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Foster, K.R. and Ratnieks, F.L.W. (2001) The effect of sex-allocation biasing on the evolution of worker policing in hymenopteran societies. *American Naturalist*, 158 (6). pp. 615-623. ISSN 0003-0147

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# The Effect of Sex-Allocation Biasing on the Evolution of Worker Policing in Hymenopteran Societies

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Submitted December 15, 2000; Accepted June 15, 2001

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**ABSTRACT:** Mutual policing is thought to be important in conflict suppression at all levels of biological organization. In hymenopteran societies (bees, ants, and wasps), multiple mating by queens favors mutual policing of male production among workers (worker policing). However, worker policing of male production is proving to be more widespread than predicted by relatedness patterns, occurring in societies headed by single-mated queens in which, paradoxically, workers are more related to the workers' sons that they kill than the queen's sons that they spare. Here we develop an inclusive-fitness model to show that a second reproductive conflict, the conflict over sex allocation, can explain the evolution of worker policing contrary to relatedness predictions. Among ants, and probably other social Hymenoptera, workers kill males to favor their more related sisters. Importantly, males are killed at the larval stage, presumably because workers cannot determine the sex of queen-laid eggs. Sex-allocation biasing favors worker policing because policing removes some males (the workers' sons) at low cost at the egg stage rather than at higher cost at the larval stage. Our model reveals an important interaction between two reproductive conflicts in which the presence of one conflict (sex allocation) favors the suppression of the other (male production by workers).

**Keywords:** mutual policing, worker policing, sex-allocation conflict, reproductive conflict, social insects.

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Mutual policing, where group members suppress each other's reproduction, is thought to have played an important role in the rise of biological complexity (Frank 1995; Maynard Smith and Szathmáry 1995; Keller 1999).

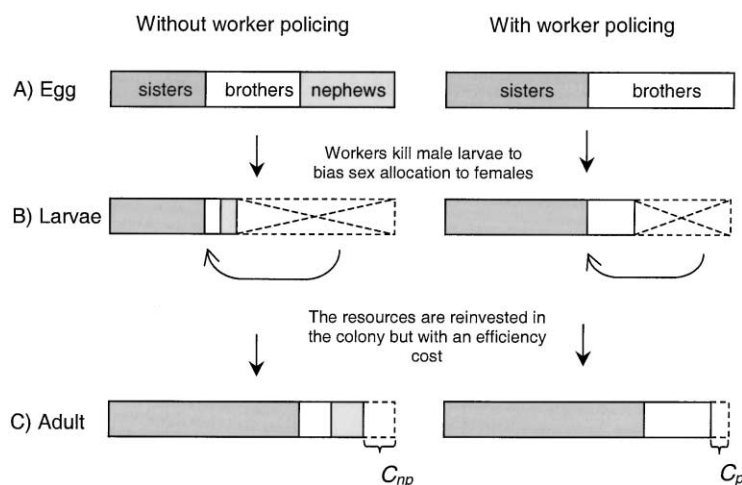
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Multiple mating by queens in the eusocial Hymenoptera (bees, ants, and wasps) is predicted to result in mutual policing of reproduction among workers (worker policing; Starr 1984; Ratnieks 1988; Crozier and Pamilo 1996). Although typically unable to mate, workers in most species can compete with the queen over male production by laying unfertilized eggs, which are male. However, in a colony with more than two worker patrines (effective paternity  $> 2$ ), workers are more related to the queen's sons (brothers;  $r = 0.25$ ) than to other workers' sons (nephews;  $r < 0.25$ ), so worker policing is selectively favored.

