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Source: *The American Naturalist*, Vol. 184, No. 3 (September 2014), pp. 303-317

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/677283>

Accessed: 18/09/2014 05:51

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Haplodiploidy and the Evolution of Eusociality: Worker Revolution

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Submitted August 5, 2013; Accepted March 7, 2014; Electronically published August 4, 2014

Online enhancements: appendices.

ABSTRACT: Hamilton suggested that inflated relatedness between sisters promotes the evolution of eusociality in haplodiploid populations. Trivers and Hare observed that for this to occur, workers have to direct helping preferentially toward the production of sisters. Building on this, they proposed two biological scenarios whereby haplodiploidy could act to promote the evolution of eusociality: (a) workers biasing the sex allocation of the queen's brood toward females and (b) workers replacing the queen's sons with their own sons. This "worker revolution," whereby the worker class seizes control of sex allocation and reproduction, is expected to lead to helping being promoted in worker-controlled colonies. Here, we use a kin-selection approach to model the two scenarios suggested by Trivers and Hare. We show that (1) worker control of sex allocation may promote helping, but this effect is likely to be weak and short lived; and (2) worker reproduction tends to inhibit rather than promote helping. Furthermore, the promotion of helping is reduced by a number of biologically likely factors, including the presence of workers increasing colony productivity, workers being unmated, and worker control of sex allocation being underpinned by many loci each having a small effect. Overall, our results suggest that haplodiploidy has had a negligible influence on the evolution of eusociality.

Keywords: kin selection, sex allocation, inclusive fitness, social evolution, helping, altruism.

Introduction

The eusocial world is dominated by the social Hymenoptera: the ants, bees, and wasps (Crozier 2008). Hamilton (1964, 1972) suggested that this owes to their haplodiploid genetics, whereby unfertilized (haploid) eggs develop into males and fertilized (diploid) eggs develop into females. All workers are female, and haplodiploidy leads to a worker being more related to her full sisters (life-for-life relatedness $R = 3/4$, assuming unbiased sex allocation) than

to her own daughters ($R = 1/2$). That is, the worker would prefer to rear a sister instead of a daughter, all else being equal. However, things are not so simple, because haplodiploidy also makes a worker less related to her brothers ($R = 1/4$) than to her sons ($R = 1/2$). Thus, with an unbiased sex allocation, the average relatedness to siblings is exactly equal to the average relatedness to offspring ($R = 1/2$; Hamilton 1972; Trivers and Hare 1976). Furthermore, while a female-biased sex ratio would lead to workers rearing more sisters, the subsequent increase in relatedness is exactly negated by the fact that a female-biased sex ratio also increases the mating success of males, making females worth relatively less (Trivers and Hare 1976; Craig 1979; Iwasa 1981).

Trivers and Hare (1976) suggested Hamilton's "haplodiploidy hypothesis" could be rescued in two ways. First, they showed that the higher relatedness between two sisters ($R = 3/4$) than between a female and her brother ($R = 1/4$) means that workers will be favored to bias the sex allocation of their colony toward females. They suggested that, as helping spreads through a population, an association between helping and the production of female-biased broods would increase the relatedness of workers to the siblings that they were helping rear, without the overall population sex ratio becoming sufficiently female biased to completely negate this relatedness benefit. Second, they suggested that workers might replace the queen's sons with their own sons. This could further raise the relatedness between workers and the offspring that they help to rear, because they are more related to the sons of their sisters (nephews, $R = 3/8$) than to the sons of their mother (brothers, $R = 1/4$).

Trivers and Hare's (1976) article has been hugely influential. In particular, a number of relatively general models have shown that an association between helping and the production of relatively female-biased broods, termed "split sex ratios," promotes helping (Charnov 1978; Charlesworth 1980; Iwasa 1981; Grafen 1986; Boomsma

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and Grafen 1990, 1991; Pamilo 1991, Crozier and Pamilo 1993). However, we now have a better understanding of the life histories associated with the evolution of eusociality (West 2009; Boomsma et al. 2011), allowing us to ask more specific questions about the relative magnitude of the haplodiploidy effect in the most biologically relevant scenarios (e.g., monogamy, subsociality, sex allocation; Boomsma 2007, 2009; Hughes et al. 2008; West 2009; Boomsma et al. 2011). Biological details matter, because they will determine how helping is associated with the brood sex ratio but also because factors such as biased sex allocation and worker reproduction have multiple consequences for genetic similarity of nestmates and the reproductive values of different classes of individuals.

Here, we examine Trivers and Hare's (1976) version of the haplodiploidy hypothesis and determine the magnitude of the effect of haplodiploidy, in different biological scenarios. We model the evolution of altruistic helping, where a worker rears her colony's offspring instead of her own. We focus on the two scenarios suggested by Trivers and Hare: workers' control of the colony sex ratio spreading through a population and workers replacing the queen's sons with their own. We consider the consequences of variation in biological details that could alter the association between helping and biased sex ratios, such as the underlying genetics, strength of selection, extent of worker reproduction, and rate of sex ratio evolution. We focus on the two Trivers and Hare (1976) scenarios because these have been so influential and because we have already examined the other factors that could lead to split sex ratios elsewhere, finding them unlikely to have played a major role in the evolution of eusociality (Gardner et al. 2012a, 2012b; Alpedrinha et al. 2013). In addition, they are different classes of scenarios, in that Trivers and Hare (1976) focused on how split sex ratios may arise transiently, as worker control spreads, whereas other scenarios involve split sex ratios being maintained at equilibrium, as evolutionarily stable strategies (reviewed by Gardner et al. 2012a).

Methods

In the following sections, we study the evolution of altruistic helping by investigating the impact that the emergence and spread of helpers and worker control of sex allocation has on the genetic structure of the population and the adaptive value of altruistic helping. We then consider the emergence of worker reproduction in populations where both the presence of helpers and also worker control are already established. We consider three scenarios by which worker reproduction could occur: replacing brothers with sons, replacing sisters and brothers with sons, and replacing sisters and brothers with sons and daughters.

The evolution of eusociality is a highly complex long-term process in which many traits coevolve in a coordinated fashion to bring about a new level of individuality. This complexity and the fact that costs and benefits of helping are themselves expected to evolve over such time-scales mean that it is inappropriate to perform an analysis of the evolutionary stable level of worker altruism. Instead, we investigate the evolutionary incentive of a female who is deciding whether to help rear b additional juveniles in her mother's nest at a personal cost of c own offspring (this may or may not involve the female giving up all of her personal reproduction). We consider scenarios where the juveniles that the worker could help raise in her mother's nest are siblings or a mixture of siblings and nephews/nieces.

Hamilton (1972) showed that the value of a social partner to a focal actor is measured by how well the former transmits copies of the latter's genes to future generations. This is the product of two quantities: the concentration of the actor's genes in the recipient, termed consanguinity (p ; Bulmer 1994), and the expected asymptotic genetic contribution made by the recipient to future generations, termed reproductive value (v ; Fisher 1930). We assume weak selection, which allows us to calculate quasi-equilibrium values for these quantities (Taylor 1996, Taylor and Frank 1996). We denote the sex ratio (proportion male) among the juvenile reproductives in the mother's nest as z_c and the sex ratio of workers who decide to breed independently as z_o . The worker has an average consanguinity p_m to the juvenile males in her mother's nest, p_f to the juvenile females in her mother's nest, p_s to her sons and p_d to her daughters. We calculate these coefficients of consanguinity in terms of population parameters in appendix A (apps. A–D available online). The reproductive values of juvenile reproductive males and females are v_m and v_f , respectively, and we calculate these in terms of population parameters in appendix B. Table 1 summarizes the notation we use in this article.

