex and caste ratios imposed by the workers (*thick curve*) yield the highest possible payoff to themselves (*black arrows*). Initially fixed parameter values:  $\mu = 10$ ,  $K = 200,000$ ,  $c_r = 16.4$ ,  $c_m = 7.4$ ,  $c_w = 1$ . We then adjusted  $X$  to the value for which both maxima of the queen's payoff function reached the same height; thus,  $X = 0.6911$ . *Thin black arrows*,  $N = N^*$ ; *white arrows*,  $N = N^{\dagger}$ ; *thick black arrows*,  $N = N_{\max}$ . Segments A–D correspond to qualitative differences in the selected sex allocation strategies, as explained in text.

calculate the strategies maximizing the workers' and the queen's payoffs, it is clear that they did not allow for the possible existence of two genetic payoff maxima for the queen: the modeled colony was constrained to reach a stable sex allocation ratio, obeying  $0.25 \leq \sigma \leq 0.5$ , and deemed to represent the ESS if this ratio was equal to that of the population. Their equilibrium values appear unlikely according to our model. For instance, for an equal cost of gynes and workers ( $c_f = c_w$ ), Bulmer and Taylor (1981) obtained the equilibrium for  $s = 0.499$  (or  $X = 0.501$ ). With such a value, our model unequivocally predicts that a queen laying diploid eggs ad lib. should invade. This can easily be understood intuitively: since there is almost no cost to the queen if workers raise gynes instead of males, the queen should just let the workers reach the maximum colony productivity and not restrain the number of diploid eggs to force the production of males.

A possible limitation of the present model is that it applies to perennial colonies that allegedly go through an infinite series of identical cycles, during which their worker population is kept stable by the replacement of dead or lost individuals, and that a steady flow of dispersing propagules (males and/or gynes) are released. Therefore, the optimal strategy for all parties is to reach the highest genetic payoff that can be repeated at each reproductive episode. Intuitively, this situation is the one that gives the least power of control to the queen because there is a high pressure for perpetuating the colony and thus a constant need of diploid eggs. At the opposite extreme, colonies with a single, terminal phase of sexual production should be totally under queen control. The next-to-trivial case of a bigenerational colony, in which resources of the first generation may be invested in all castes whereas second-generation resources are all invested into sexuals, also favors the queen (Bulmer 1981), but we are now extending this model to determine the range of conditions under which two types of colonies (egg limited, male producing vs. non-egg limited, gyne producing) are expected.

The model of Reuter and Keller (2001) suggests that under mixed control of sex allocation, a stable equilibrium should be reached for a definite value of the sex ratio (controlled by the queen) and a definite value of the proportion of females raised as workers (controlled by workers). The sex allocation ratio should stabilize at some point between the queen's and the workers' optima, and all colonies are expected to converge toward the ESS values. A major constraint of the Reuter-Keller model is that in their mixed control case, the adult sex ratio (workers + gynes vs. males) remains under full queen control. Despite the fact that elimination of male brood is a common feature of ant colonies (Aron et al. 1994, 1995, 1999; Keller et al. 1996; Sundström et al. 1996), workers are not allowed to eliminate males: they can influence sex allocation (gynes

vs. males) solely by modifying the proportion of diploid eggs raised as gynes rather than as workers. Another restriction of the Reuter-Keller model is that the genetic payoffs are calculated according to the relative quantities of each caste or sex raised, thereby severely restraining potential effects of absolute differences in productivity between colonies. In our model, such differences are essential.

Our model suggests that split sex ratios in ants could fundamentally result from queens adopting a mixed ESS (Maynard Smith 1982). At the population equilibrium, queens are faced with a choice between two alternatives yielding an equal genetic payoff. If the population stands away from the equilibrium, the payoffs become unequal. Since individual queens are unlikely to be able to detect which option is better, they must "play the field." The return to the equilibrium will be driven by frequency-dependent selection. These conditions are characteristic of a mixed ESS (Maynard Smith 1982, p. 69). A remarkable feature of a mixed ESS is that it can be reached through several processes. The decision of being either a male producer or a gyne producer can be everything from purely genetic to purely environmental, provided that the probability of expressing either phenotype is constant. The possibility of shifting from one strategy to the other is also theoretically open. In *Solenopsis invicta*, further research should determine whether the switch is under genetic control or not, and if not, whether any environmental cue influences the queen's choice and whether she can shift strategies at some point of her life or not. Among colonies of *S. invicta* monitored over 1 yr, a minority were found to shift their sex allocation during the observation period, but whether such shifts occurred with or without queen replacement is not known (Markin and Dillier 1971; Morrill 1974). Long-term studies on this topic are badly needed.