Consistent with theoretical prediction, worker policing by egg eating has been found in the multiple-mated honeybees *Apis mellifera*, *Apis cerana*, and *Apis florea* (Ratnieks and Visscher 1989; Barron et al. 2001), while in the typically single-mated stingless bees and bumblebees, worker policing appears to be absent because workers' sons are reared (van Honk et al. 1981; Estoup et al. 1995; Peters et al. 1999). In addition, evidence for worker policing has been found in multiple- but not single-paternity colonies of the wasp *Dolichovespula saxonica* (Foster and Ratnieks 2000). However, nonequal paternity in the offspring of some multiple-mated *D. saxonica* queens makes effective paternity  $< 2$ , so that workers are in fact slightly more related to nephews than brothers. Worker policing has also been found in the European hornet *Vespa crabro* (effective paternity = 1.11; Foster et al. 1999, 2002; Foster 2000) and the common wasp *Vespula vulgaris* (effective paternity = 1.90; Foster and Ratnieks 2001). Furthermore, worker policing occurs in three species of queenless ant, where, although genetic studies are required, it may also have evolved contrary to relatedness predictions (Gobin et al. 1999; Kikuta and Tsuji 1999; Liebig et al. 1999). In many colonies, therefore, workers are paradoxically causing the replacement of their more-related nephews ( $r > 0.25$ ) by less-related brothers.

In addition to conflict over male production, queen-worker conflict over sex allocation also occurs in hymenopteran societies (Hamilton 1964; Trivers and Hare 1976). Workers typically favor a more female-biased sex



**Figure 1:** How worker policing reduces the cost of sex-allocation biasing (i.e.,  $C_p < C_{np}$ ; eq. [5]). Three stages are shown. A, Egg stage, during which worker policing occurs and worker-laid eggs are targeted. B, Larval stage, during which sex-allocation biasing is performed by killing a proportion of the male brood (the final sex ratio shown is three females to one male). C, Adult stage, during which workers reinvest the resources from the killed male larvae into the remaining brood, but at an efficiency cost of 20%.

ratio than the queen. This is because workers are more related to the queen's daughters (sisters;  $r = 0.25 + 0.5/k$ , where  $k$  is effective paternity) than the queen's sons (brothers;  $r = 0.25$ ), while the queen is equally related to both sexes ( $r = 0.5$ ; Hamilton 1964; Trivers and Hare 1976). Consistent with worker-control of sex-allocation biasing, sex allocation in most ant species is female biased (Trivers and Hare 1976; Boomsma 1989; Pamilo 1990; Bourke and Franks 1995). In the few species where the mechanism of sex-allocation biasing by workers has been investigated, biasing occurs by the killing of males. Killing of male larvae has been demonstrated in the wood ant *Formica exsecta* (Sundström et al. 1996; Chapuisat et al. 1997) and the Argentine ant *Linepithema humile* (Aron et al. 1994; Passera and Aron 1996). In addition, evidence for the removal of males between the egg and pupae stages occurs in *Formica truncorum* (L. Sundström, personal communication), the fire ant *Solenopsis invicta* (Aron et al. 1995), and the ants *Myrmica tahoensis* (Evans 1995) and *Pheidole pallidula* (Keller et al. 1996). It has been suggested that workers remove male larvae rather than eggs because they are unable to identify the sex of eggs (Nonacs 1993). Evidence that workers have difficulty identifying the sex of young brood was provided by Nonacs and Carlin (1990), who showed that workers of the Florida carpenter ant *Camponotus floridanus* failed to discriminate the sex of brood until the pupal stage.

Here we consider the effect of the queen-worker conflict over sex allocation on the evolution of mutual policing among workers. We model a situation in which workers kill male larvae to bias sex allocation and examine the

conditions under which worker policing, that is, the killing of worker-laid male eggs, is selected. We show that sex-allocation manipulation can select for worker policing when the queen is singly mated because policing reduces the cost of male killing by removing some of the males at very low cost as eggs.

## The Model

### Overview

We consider a situation in which workers remove excess males to cause a female-biased sex-allocation ratio (fig. 1). They can either start killing males at the egg stage or in the larval stage. Consistent with the empirical data (above), we assume that in the egg stage the only eggs that they know to be male are those laid by workers. That is, workers cannot recognize the gender of queen-laid eggs, but they can recognize whether an egg is queen or worker laid. In the larval stage, we assume that workers can recognize the gender of larvae but not their maternal origin. The latter is supported by Ratnieks and Visscher (1989), who showed that honeybees accepted both workers' and queen's sons in the larval stage but preferentially killed workers' sons at the egg stage. We assume that there is a negligible cost in killing eggs but that larvae that are killed incur a cost of  $c$ . That is, only  $1 - c$  of energy in males can be reallocated by killing. The reinvested resources can be reallocated either to reproductives of both sexes (males and queens, as in fig. 1) or only to females (queens).