Helping increases the worker's inclusive fitness when the value of the extra juveniles reared by the worker outweighs the value of the offspring that she could have produced had she bred independently, that is, when $b[z_c p_m v_m + (1 - z_c) p_f v_f] > c[z_o p_s v_m + (1 - z_o) p_d v_f]$. We may rewrite this condition as $c/b < \alpha$, where α defines the "potential for helping" (Gardner et al. 2012a) and is given by

$$\alpha = \frac{z_c p_m v_m + (1 - z_c) p_f v_f}{z_o p_s v_m + (1 - z_o) p_d v_f}. \quad (1)$$

The potential for helping (α) represents the threshold value of c/b at which the worker is indifferent between raising juveniles in her mother's nest versus her own off-

Table 1: Summary of model notation

Symbol	Definition
z	Population sex ratio
z_C	Colony offspring sex ratio
z_O	Sex ratio strategy of a focal worker breeding independently (new colony)
z_Q	Queen-controlled colony sex ratio strategy for queen-derived offspring
z_W	Worker-controlled colony sex ratio strategy for queen-derived offspring
z_A	Sex ratio strategy of workers for worker-derived offspring
h	Proportion of colonies with workers
μ	Proportion of worker reproduction in the population
v	Proportion of colonies where queen-derived offspring is worker controlled
ϕ	Paternal kinship index. The probability that any two sperm cells present in the queen spermatheca derive from the same male
p	Consanguinity of an outbred female to herself; $p = 1/2$
p_x	Consanguinity between a focal female and a reproductive individual $x \in \{D, S, F, M, Ni, Ne\}$, present in the same colony
r	Regression coefficient of relatedness of a relative Y to the actor X ($r = p_{YX}/p_{XX}$): the consanguinity of the actor and recipient (p_{YX}) divided by the consanguinity of the actor to herself (p_{XX})
$R_{x,W}$	Life-for-life relatedness coefficient of a relative Y ($Y \in \{D, S, F, M, Ni, Ne\}$) to a worker W; $R_{Y,W} = [(p_{Y,W}/p_{W,W}) \times (V_Y/V_P)]$
v_m	Value of a male, given by the class reproductive value c_m over the number of males in the population z
v_f	Value of a female, given by the class reproductive value c_f over the number of females in the population $1 - z$
c_m	Male class reproductive value
c_f	Female class reproductive value
N	Total number of individuals in the population
K	Number of colonies in the population
f	Female
m	Male
D	Daughter
S	Son
F	Sister
B	Brother
Ni	Niece
Ne	Nephew

spring in her own nest (Charnov 1978; Grafen 1986). The reciprocal of this quantity ($1/\alpha$) coincides with Iwasa's (1981) "sociality threshold" and Pamilo's (1991) "efficiency threshold." In an outbred diploid population, strict monogamy leads an individual to be equally related to her siblings and her own offspring, such that helping is favored when $d/b < 1$. Hence, haplodiploidy promotes the evolution of helping (relative to diploidy) if $\alpha > 1$ and inhibits the evolution of helping if $\alpha < 1$. Throughout our analysis, we will assume outbreeding. In addition, while we present general results for the potential for helping (α), allowing for both single and multiple mating ($0 \leq \phi \leq 1$, where ϕ is the consanguinity of the sperm cells that are used to fertilize the queen's eggs; e.g., $\phi = 1/n$ if the queen uses an equal amount of sperm from n unrelated males), we focus on monogamy ($\phi = 1$). We do this because (1)

while both inbreeding and monogamy increase relatedness within the colony, hymenopteran eusociality has evolved only in outbred monogamous populations (Boomsma 2007, 2009; Hughes et al 2008); and (2) multiple mating reduces relatedness between maternal siblings and hence reduces selection for cooperation (Charnov 1982).

Often, it is convenient to express genetic similarity in terms of coefficients of relatedness, rather than coefficients of consanguinity. Throughout this article, we use Hamilton's (1970) regression coefficient of relatedness ($r = p'/p$), which is simply the consanguinity of the actor and recipient (p') divided by the consanguinity of the actor to herself (p ; Bulmer 1994). The consanguinity of a female and her full sister is $p_f = 3/8$, and the consanguinity to herself is $p = 1/2$ (app. A); hence, the relatedness to her full sister is $r = (3/8)/(1/2) = 3/4$. Similarly, consan-

guinity of a female and her brother is $p_M = 1/4$ (app. A), and so the relatedness to her brother is $r = (1/4)/(1/2) = 1/2$. This regression form provides the general definition of relatedness (Grafen 1985), which is at the heart of modern theoretical methodology (Taylor and Frank 1996; Frank 1998; Grafen 2006; Rousset 2004), and is the basis for how relatedness is measured in empirical studies, using molecular markers such as a microsatellites (Queller and Goodnight 1989). The relationship between regression relatedness and life-for-life relatedness are discussed by Gardner et al. (2012a).

Split Sex Ratios and Helping

We first consider a general model for the evolution of altruistic helping. We consider a population with negligible worker reproduction ($\mu = 0$) to determine the potential for helping when the sex ratio among the focal worker's offspring is z_O , the colony z_C and the population average \bar{z} . Substituting the appropriate consanguinities and reproductive values (apps. A and B) into equation (1), we obtain

$$\alpha = \frac{z_C - 2\bar{z}z_C(1 + \phi) + \bar{z}(1 + 2\phi)}{2\bar{z} + 2z_O - 4\bar{z}z_O}. \quad (2)$$

This allows us to assess the overall impact of the sex ratio (z_O, z_C, \bar{z}) on the potential for helping. If we assume that there is no variation in sex allocation across colonies ($z_C = z_O = \bar{z}$), then we find that the potential for helping is unity ($\alpha = 1$), irrespective of the population sex ratio ($0 < \bar{z} < 1$). That is, in the absence of split sex ratios, haplodiploidy neither promotes nor inhibits the evolution of helping (Grafen 1986).

In contrast, if different colonies exhibit different sex ratios ($z_O \neq z_C$), then we find that haplodiploidy can either promote ($\alpha > 1$) or inhibit ($\alpha < 1$) the evolution of helping. First, assuming only minor variation across colonies ($z_C \approx z_O \approx \bar{z}$), we find that if the sex ratio among the offspring in the individual's mother's colony is female biased relative to the population average, then helping is promoted, except in populations with extreme female bias ($\partial\alpha/\partial z_C|_{z_C=z_O=\bar{z}} < 0$ if $\bar{z} > 1/4$). This is because workers are more related to their sisters than to their brothers, so all else being equal, the value of a sibling is higher than the value of a worker's own offspring. However, this effect is counterbalanced by an increase in the reproductive value of males, if the population sex ratio is female biased. If the sex ratio of the population is strongly female biased ($\bar{z} < 1/4$), then helping is promoted in colonies where the sex ratio is less female biased than the population as a whole ($\partial\alpha/\partial z_C|_{z_C=z_O=\bar{z}} > 0$ if $\bar{z} < 1/4$).

Second, if the worker can bias her own offspring sex ratio toward the rarer sex, then this makes her own off-

spring relatively more valuable and hence inhibits helping (Iwasa 1981; Pamilo 1991). Specifically, if the population consists mainly of males, the potential for helping decreases as the worker produces more sons over daughters ($\partial\alpha/\partial z_O|_{z_C=z_O=\bar{z}} > 0$ if $\bar{z} < 1/2$ and $\partial\alpha/\partial z_O|_{z_C=z_O=\bar{z}} > 0$ if $\bar{z} > 1/2$). Third, we find that the potential for helping increases with increasing population male bias in sex allocation ($\partial\alpha/\partial \bar{z}|_{z_C=z_O=\bar{z}} > 0$ for all $0 < \bar{z} < 1$). That is, if the sex allocation among the worker's own offspring and among her siblings are both slightly female biased relative to the population average, then this promotes the evolution of helping. These results illustrate that haplodiploidy can promote or inhibit the evolution of helping, depending on the inclusive fitness value of own versus the colony offspring, which is determined by sex allocation.