Our model predicts that male-producing colonies should realize a lower investment in sexuals than gyne-producing ones. Such a pattern is commonplace in ants (Nonacs 1986; Crozier and Pamilo 1996). To explain this, several authors have put forward hypotheses based on resource abundance, assuming that an increased amount of resources could more easily (e.g., by switching the development of diploid larvae toward the gyne caste) or more profitably (e.g., if gynes benefit more than males from an increased amount of body reserves, or if males engage in local mate competition) be invested into gynes than into males (Nonacs 1986; Frank 1987; Rosenheim et al. 1996; Chapuisat and Keller 1999; Aron et al. 2001; Ode and Rissing 2002). However, these hypotheses do not fit well with extremely biased sex ratios. Our model suggests that male specialization does not necessarily follow from lower productivity but that both characteristics may be consequences of diploid egg limitation by the queen. The model

also predicts that female-biased sex allocation at the population level results from male-specialized colonies being less productive, but not less abundant, than gyne-specialized ones. In monogynous populations of *S. invicta*, available data suggest that this is actually the case (Morrill 1974; Vargo 1996), although sampling biases and high variance in sexual productivity between colonies make it problematic to obtain fully reliable, statistically significant results. An indirect way to solve this problem could be through the comparison of worker populations between male- and gyne-producing colonies: our model indeed predicts that differences in worker force should be more pronounced than differences in colony productivity, because the productivity per worker should be higher in the less populous male-producing colonies. For instance, in the simulation presented above, the worker force ratio between gyne-producing and male-producing colonies reaches 5.5 : 1, whereas the sexual productivity ratio is only 2.2 : 1.

At this point, formulating quantitative predictions still remains very hazardous. The numerical simulation had no other aim than illustrating the qualitative results of the analytical model. Even for a well-studied species such as *S. invicta*, only crude estimates of life-history parameters are available, and environmental effects, which are necessarily complex, are extremely difficult to incorporate into the model. For this reason, a close fit could not be expected between the numerical results of our model and the actual data recorded for *S. invicta*. For instance, the model predicts a proportional investment in gynes of 0.69 in *S. invicta*, which is substantially higher than the mean value of 0.607 provided by Vargo (1996), although the confidence interval on this mean is not known. Further sampling is needed to determine whether the high ratio between the worker force of gyne-producing versus male-producing colonies (5.5 : 1) predicted by the simulation is realistic or not. In any case, the qualitative predictions that emerged as to the relative size, abundance, and productivity of male- and gyne-producing colonies within a population are testable. Across populations or species, our model predicts a positive relationship between female bias at equilibrium and female caste dimorphism (gynes vs. workers), but this prediction is harder to test because many other factors may concurrently influence population-wide sex allocation (Bourke and Franks 1995; Crozier and Pamilo 1996; Chapuisat and Keller 1999).

Hypotheses based on relatedness asymmetries have thus far been very successful in explaining some but not all cases of split sex ratios in social Hymenoptera (review in Queller and Strassmann 1998). The model developed here discloses another possible pathway for the evolution of this phenomenon. The possibility of strongly bimodal sex ratios resulting from the adoption of a mixed ESS by the

queens under very simple assumptions is a major result of this study. In view of this hypothesis, it would be of utmost interest to study the mechanisms underlying the queen's choice in monogyne *S. invicta* or in other species, wherever the primary sex ratio imposed by the queen determines the colony's sex allocation. Further theoretical developments of this model are also needed. We are now attempting, on the one hand, to include a limited life expectancy of the colonies and, on the other hand, to deal with bimodal sex ratios in more complicated genetic structures, such as the facultative oligogyny displayed by some ant species (Fournier et al. 2003).

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