Our model reveals a novel benefit to worker policing.

In colonies with worker policing, the cost of sex-allocation biasing is reduced because some males are removed at low cost as eggs rather than at higher cost as larvae (fig. 1;  $C_p < C_{np}$ ).

### Inclusive-Fitness Equations

The model follows Pamilo's (1991a, 1991b) formulation of inclusive fitness and compares the "allocation component of fitness" ( $V$ ) of a nonlaying worker in a colony with worker policing to a nonlaying worker in a colony without worker policing. All parameters used in the model are shown in table 1. The allocation component of fitness is the sum of the fitness gained from each class of offspring or relative. With worker reproduction, there are three classes of reproductive relatives of the focal nonlaying worker: queen's daughters (the focal worker's sisters), queen's sons (the focal worker's brothers), and workers' sons (the focal worker's nephews), so that

$$V = \frac{g_s v_f x}{X} + \frac{(1 - W_c) g_b v_m y}{Y} + \frac{W_c g_n v_m y}{Y},$$

or

$$V = \frac{g_s v_f x}{X} + \frac{[(1 - W_c) g_b + W_c g_n] v_m y}{Y}, \quad (1)$$

where  $v_f$  and  $v_m$  are the sex-specific reproductive values of females and males,  $x$  and  $y$  are the proportional allocations to each sex in the focal colony,  $X$  and  $Y$  are the proportional

allocations to each sex in the whole population,  $W_c$  is the proportion of males in the colony that are workers' sons, and  $g_s$ ,  $g_b$ , and  $g_n$  are the regression relatednesses of sisters, brothers, and nephews to the focal worker. Worker policing will be selected if the inclusive fitness of the focal worker in a policing colony is greater than that of a focal worker in a nonpolicing colony.

First, we calculate the allocation component of fitness for a focal worker in nonpolicing ( $V_{np}$ ) and policing ( $V_p$ ) colonies :

$$V_{np} = g_s v_f + [(1 - W_c) g_b + W_c g_n] v_m, \quad (2)$$

$$V_p = g_s v_f + g_b v_m. \quad (3)$$

We assume that all colonies in the population have the same sex-allocation ratio, so that  $x = X$  and  $y = Y$  in equations (2) and (3), which cancels equation (1). (We discuss the effect of relaxing this assumption below.) Next, we incorporate an efficiency cost of sex allocation ( $C$ ):

$$C = y_{\text{change}} c, \quad (4)$$

where  $c$  is the inefficiency of energy transfer between the killed larval males and the colony and  $y_{\text{change}}$  is the change in the proportional allocation to males (change in male allocation as a proportion of all the brood). We can now compare the inclusive fitness of nonlaying workers in policing versus nonpolicing colonies ( $B_{\text{policing}}$ ):

$$B_{\text{policing}} = (1 - C_p) V_p - (1 - C_{np}) V_{np}, \quad (5)$$

**Table 1:** Parameters and variables used in the model

Value	Description
$V_{np}, V_p$	Allocation component of fitness in nonpolicing and policing colonies
$g_s, g_b, g_n$	Relatedness of focal worker to sisters, brothers, and nephews
$v_f, v_m$	Sex-specific reproductive values of females and males
$x, y$	Proportions of colony sex allocation to females and males
$X, Y$	Proportions of population sex allocation to females and males
$W_c$	Proportion of males that are workers' sons in the colony
$W_{\text{pop}}$	Proportion of males that are workers' sons in the population
$y_{\text{change}}$	Reduction in the allocation to males by male killing as a proportion of all the brood
$c$	Proportion of the energy invested in an adult male that is lost if he is killed
$B_{\text{policing}}$	Difference in inclusive fitness of a worker in a policing versus a nonpolicing colony
$C_p, C_{np}$	Proportional reduction in total colony productivity resulting from male killing
$k$	Effective paternity in colonies and the population
$w$	Proportion of eggs that are laid by workers
$x_q, y_q$	Proportions of queen-laid eggs that are female and male
$x_1, y_1$	Proportions of females and males before sex-allocation biasing
$x_2, y_2$	Proportions of adult females and males after sex-allocation biasing
$P$	Frequency of policing colonies versus nonpolicing colonies
$X_{\text{opt}}$	Stable sex-allocation ratio for workers