Worker Control of Sex Allocation

We now consider the early evolution of the eusociality scenario envisaged by Trivers and Hare (1976, pp. 251–252), where helping already occurs in some colonies but not in others. Trivers and Hare (1976) argued that as worker control of sex allocation spreads through a population, this worker revolution over the control of sex allocation allows haplodiploidy to promote the evolution of eusociality. Their scenario involves the following steps.

Step 1: some daughters stay and help their mothers, rather than breeding independently. Step 2: the queen allocates equal resources into male and female offspring. Step 3: a mutation (or a small number of mutations) occurs that allows workers to bias the sex ratio of the brood that they are helping to raise toward females (sisters). Step 4: while the mutation is spreading, colonies that contain workers with the mutation will be raising broods of reproductive offspring that are biased toward females, relative to the population as a whole. Step 5: consequently, these workers gain the relatedness benefit of rearing a greater proportion of sisters, without this being exactly canceled by an increased reproductive success of males, and so workers are favored to increase altruistic helping. Step 6: as worker control spreads, workers evolve specialized adaptations to cooperative breeding, which increases the efficiency benefit of cooperation (lower c/b , which helps drive the evolution of eusociality).

This scenario focuses on the early stages of evolution toward eusociality, when both the presence of workers and worker control over the sex ratio need not be fixed in the population. We assume that a juvenile female has the opportunity to either stay at her mother's colony and help rear siblings or leave her mother's colony to start a new colony of her own. We assume that (a) a proportion h of colonies contain workers and a proportion $1 - h$ of colonies are workerless and (b) a proportion v of colonies

that contain workers have their sex allocation controlled by those workers, whereas a proportion $1 - v$ of colonies that contain workers have their sex allocation controlled by the queen. All workerless colonies have their sex allocation controlled by the queen. We denote the sex ratio of worker-controlled colonies by z_w and the sex ratio of queen-controlled colonies by z_q .

We assume that any differences in productivity between colonies with and without workers are negligible, and so the average sex allocation in the population is $\bar{z} = hvz_w + (1 - hv)z_q$. We make this assumption for ease of analysis and also because we wish to consider the best-case scenario for the evolution of helping—differences in productivity would reduce the effective variance in sex-allocation strategies in the population, leading to lower potential for helping and hence inhibit helping (Abugov 1981; Iwasa 1981; Andersson 1984; Grafen 1986; Pamilo 1991; Gardner et al. 2012a). From equation (1), it is clear that the potential for helping depends on the population sex ratio (and also on the colony sex ratio, if helping is facultative). However, the proportion of colonies with helpers h also affects sex allocation. Thus, we consider two scenarios that represent the two extreme end points of the possible continuum, that sex ratios remain relatively constant over the course of the worker revolution (“fast worker revolution”) or that sex ratios attain their convergence-stable values (Eshel and Motro 1981) effectively instantaneously over the course of the worker revolution (“slow worker revolution”).

Fast Worker Revolution

We start by assuming that worker control of sex ratio spreads rapidly relative to the timescale of sex ratio evolution, such that we can consider sex ratio strategies as fixed parameters. We assume that queen-controlled colonies exhibit an unbiased sex ratio ($z_q = 1/2$), and worker-controlled colonies exhibit a female-biased sex ratio ($0 < z_w < 1/2$). We consider two different scenarios, which differ in whether helping behavior is linked to the colony sex ratio. First, we consider the potential for obligate helping, which is enacted independently of whether the colony’s sex allocation is under worker or queen control. Second, we consider the potential for facultative helping, which is enacted only in colonies where workers control sex allocation. This could occur either via conditional adjustment of helping behavior or if helping and sex ratio biasing were genetically linked.

Obligate Helping. Our first task is to calculate the offspring sex ratio that the worker would produce, were she to leave her mother’s nest and breed independently (z_o). She would gain workers with a probability h , who would control the

colony sex allocation with probability v . Consequently, her offspring sex ratio would be worker-controlled with a probability hv , leading to a sex ratio of z_w , and would be under her own control with probability $1 - hv$, leading to a sex ratio of z_q . Hence, her average expected sex ratio is given by $z_o = hvz_w + (1 - hv)z_q$, which is also the expected population sex ratio \bar{z} .

Our next task is to calculate the sex ratio of the siblings that the worker could help rear were she to stay and help at her mother’s nest. The colony sex ratio would be under worker control with probability v and queen control with probability $1 - v$, leading to a average sex ratio of $z_c = vz_w + (1 - v)z_q$.

We now examine the consequences of this sex ratio variation across colonies for the evolution of helping. We substitute the appropriate consanguinities and reproductive values (apps. A and B) into equation (1), which gives

$$\alpha = \frac{1 + \phi - v(1 - 2z_w)(hv(1 - 2z_w) - \phi(1 - h[1 + v(1 - 2z_w)]))}{2 - 2[hv(1 - 2z_w)]^2}. \quad (3)$$

Helping is favored so long as both the frequencies of colonies with workers and with worker control are low, specifically, $\alpha > 1$ if $v < 1/[2h(1 - 2z_w)]$. We illustrate the results from equation (3) in figure 1a, assuming that the sex ratio in worker-controlled colonies is 75% female ($z_w = 1/4$), which is the convergence-stable sex ratio for a population where all colonies are worker controlled (a greater female bias would lead to a higher α). We find that worker control of sex allocation can promote helping and that this effect is greater when (a) the proportion of colonies with workers is lower (lower h) and (b) workers are in control of sex allocation at a higher proportion of the colonies with workers (higher v).

Why is obligate helping less readily promoted as workers become more common? As long as there is some worker control of sex allocation ($v > 0$), then a higher frequency of workers (higher h) leads to a more female-biased sex ratio at the population level, which reduces the reproductive value of females and increases the reproductive value of males. As the sex ratio of siblings is more female biased than that of offspring ($z_c < z_o$, when $h < 1$), this reduces the relative value of helping relative to breeding independently.

Why is obligate helping more readily promoted as worker control becomes more common? Greater worker control of sex allocation has two consequences. First, it leads to workers helping rear, on average, a more female-biased mixture of brothers and sisters. This increases the relatedness between helpers and the offspring that they help raise and hence promotes helping. Second, it leads to a more female-biased sex ratio at the population level,

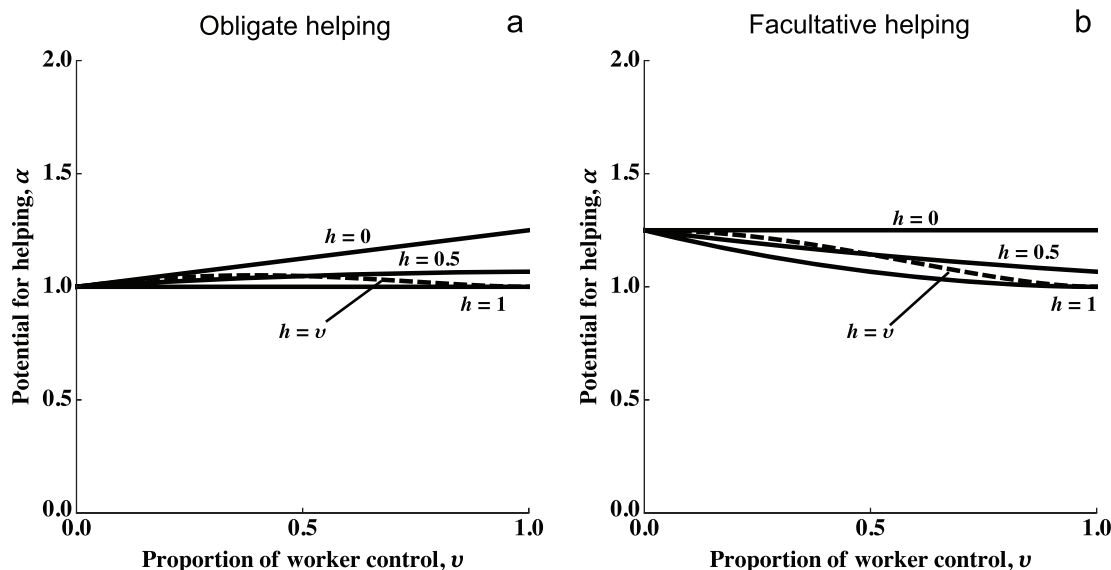


Figure 1: Worker control and the evolution of helping with fixed sex ratios. Shown are the predictions for the potential for helping, for the scenario where colonies in which queens control sex allocation produce 50% females ($z_Q = 1/2$) and colonies in which workers control the sex ratio produce 75% females ($z_W = 1/4$). *a*, Obligate helping, given independent of sex allocation in the colony: the potential for helping increases with the proportion of colonies where workers control sex allocation and decreases with the proportion of colonies with workers. *b*, Facultative helping, directed only at colonies where workers control sex allocation: the potential for helping decreases with both the proportion of colonies where there are workers (h) and the proportion of those colonies where workers control sex allocation (v).

which reduces the relative value of females and hence inhibits helping as described in the above paragraph. Overall, so long as the population sex ratio is not extremely female biased, the first effect is larger and increased worker control promotes helping ($d\alpha/dv > 0$ if $z_C < z_Q$ and $\bar{z} > 1/4$).

Facultative Helping. We now consider the evolution of facultative helping, which is enacted only in colonies where workers control sex allocation. The difference here is that we are considering the relative value of an additional amount of helping directed at offspring with a female-biased sex ratio of $z_C = z_W$, which does not vary with h and v . We substitute the appropriate consanguinities and reproductive values (apps. A and B) into equation (1), and obtain

$$\alpha = \frac{1}{4} \left[\frac{2z_W}{1 - hv(1 - 2z_W)} + \frac{2(1 - z_W)(1 + 2\phi)}{1 + hv(1 - 2z_W)} \right]. \quad (4)$$

If workers produce a moderately female-biased sex ratio ($1/4 \leq z_W \leq 1/2$), facultative helping is always promoted. More generally, $\alpha > 1$ if $v < 1/[2h(1 - 2z_W)]$. We illustrate the predictions from equation (4) in figure 1*b*, assuming that the sex ratio in worker-controlled colonies is 75% female ($z_W = 1/4$).

As with obligate helping, an increase in the proportion of colonies with workers (h) reduces the extent to which

helping is promoted ($d\alpha/dh \leq 0$), because it leads to a decrease in the relative reproductive value of females (fig. 1*b*). This inhibits facultative helping because the sex ratio of siblings that could be helped will be more female biased than the sex ratio of offspring that could be produced ($z_C < z_Q$ when $h < 1$). However, in contrast to obligate helping, we now find that an increased frequency of colonies with workers (h) also leads to a reduced promotion of helping ($d\alpha/dv \leq 0$; fig. 1*b*). The reason for this is that we are only examining selection on helping at worker-controlled colonies, and so the frequency of worker control (v) does not influence the sex ratio of siblings helped. Consequently, the only influence of a greater proportion of colonies with workers is to reduce the relative reproductive value of females, which reduces the relative value of helping (because $z_C < z_Q$ when $h < 1$). Overall, the maximum value for the potential for facultative helping is reached when both the proportion of colonies with workers and the frequency of worker control are vanishingly small ($\alpha = 1.25$ when $h \approx 0$ and $v \approx 0$).

Slow Worker Revolution

We now relax the assumption that sex ratio strategies are fixed, and instead assume that the presence of workers and worker control spreads slowly relative to the timescale of sex ratio evolution. More specifically, we assume that

worker-controlled (z_w) and queen-controlled (z_Q) sex ratios are always at their convergence-stable values, with respect to the frequency of both workers (h) and worker control (v). In this scenario, the colony sex ratios emerge from the other population parameters, rather than being left as free variables (i.e., it is a more “closed” model; Gardner and West 2006). This does not mean the model is necessarily more accurate but rather emphasizes that it considers a different scenario.

In appendix C, we show that the joint convergence-stable sex ratio strategies for queen-control and worker-control colonies are given by

$$(z_Q, z_w) = \begin{cases} \left[\frac{1}{2(1-hw)}, 0 \right] & \text{if } h < \frac{1}{2v} \\ (1, 0) & \text{if } \frac{1}{2v} \leq h \leq \frac{1+2\phi}{2v(1+\phi)} \\ \left[1, \frac{1-2(1+hw)(1+\phi)}{2hw(1+\phi)} \right] & \text{if } h > \frac{1+2\phi}{2v(1+\phi)} \end{cases} \quad (5)$$

We illustrate the predictions from equation (5) in figure 2. In a population with a low proportion of colonies with worker control (i.e., low h or low v), queen-controlled colonies produce an unbiased sex ratio, while worker-controlled colonies produce only female offspring. As the proportion of colonies with worker control (hw) increases in the population, the sex ratio produced by queen-control colonies becomes increasingly male biased, to compensate for the excess of females produced in worker-controlled colonies. As a result, the population sex ratio becomes female biased only when worker control of sex allocation is sufficiently common ($\bar{z} < 1/2$ if $h > [1/2]v$; fig. 2c).

We assume the sex ratio strategies given in equation (5), the appropriate consanguinities and reproductive values (apps. A and B), and substitute these into equation (1). In this case, the potential for helping (α) is given by

$$\alpha = \begin{cases} \frac{1+\phi(1+v)-hw(1+2\phi)}{2(1-hw)} & \text{if } h < \frac{1}{2v} \\ \frac{1+h(1-2v)+2\phi(1-2hw)}{4h(1-hw)} & \text{if } \frac{1}{2v} \leq h \leq \frac{1+2\phi}{2v(1+\phi)} \\ \frac{1+\phi}{2} & \text{if } h > \frac{1+2\phi}{2v(1+\phi)} \end{cases} \quad (6)$$

for obligate helping (fig. 3a), and

$$\alpha = \begin{cases} \frac{1+2\phi}{2} & \text{if } h < \frac{1}{2v} \\ \frac{1+2\phi}{4hw} & \text{if } \frac{1}{2v} \leq h \leq \frac{1+2\phi}{2v(1+\phi)} \\ \frac{1+\phi}{2} & \text{if } h > \frac{1+2\phi}{2v(1+\phi)} \end{cases} \quad (7)$$

for facultative helping (fig. 3b).

Both obligate and facultative helping are promoted as long as the frequency of worker control is below a threshold ($\alpha > 1$ if $v < [3/4]h$). The main difference between the two scenarios is that helping reaches higher values for a wider range of parameters for facultative helping ($\alpha = 1.5$ only if $h \approx 1$ for obligate helping and if $h < [1/2]v$ for facultative helping).

The evolving sex ratios scenario (fig. 3) leads to a higher potential for helping compared with the fixed ratio scenario (fig. 1; $z_Q = 1/2$, $z_w = [1/4]$). This difference arises because the evolving sex ratios model leads to greater sex ratio variation between the colony types.