where  $C_p$  and  $C_{np}$  are the costs of sex allocation in policing and nonpolicing colonies, and, conversely,  $1 - C_p$  and  $1 - C_{np}$  are the relative productivity of each colony type. Worker policing is selected when  $B_{\text{policing}}$  is positive.

*Model Parameters*

We now have an equation that calculates the fitness effect of worker policing in colonies where sex-allocation biasing occurs. We are interested in the effect of six key factors on  $B_{\text{policing}}$ , which need to be incorporated into equations (2)–(5):  $k$  (effective paternity; the basis of the original worker policing predictions; Ratnieks 1988),  $c$  (cost of recycling male larvae),  $w$  (amount of worker laying, as this varies greatly between species; Bourke and Franks 1995),  $x_q$  (primary sex ratio of queen-laid eggs—the proportion of eggs that are female),  $x_2$  (final allocation to females, after workers have performed sex-allocation biasing), and  $P$  (proportion of policing colonies in the population). We now define the values in equations (2)–(5) in terms of these factors.

*Regression relatedness* (Hamilton 1970; Grafen 1985). We base the model on single-queen societies because colony kin structure can be defined in terms of a single variable, “effective paternity,” itself determined by queen mating frequency and sperm use (Boomsma and Ratnieks 1996). However, the method is also applicable to multiple-queen societies where relatedness patterns that favor policing or disfavor policing also occur dependent on the number and relatedness of queens (Pamilo 1991b):

$$g_s = 0.25 + 0.5(1/k), \tag{6a}$$

$$g_b = 0.5, \tag{6b}$$

$$g_n = 0.25 + 0.5(1/k). \tag{6c}$$

*The proportion of males in the population that are workers’ sons* ( $W_{\text{pop}}$ ). This is dependent on two factors: the proportion of males that are workers’ sons in the nonpolicing colonies  $W_c$  (fig. 2),

$$\begin{aligned} W_c &= \frac{w}{w + (1 - w)y_q} \\ &= \frac{w}{w + (1 - w)(1 - x_q)}, \end{aligned} \tag{7a}$$

and the frequency of policing colonies ( $P$ ), for which we assume that no workers’ sons are reared, versus nonpolicing colonies ( $1 - P$ ),

$$W_{\text{pop}} = (1 - P)W_c. \tag{7b}$$

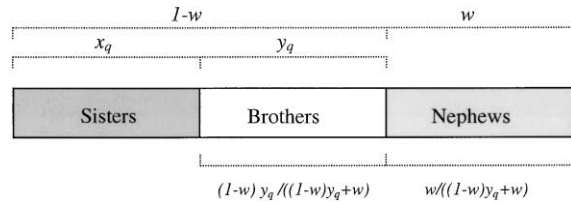


Figure 2: The proportion of males that are workers’ sons if the workers lay a proportion  $w$  of the total eggs,  $x_q$  of the queen’s eggs are female, and  $y_q = 1 - x_q$  are male ( $W_c$ ; eq. [7a]).

*Reproductive value* (Fisher 1930). When all males in the population are queen’s sons, females have twice the reproductive value of males because males contribute only genes to females of the next generation. With worker reproduction, however, father males also contribute genes to males, thereby raising male reproductive value (see Bourke and Franks 1995 and Crozier and Pamilo 1996 for a summary of reproductive value and relatedness):

$$v_f = 1, \tag{8a}$$

$$v_m = \frac{1}{2 - W_{\text{pop}}}. \tag{8b}$$

*The amount of male killing needed to change the primary sex ratio to the sex ratio after sex-allocation biasing* ( $y_{\text{change}}$ ; eq. [4]). The primary sex allocation to females (fig. 2) is