Worker Reproduction

The other scenario that Trivers and Hare (1976; pp. 250–251) suggested could lead to haplodiploidy promoting the evolution of eusociality is if workers “deny to the queen the production of males.” The idea here is that workers replace the sons of the queen with their own sons and that this would favor helping because workers are more related to the sons of their sisters (nephews, $r = 3/4$) than to the sons of their mother (brothers, $r = 1/2$). Consequently, workers could benefit by raising sisters and nephews rather than sisters and brothers. This idea implies that a worker caste is already established in the population, and the question changes to what extent does haplodiploidy promote the maintenance of helping (Gardner et al. 2012a).

Worker reproduction has two consequences. First, it means that workers increasingly rear nephews instead of siblings, which changes the relatedness of a worker to the larvae she could help to rear (Trivers and Hare 1976). Second, it changes male gene transmission and hence the class reproductive values of males and females (Trivers and Hare 1976; Grafen 1986, Pamilo 1991). In a haplodiploid system with no worker reproduction, males censused in each generation trace none of their genes to males in the previous census, leading the total reproductive value of males to be half that of females. However, when there is worker reproduction a male can contribute genes to the next generation of reproductive males via the reproduction of his worker’s daughters, and this increases the reproductive value of males to more than half that of females (Gardner et al. 2012a, 2012b).

Here, we study three scenarios: replacement of brothers

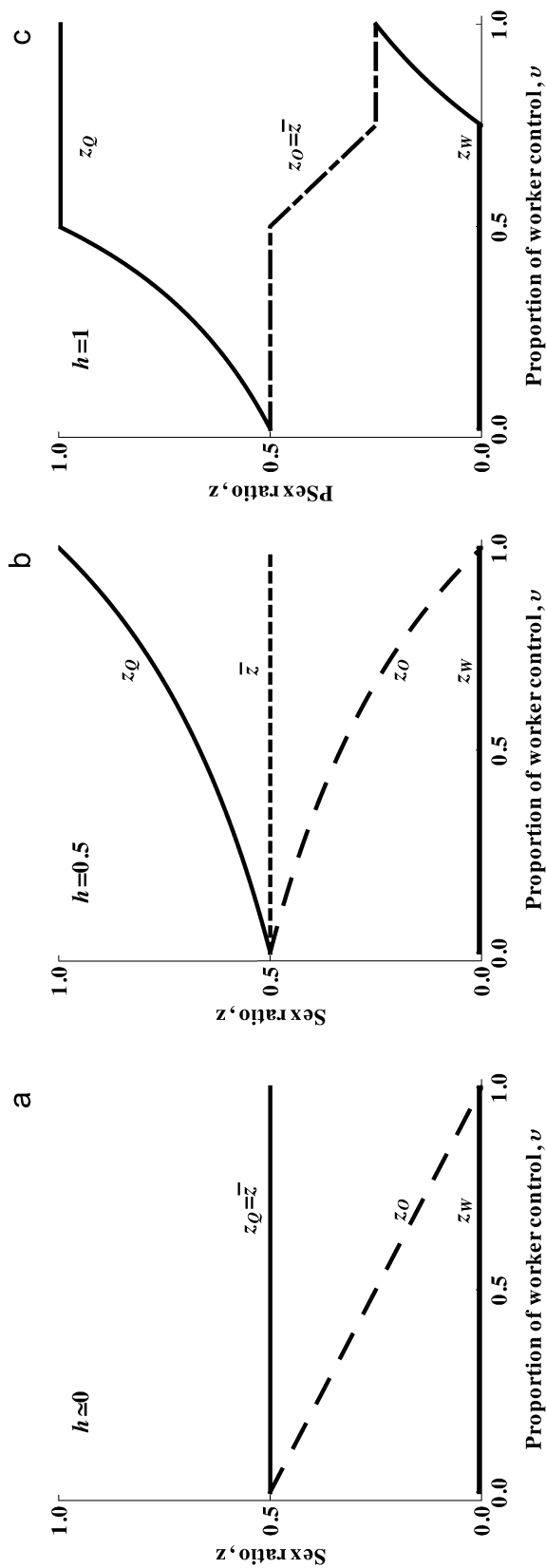


Figure 2: Worker control and the evolution of sex allocation. Shown are the predictions for the convergence sex ratio strategies, for the scenario where sex ratio strategies for queen-controlled colonies and for worker-controlled colonies evolve. Colonies where the sex allocation is controlled by the queen exhibit a male-biased sex ratio, whereas colonies where workers control sex allocation exhibit a female-biased sex ratio. Male bias in queen-controlled colonies increases with the proportion of colonies where workers control the sex ratio (h) and with the proportion of colonies with workers (v). Female bias in worker-controlled colonies decreases with the same factors. The average sex ratio of queen-laid offspring becomes more female biased with the proportion of worker control (v). The three panels describe when the proportion of colonies with workers approaches zero (a), 50% of the colonies have workers (b), and the proportion of colonies with workers approaches 100% (c).

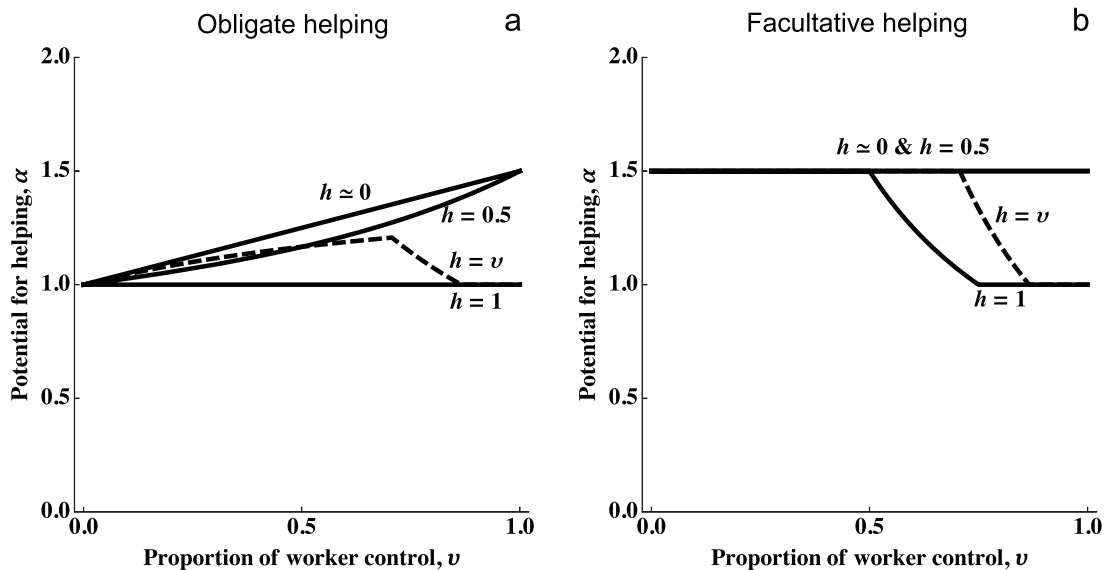


Figure 3: Worker control and the evolution of helping with evolving sex ratios. Shown are the predictions for the potential for helping, for the scenario where sex ratio strategies for queen-controlled colonies and for worker-controlled colonies evolve. *a*, Obligate helping as a function of sex ratio evolution: the potential for helping increases with the proportion of worker control and decreases with the proportion of colonies with workers. *b*, Facultative helping, directed only at colonies where workers control sex allocation: the potential for helping decreases with both the proportion of colonies where there are workers (h) and the proportion of those colonies where workers control sex allocation (v).

with nephews, replacement of brothers and sisters with nephews, and replacement of brothers and sisters with nephews and nieces. We focus our attention on the scenario where all colonies have workers ($h = 1$) and workers have complete control of sex allocation ($v = 1$). Also, as all colonies have workers, the potential for helping considers the decision of a focal worker faced with the option of either helping to rear b of the queen's offspring or produce c of her own offspring within the colony. We assume a large number of workers, so that the probability of a focal worker aiding her own offspring is rare. Consequently, from the perspective of a worker, the colony offspring comprises mainly siblings and nephews. More generally, any benefits of helping that accrue to the worker's own offspring can be considered as mediating the net direct effect of helping (c) rather than its indirect benefit (rb).