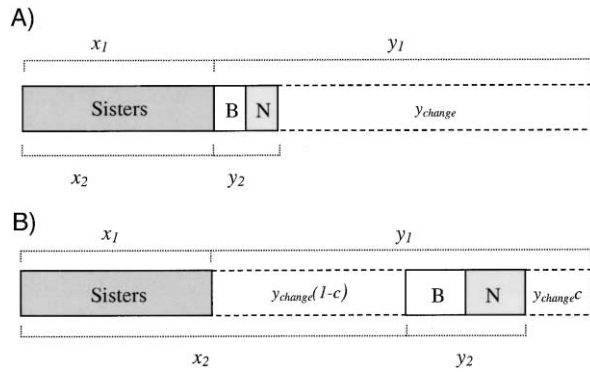
$$x_1 = (1 - w)x_q, \tag{9}$$

where  $w = 0$  in policing colonies. We consider the two extreme cases of male reinvestment into reproductives of both sexes or only into queens: first, if resources are reinvested into reproductives of both sexes (fig. 3A)

$$\begin{aligned} \frac{(y_1 - y_{\text{change}})}{x_1} &= \frac{y_2}{x_2}, \\ y_{\text{change}} &= 1 - \frac{x_1}{x_2}, \end{aligned} \tag{10a}$$

and, second, if resources are reinvested only into queens (fig. 3B),

$$\begin{aligned} \frac{y_1 - y_{\text{change}}}{x_1 + (1 - c)y_{\text{change}}} &= \frac{y_2}{x_2}, \\ y_{\text{change}} &= \frac{x_2 - x_1}{1 + cx_2 - c}. \end{aligned} \tag{10b}$$



**Figure 3:** Calculation of  $y_{\text{change}}$ , the number of males that must be killed to produce a given secondary sex-allocation ratio. Values  $x_1$  and  $y_1$  are the proportions of females and males before, and  $x_2$  and  $y_2$  after, sex-allocation biasing. A, Sex allocation with reinvestment back into the colony as a whole (eq. [10a]). B, Sex allocation with reinvestment back into females (eq. [10b]). Reinvestment of a proportion  $y_{\text{change}}$  of the males results in the production of  $(1-c)y_{\text{change}}$  new brood (females and males in A and females only in B) and a waste of  $y_{\text{change}}c$ .

The stable sex-allocation ratio for workers ( $X_{\text{opt}}$ ). The stable sex-allocation ratio for workers is determined by the relative kin value of males versus females (Fisher 1930; Trivers and Hare 1976; Benford 1978; Pamilo 1991a):

$$X_{\text{opt}} = \frac{gf.vf.}{gf.vf. + [v_m(1 - W_{\text{pop}})g_b + W_{\text{pop}}g_n]}. \quad (11)$$

## Results

The equations were combined, and  $B_{\text{policing}}$  was evaluated using Mathematica 3.0 (Wolfram Research 1996; fig. 4). Our aim was to determine the effect of the cost of sex-allocation biasing  $c$  on the paternity frequency at which worker policing is selected (when  $B_{\text{policing}} > 0$ ) and to see how robust the results are with respect to parameters  $w$ ,  $x_2$ ,  $x_q$ , and  $P$ . Unless otherwise stated, the results are for  $c = 0.1$  (10% of the investment in a male that is killed cannot be recovered),  $w = 0.5$  (half of all eggs are laid by workers),  $x_q = 0.5$  (the queen lays eggs at an equal sex ratio),  $x_2 = X_{\text{opt}}$  (colony and population sex allocation is at the worker optimum),  $P = 0$  (worker policing is invading), and  $y_{\text{change}}$  is for killed male larvae reinvested into both females and males.

### Cost of Sex-Allocation Biasing (Fig. 4A)

Introducing an efficiency cost of 10% or 20% to the recycling of males killed during sex allocation has a large effect on the threshold at which worker policing is favored.

An efficiency cost of  $>23\%$  results in policing being favored at all paternities. With no efficiency cost, the classic result that worker policing is selected when effective paternity is  $>2$  (Starr 1984; Ratnieks 1988) is recovered.