Brothers Replaced by Nephews

We assume that workers are able to distinguish between male and female juveniles and that a fraction μ of the queen's sons are replaced by the workers' sons. We assume that workers do not mate and are constrained to produce sons ($z_o = 1$). Thus, following equation (1), the potential for helping (α) is given by $\alpha = \{z_w v_m [\mu p_{Nc} + (1 - \mu) p_M] + (1 - z_w) v_f p_F\} / v_m p_S$.

Fast Worker Revolution. As with our spread of worker control model, we now need to make assumptions about the sex ratios produced in different colonies. If we assume that the sex ratio produced in colonies is a fixed variable z_w , then the potential for helping simplifies to $\alpha = z_w(2 - \mu + 2\phi)/2$. In this case, if workers produce a female-biased sex ratio, then helping is inhibited (if $z_w \leq 1/2$, then $\alpha \leq 1$) and the potential for helping decreases with the frequency of worker replacement ($d\alpha/d\mu \leq 0$; fig. 4a).

Why is helping inhibited when workers produce sons at the expense of brothers? We are comparing, for a worker, the relative value of producing a female-biased mixture of siblings and nephews versus the production of sons. Considering the siblings and nephews, both the female-biased sex ratio and the substitution of nephews for brothers leads to an increase in relatedness to the individuals that she could be helping to raise. However, at the same time, both the overall female bias in the population sex ratio and worker reproduction (see below) lead to a relative increase in the reproductive value of males. This increase in the relative value of males is so great that sons are worth relatively more than a mixture of siblings and nephews.

Why does helping become more inhibited as the amount of worker reproduction increases? An increase of worker reproduction frequency has two consequences. First, it increases the average relatedness of potential helpers to the offspring they could be helping raise. Second, worker re-

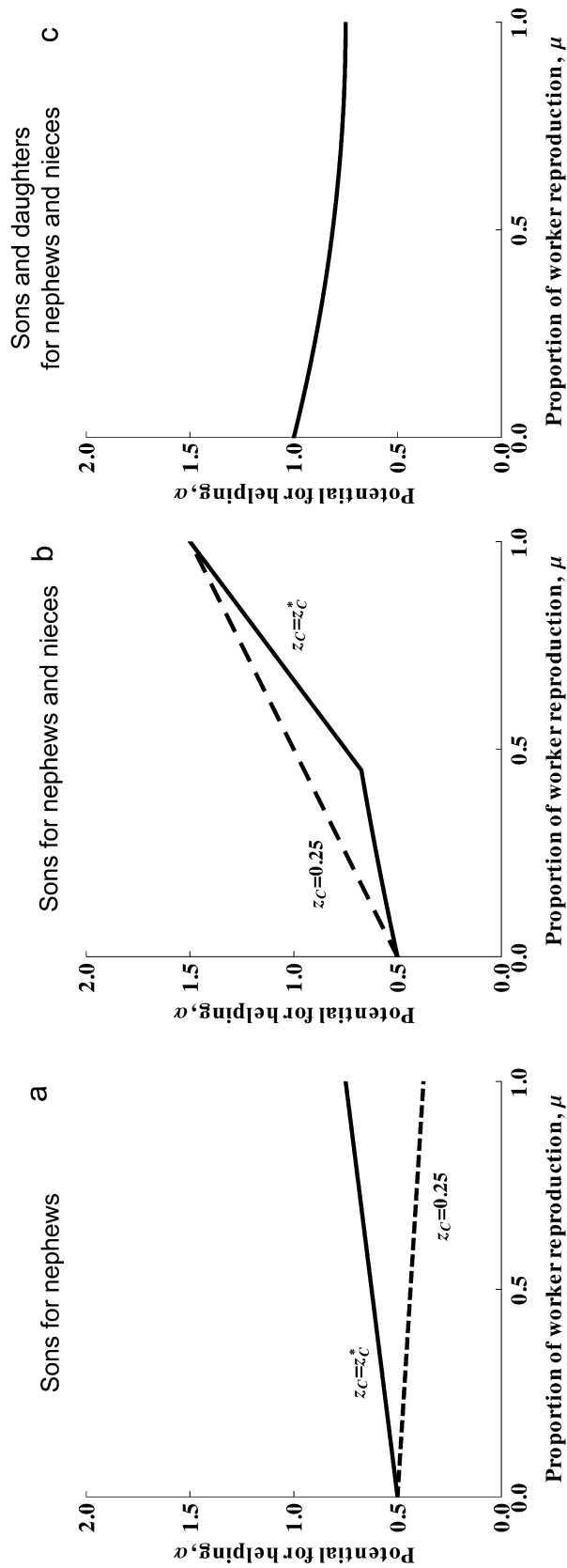


Figure 4: Worker reproduction and the evolution of helping. Shown are the predictions for the convergence sex ratio strategy, for the scenario where workers control the colony sex allocation and also produce a proportion μ of the colony offspring. The dashed lines represent populations where colony sex ratio is fixed ($z_w = 1/4$), whereas solid lines represent populations where the sex ratio evolves to the convergence-stable strategy. *a*, Workers replace nephews with sons: haplodiploidy inhibits helping in both populations with fixed and evolving sex ratios. *b*, Workers replace nephews and nieces with sons: as the colony sex ratio becomes male biased due to worker replacement, the value of females increases driving helping to be promoted by haplodiploidy ($\alpha > 1$ if $\mu > 1/2$ in populations with fixed sex ratio at $z_w = 1/4$, and $\alpha > 1$ if $\mu > 2/3$ in populations where the sex ratio evolves). *c*, Workers replace nephews and nieces with sons and daughters: as the proportion of worker reproduction increases, the relatedness of a focal worker to her colony decreases and, as a result, helping is never promoted by haplodiploidy in both populations with fixed and evolving sex ratios.

production increases the reproductive value of males, which goes from $c_m = 1/3$ when $\mu = 0$ to $c_m = 1/2$, when $\mu = 1$. This change in reproductive value occurs because, in a haplodiploid genetic system, males transmit genes only through their daughters. Consequently, if brothers are replaced with nephews, this means that males also transmit genes to males from the next generation, through their daughters (workers), raising the reproductive value of males. Overall, this second effect is greater, and so greater levels of worker reproduction select against helping (fig. 4a).

Slow Worker Revolution. We now relax the assumption that colony sex ratios are fixed strategies and instead assume that sex ratios evolve rapidly relative to other life-history variables. More specifically, we assume that the colony sex ratio is always at its convergence-stable values, with respect to the fraction of the queen's sons that are replaced by the workers' sons (μ). In this case, the convergence-stable strategy for the colonies' sex ratio is given by $z_w^* = [2 - \mu(1 - 2\phi)]/[2(2 - \mu + 2\phi)]$ (see app. D for derivation). As the frequency of worker production (μ) increases, this raises the relatedness between workers and the males that they could help rear, leading to a less female-biased sex ratio. In the extreme, if all male offspring were replaced by workers ($\mu = 1$), workers would favor an unbiased colony sex ratio ($z_w^* = 1/2$).

In this scenario, the potential for helping is given by $\alpha = [2 - \mu(1 - 2\phi)]/4$. As with fixed sex ratio strategies, a mixture of siblings and nephews is also worth less than sons, and so helping is inhibited ($\alpha < 1$; fig. 4a). However, in contrast to the situation with fixed sex ratios, the relative advantage of helping increases with the extent of worker reproduction ($d\alpha/d\mu > 0$; fig. 4a). The reason for this is that, with evolving sex ratios, worker reproduction leads to less female-biased sex ratios, as described above. This, in turn, reduces the relative reproduction value of males, decreasing the value of sons relative to a mixture of sibling and nephews.