### Reinvestment Directly into Females (Fig. 4B)

If killed males are reinvested directly into new queens, the benefit of worker policing is reduced. That is, for a given efficiency cost ( $c$ ), the paternity at which worker policing is favored is higher than in figure 4A. This is expected because reinvestment directly into queens makes sex-allocation biasing by male larvae killing more efficient, thereby reducing the benefit of worker policing.

### The Amount of Worker Laying (Fig. 4C)

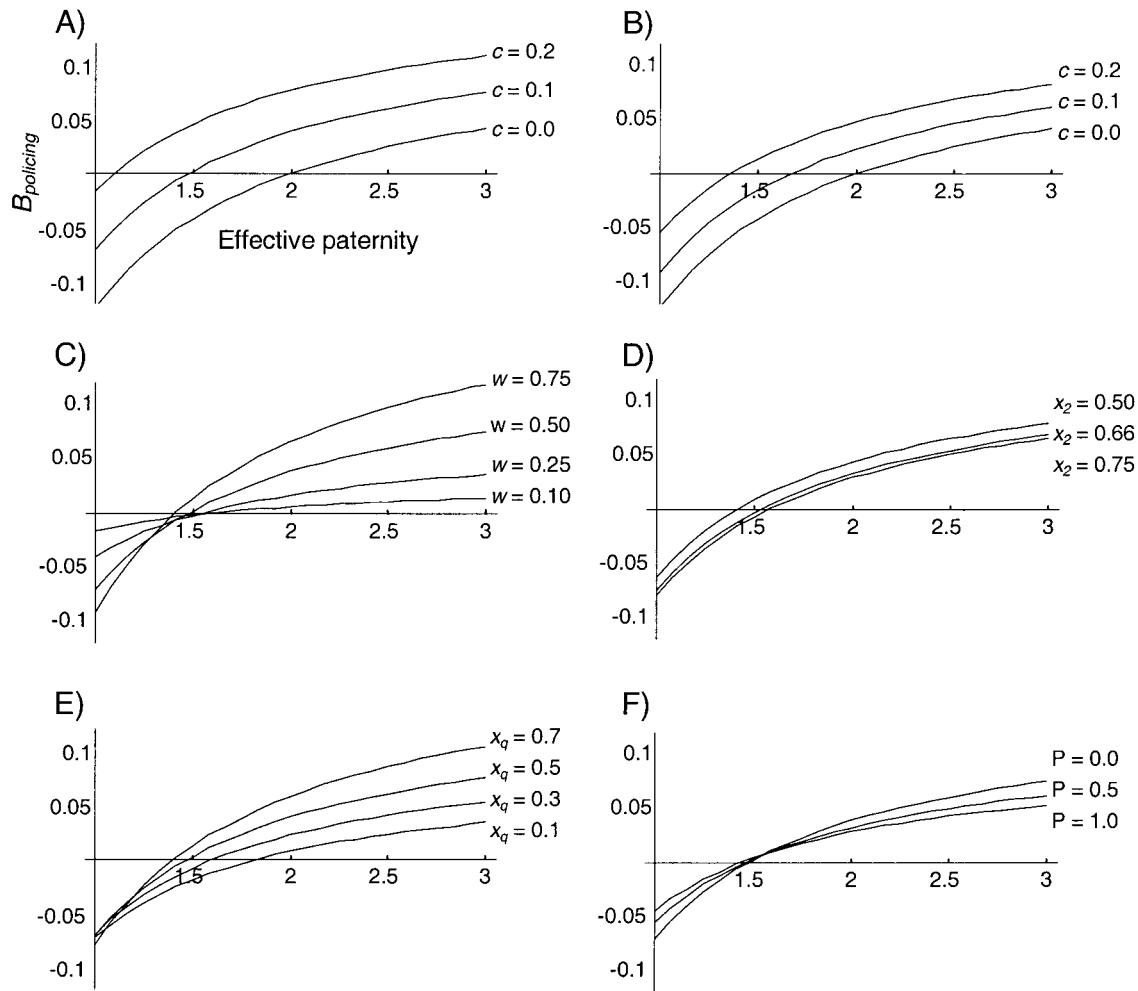
Worker policing is favored by increased worker egg laying. This is because more worker-laid eggs results in more male larvae to kill, which raises the cost of sex-allocation biasing in nonpolicing colonies. Importantly, worker policing is always selected for at paternities  $<2$  at all levels of worker reproduction. This is logical because worker policing of eggs can only reduce the cost of killing male larvae.

### The Proportion of Females Raised by the Workers (Fig. 4D)

The final sex-allocation ratio slightly affects the paternity frequency at which policing is favored. The more female biased the final sex-allocation ratio (closer to the worker optimum), the more difficult it is for worker policing to evolve. This is because a female bias requires more male killing in both policing and nonpolicing colonies, which decreases the difference in the amount of male larvae killing in nonpolicing versus policing colonies. That is,  $C_{\text{np}} - C_{\text{p}}$  is slightly reduced (see fig. 1), which reduces the relative benefit of worker policing.

### The Proportion of Female Eggs Laid by the Queen (Fig. 4E)

Figure 4E shows that if the queen lays a male-biased sex ratio, the benefit of worker policing is reduced. As with a female-biased final sex ratio (fig. 4D), a male-biased primary sex ratio causes more killing of male larvae in both policing and nonpolicing colonies, thereby decreasing the difference between the two colony types.



**Figure 4:** A, Effect of an efficiency cost of male killing,  $c$ , on the paternity frequency at which worker policing is selected. Positive values of  $B_{\text{policing}}$  indicate a benefit to nonlaying workers from worker policing. With no cost ( $c = 0$ ), the classic worker-policing result that workers will police at effective paternity  $>2$  is recovered (Ratnieks 1988). B, Resources reinvested directly into new queens. C, Effect of the amount of worker laying. D, Effect of the final sex-allocation ratio. E, Effect of the queen-laid sex ratio. F, Effect of the frequency of colonies with worker policing in the population. Unless otherwise stated, killed males are reinvested into both sexes;  $c = 0.1$ ,  $w = 0.5$ ,  $x_2 = X_{\text{opt}}$ ,  $x_q = 0.5$ , and  $P = 0$ .

#### *The Frequency of Worker Policing in the Population (Fig. 4F)*

The frequency of policing colonies in the population has little effect on the paternity at which policing is selected. There is, however, a difference in the gradient of the curves in figure 4F. This is because worker policing ( $P > 0$ ) reduces male production by workers, which lowers the reproductive value of males (eq. [8]). This reduces the allocation component of fitness of workers ( $V$ ; eq. [1]) in all colonies and decreases the magnitude of  $B_{\text{policing}}$  at all paternitys.

#### **Discussion**

The results show that worker policing can be selected at low paternity when worker sex-allocation biasing by the killing of male larvae occurs. That is, worker policing is favored even when workers are more related to other workers' sons than to the queen's sons. Worker policing is favored because it reduces the cost of sex-allocation biasing by removing males at low cost in the egg stage. This conclusion is robust whether reinvestment of killed males is into both sexes or into young queens alone, for any amount of worker laying, at both the queen and worker sex-allocation optima, when policing is either rare or com-

mon, and for all but extremely male-biased primary sex ratios of queen-laid eggs ( $x_q < 0.1$ ; fig. 4).

Our model does not consider costs to either worker reproduction or worker policing. If worker reproduction reduces colony productivity, this will also favor the evolution of policing, and, like the effect shown in our model, this can also cause policing to evolve at low paternity (Ratnieks 1988). A cost to worker policing itself, conversely, will disfavor its evolution. However, such costs do not affect our prediction that sex-allocation biasing facilitates the evolution of worker policing, except in the extreme case that worker policing is more costly than male larvae killing. This is highly unlikely given that much more energy will be lost from killing larvae than eggs, while other costs, such as searching the brood, are likely to be comparable.