Brothers and Sisters Replaced by Nephews

We now relax the assumption that workers are able to discriminate between male and female eggs laid by the queen. Instead, we assume that workers replace siblings of both sexes with sons (or, equivalently, just add their sons to the brood of the queen). In this case, the colony offspring is composed of a fraction μ of worker-derived offspring and a fraction $1 - \mu$ of queen-derived offspring, and the potential for helping is given by $\alpha = \{\mu v_m p_{Ne} + (1 - \mu)[z_w v_m p_M + (1 - z_w) v_f p_F]\} / v_m p_S$. If we assume that the sex ratio produced in colonies is a fixed variable z_w , then the potential for helping is $\alpha = [\mu + 2\phi\mu + 2z_w \times$

$(1 - \mu)(1 + \phi)]/2$. In this case, the potential for helping increases with the frequency of worker reproduction ($d\alpha/d\mu \geq 0$) and decreases with an increase of the sex ratio female bias ($d\alpha/dz_w \leq 0$). Thus, helping is promoted by haplodiploidy when there is a high frequency of worker reproduction and low female-bias in the sex ratio ($\alpha > 1$ if $\mu > [2 - 4z_w]/(3 - 4z_w)$; fig. 4b). If we assume that sex allocation is an evolving trait (see app. D, eq. [D1]), then the potential for helping is

$$\alpha = \begin{cases} \frac{2 + \mu\phi}{2 + 2\phi} & \text{if } \mu \leq \frac{2}{3 + 2\phi} \\ \frac{3\mu}{2} & \text{if } \mu \leq \frac{2}{3 + 2\phi} \end{cases} \quad (8)$$

In this case, helping is promoted by sufficiently high frequencies of worker replacement ($\alpha > 1$ if $\mu > 2/3$ and $d\alpha/d\mu \geq 0$; fig. 4b).

As with the previous scenario, and for the same reasons, we find that worker replacement generally led to an inhibition of helping ($\alpha < 1$). There are, however, two qualitative differences. First, in the scenario with fixed sex ratios, the potential for helping increases with the extent of worker reproduction. As worker reproduction (sons) becomes more common, the sex ratio becomes less female biased and eventually male biased. This increases the relative reproductive value of females and hence increases the relative advantage of raising siblings relative to sons. Second, when the extent of worker reproduction is sufficiently high, then helping is promoted rather than inhibited. This is because (a) the reproductive value of females increases, and (b) at very high levels of worker reproduction, workers are effectively comparing nephews versus sons, and they are more related to the former. However, the extent of worker reproduction required to give $\alpha > 1$ is unrealistic, because it requires that colonies raise predominantly sons of workers, and so there would be a huge advantage to raising females (i.e., for lower μ or for workers to mate).

Brothers and Sisters Replaced by Nephews and Nieces

We now relax the assumption that workers can produce only sons and examine the scenario where workers replace siblings with a mixture of sons and daughters. We assume that both queen-produced and worker-produced offspring are under worker control such that both types of offspring are produced with the same sex ratio. In the supplementary information, we show that the potential for helping is the same in the fixed and evolving sex ratio scenarios and is given by $\alpha = \{2 - \mu + \phi [2 - \mu(1 - \mu)]\}/4$ (fig. 4c). If worker reproduction is very low $\mu \approx 0$, we recover the result from Gardner et al. (2012a, 2012b) that workers

value equally the colony and their own offspring and helping is not promoted or inhibited by haplodiploidy. As worker reproduction increases in the population, the potential for helping decreases due to an overall decrease in relatedness of the colony offspring to a focal worker. As a result, helping is inhibited if workers produce a proportion of the colony offspring (see app. D for derivation).

Empirical studies find rates of worker reproduction from 0% to 100%, with an average of 12% (Ratnieks et al. 2006; Wenseleers and Ratnieks 2006), which would lead to worker reproduction inhibiting helping ($\alpha \approx 0.6$ if $z_w = 1/4$, and $\alpha \approx 0.5$ if $z_w = z_w^*$). Thus, our results suggest that the evolution of helping is not facilitated in the scenarios in which workers replace some of the queen's sons with their own sons (fig. 4a). Only the replacement of sons with nephews and nieces can provide the conditions for helping to be promoted (fig. 4c).

Discussion

We have quantified the possible role for haplodiploidy to promote the evolution of eusociality in the classic haplodiploidy hypothesis, as described by Trivers and Hare (1976). We found that (1) worker control of sex allocation can facilitate the evolution of helping, but this effect is likely to be relatively minor and only temporary (figs. 1, 3); and (2) worker reproduction does not promote the evolution of helping, because a female-biased population sex ratio leads workers to value their sons more than they value a mixture of siblings and nephews (i.e., $\alpha \leq 1$; fig. 4). Overall, our results suggest that haplodiploidy is unlikely to have played a major role in facilitating the evolution of eusociality in such scenarios.

Worker Control

We found that worker control of sex allocation can facilitate the evolution of helping but that this is appreciable only when the proportion of worker-controlled colonies (hw) is low (figs. 1 and 3). This means that the spread of worker control would negate any facilitation of helping. The proportion of colonies harboring workers (h) and the proportion of such colonies in which the workers have seized control of sex allocation (v) are unlikely to both be small, as selection for worker control of sex allocation can occur only when some individuals are acting as workers. Consequently, the scenario where haplodiploidy could have the greatest influence (low h and low v) is unlikely to occur. Overall, as worker control spreads, the benefit to helping will initially be small (low v , medium to high h), and then disappear (high v , high h).

As suggested by Trivers and Hare (1976), we found that facultative helping, occurring only in colonies with worker

control of sex allocation, is more strongly promoted than is helping that occurs in all colonies that contain workers (cf. figs. 1, 3). However, this link between sex allocation and helping would require one of two further assumptions, both of which limit its importance. First, workers could conditionally adjust their behavior depending on the type of colony in which they find themselves. Even if workers could assess their colony type, this would only facilitate the evolution of facultative helping behaviors and not obligate traits such as sterility, which are the hallmark of eusociality (Crespi and Yanega 1995; Boomsma 2009). Second, the helping and sex allocation behaviors of workers might be genetically linked. There is no reason to expect genetic linkage to be common across these traits, let alone that this should be the norm. Moreover, in this scenario helping is favored transitively, as the potential for helping (α) decreases with an increase of the frequencies of colonies with workers and worker control.

Productivity and Sex Ratio Control

Haplodiploidy and worker control of sex allocation are much less likely to facilitate the evolution of helping than suggested by our results (figs. 1, 3). First, we have assumed that any differences in productivity between colonies with and without workers are negligible. However, potential helpers would only be selected to stay and help if this led to an increase in colony productivity. While this productivity benefit promotes the evolution of helping, in both diploids and haplodiploids, it also reduces the effective variance in sex-allocation strategies in the population, which reduces the extent to which haplodiploidy promotes helping (Gardner et al. 2012a). Second, we have assumed that the sex ratio among worker-derived offspring is constrained, owing either to the absence of worker mating (such that workers produce only sons) or else to interference from other workers (such that their offspring have the same sex ratio as the queen's offspring). Worker control of sex allocation leads to a female bias at the population level, which increases the reproductive value of males. Consequently, if workers are more likely to be able to rear sons, then this would be favored over rearing a female-biased mixture of siblings (i.e., helping is inhibited rather than facilitated; see when $\mu = 0$ in fig. 4b). This could be a result of workers being unmated or less likely to obtain helpers, which might occur if they were breeding later in a season.