The paternity frequency at which policing is favored is critically dependent on the amount of investment into males that can be recovered by killing. For our parameter values, a loss of  $>23\%$  results in worker policing being favored at all paternities, that is, irrespective of relatedness to males. The amount of energy lost through male killing is dependent on four key factors: first, metabolic efficiency, which is the percentage of energy consumed that is incorporated into new biomass; second, the amount of energy in males at the time of their execution, with less energy lost the earlier that males are killed; third, the labor cost of rearing males, which is permanently lost; and, fourth, accuracy of worker recognition of the sex of larvae. If workers sometimes mistakenly kill females during sex-allocation biasing, the cost of sex-allocation biasing will increase. The importance of the third and fourth factors are unknown. However, given that metabolic efficiency in carnivorous insects is around 45% (Begon et al. 1990; Chapuisat et al. 1997) and male killing sometimes occurs late in the larval stage (Chapuisat et al. 1997), a loss greater than 20% seems realistic and is probably an underestimate.

Extension of the theory of worker policing was inspired by the Vespinae wasps, whose worker policing by egg eating occurs at paternities  $< 2$  (Foster 2000; Foster and Ratnieks 2000, 2001) and with whom female-biased sex allocation occurs (Edwards 1980; Archer 1998). However, with female-biased sex allocation common in eusocial Hymenoptera (Pamilo 1990), the potential for this interaction between worker sex-allocation biasing and policing is widespread.

Our model assumes that all colonies have the same sex allocation. This is not always true. When colonies in the same population vary in paternity, it is predicted that workers in low-paternity colonies benefit from specializing in females, while workers in higher-paternity colonies benefit by investing in males, which results in split sex ratios (Boomsma and Grafen 1990, 1991; Ratnieks 1991). This

pattern has been found in several species (Queller and Strassmann 1998), including the ants *Formica truncorum* (Sundström 1994a, 1994b) and *Formica exsecta* (Sundström et al. 1996) and the wasp *Dolichovespula arenaria* (F. L. W. Ratnieks and J. J. Boomsma, unpublished data). Facultative sex-allocation biasing also occurs when colonies vary in the number of queens in the ants *Myrmica tahoensis* (Evans 1995) and *Leptothorax acervorum* (Chan and Bourke 1994) and five epiponine wasp species (Queller et al. 1993; Hastings et al. 1998), which is in line with relatedness predictions.

The effect of facultative sex-allocation biasing on our predictions is best understood by considering the two types of colony, low paternity and high paternity, separately. In the low-paternity colonies, workers kill male larvae to bias allocation to females. As in our model, this will select for worker policing even though relatedness does not predict it. Because paternity is so low in these colonies, however, a relatively high cost to male killing is required for worker policing to evolve ( $c > 0.23$  for single paternity with our parameter values; fig. 4A). Workers in high-paternity colonies favor male-biased sex allocation, which means that less and maybe no male killing occurs (depending on the amount of worker laying  $w$  and the final allocation to females  $x_2$ ). This will reduce or remove the additional benefit to worker policing predicted by our model. However, the high paternity in these colonies increases the likelihood of worker policing due to relatedness patterns alone (Ratnieks 1988; Foster and Ratnieks 2000). Overall, facultative sex-allocation biasing will also favor the evolution of worker policing. With a high cost to male killing required in low-paternity colonies and possibly no male killing in high-paternity colonies, however, the conditions where policing will evolve are likely to be more restrictive, or at least more specific, than in our model.

This study shows the value of considering reproductive conflicts simultaneously as actually occurs in nature rather than one at a time. Our model reveals a condition under which sex allocation and male production cannot be treated separately. This study also shows the importance of considering specific details of reproductive biology, such as the timing of male killing, which is itself caused by limitations in the ability of workers to recognize the gender of brood (otherwise they would kill the queen's male eggs). Although general inclusive-fitness models are very important (Hamilton 1964), the theory should be applied with care and must often be combined with specific knowledge of the study species and the constraints on the recognition mechanisms needed to manipulate reproduction (Keller 1997).



### Acknowledgments

We thank H. Helanterä, J. M. Herbers, T. Wenseleers, and two anonymous referees for helpful advice. Funding for this study was provided by a Biotechnology and Biological Sciences Research Council Ph.D. studentship to K.R.F.

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