Third, we have implicitly assumed that there can be substantial differences between individuals in the extent to which they control and adjust sex allocation and the extent to which this could be linked with helping behavior. For example, some colonies are under complete worker control, while other colonies are under complete queen

control. However, almost all quantitative traits that have been studied, including the sex ratio behavior of a wasp, have been shown to be underpinned by many loci, each having a small effect (Lynch and Walsh 1998; Pannebakker et al 2008). In this case, we would expect relatively small differences, leading to smaller sex ratio differences between colonies and hence a lower potential for helping. For example, the spread of worker evolution would involve a more gradual change across all colonies from 50% to 75% females, rather than colonies that produce 50% females being replaced by colonies that produce 75% females. This means that split sex ratios would not really occur, and so haplodiploidy would not promote helping (if $z_Q \approx z_w$, then $\alpha \approx 1$). While there is no empirical evidence for a mixture of worker and queen control leading to substantially split sex ratios, it could be due to either this not occurring or it being a transient phenomenon.

Dynamical Assumptions

There are two important limitations to our analyses. First, we use a separation of timescales, assuming that worker evolution and/or worker reproduction evolve much faster or much slower than sex allocation (Otto and Day 2011; Rousset 2004, 2006). This allows us to focus on relatively static scenarios, where we analyze the influence of different factors separately (open model; Gardner and West 2006). In reality, parameters such as the frequency of workers (h), the extent to which workers control sex allocation (ν), and the different sex allocation strategies (z_Q , z_C , \bar{z}) could vary between individuals or coevolve over a similar timescale to the evolution of worker altruistic helping. Furthermore, the way in which these traits coevolve could depend on the distribution of alleles in the population for particular traits or genetic associations between traits, which could lead to dynamic models giving different predictions from equilibrium models (Gardner et al 2007). Second, our model parameters lack an explicit mechanistic underpinning. Mechanistic models could lead to parameters taking particular forms and being associated in specific ways. The general issue here, with both limitations, is that models developed and analyzed using different approaches, such as more mechanistic individual-based simulations, could make different predictions.

We chose an inclusive fitness approach because (a) we lack sufficient biological knowledge to make more explicit mechanistic models—although we could make more precise assumptions, they would not necessarily be valid; (b) the evolution of eusociality represents a major, long-term, open-ended transition in which multiple traits coevolve in a coordinated way to give rise to a new level of biological organization and so is less amenable to a closed-model approach; and (c) we wanted to develop models that could

provide a relatively general overview, relevant to the range of biological scenarios under which eusociality has evolved. Consequently, rather than calculate an equilibrium level of altruism for a single specific scenario, which would require that we make assumptions about what the costs and benefits of altruism are, we quantified the threshold cost/benefit ratio at which altruism would be favored. Nonetheless, we stress that if certain scenarios can be shown to be especially relevant, it would be extremely useful to analyze them with a more mechanistic, closed-model approach.

Could haplodiploidy be important, even when it leads to the potential for helping (α) being only slightly greater than 1.0? Assume that there are two species, one diploid and one haplodiploid, for which the costs and benefits of helping are the same. Now imagine that the diploid species has a potential for helping of 1 and the haplodiploid species has a potential for helping of 1.05, on account of the haplodiploidy effect. Then, if $c/b < 1.00$, helping will be favored in both species, and if $c/b > 1.05$, helping will be disfavored in both species. It is only within the narrow margin $1.00 < c/b < 1.05$ that helping is disfavored under diploidy but favored under haplodiploidy. An ideal measure of the haplodiploidy effect is the proportion of all species that find themselves in that narrow zone. However, in the absence of comprehensive data (or an explicit model) that would allow us to assess the scatter of c/b values across all species, pragmatism forces us to rely on α as a proxy of the haplodiploidy effect. An effect of 5% strikes us as quite weak, considering the dramatic effect that other factors—such as monogamy versus multiple mating—has on the potential for helping (Gardner et al 2012).

Conclusions

Our results suggest that worker control of sex allocation and worker reproduction are unlikely to have led to haplodiploidy appreciably facilitating the evolution of eusociality. We have previously argued that the other mechanisms for split sex ratios, suggested since Trivers and Hare's (1976) article, are unlikely to have played a major role in promoting the evolution of helping (Gardner et al. 2012a, 2012b; Alpedrinha et al. 2013). Consequently, while Trivers and Hare's (1976) predictions about sex ratio conflict in the social insects have led to one of the most productive areas of social evolution (West 2009), they do not succeed in rescuing the haplodiploidy hypothesis for the evolution of eusociality. While haplodiploidy could mediate the evolution of eusociality for other reasons not connected with the inflated relatedness of full sisters (Stubblefield and Charnov 1986; Wade 2001; Lehmann et al. 2008; Frohman and Kokko 2011; Johnstone et al. 2011; Gardner 2012;

Gardner and Ross 2013), the empirical evidence suggests that the distribution of eusociality is better explained by other aspects of biology, such as lifetime monogamy (Boomsma 2007, 2009, 2013; Hughes et al. 2008). Similarly, the sex ratio of helpers appears to be determined by ecology and not whether a species is diploid or haplodiploid (Ross et al. 2013; Davies and Gardner 2014). More generally, these results highlight the distinction between inclusive fitness theory, with its application across the entire tree of life (Bourke 2011; Davies et al. 2012), versus the haplodiploidy hypothesis per se.

Acknowledgments

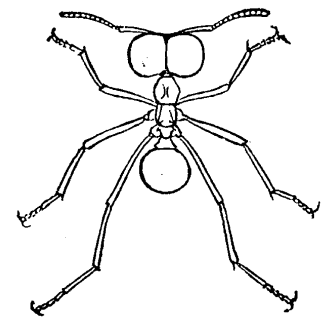
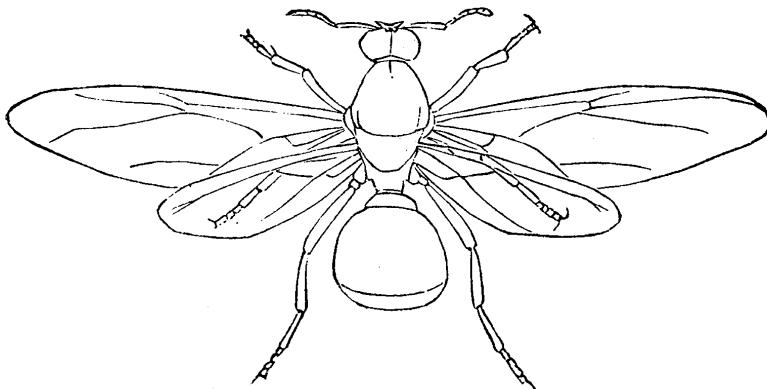
This article was inspired by numerous fruitful discussions with R. Trivers. We thank K. Boomsma, A. Grafen, I. Pen, R. Trivers, and F. Weissing for discussion and comments and Balliol College, the European Research Council, the Leverhulme Trust, the Royal Society, and the PhD Program in Computational Biology (PDBC) of the Gulbenkian Institute of Science (IGC)/Foundation for Science and Technology (FCT; SFRH/BD/33206/2007) for funding.

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Associate Editor: Franz J. Weissing
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“It seems desirable to add the testimony of Mr. Bates as to the *Cec[odoma] cephalotes*, the common species of South America. ‘This insect, from its ubiquity, immense numbers, eternal industry, and its plundering propensities, becomes one of the most important animals of Brazil. Its immense hosts are unceasingly occupied in defoliating trees [...]. They have regular divisions of laborers, numbers mounting the trees and cutting off the leaves in irregularly rounded pieces the size of a shilling, another relay carrying them off as they fall.’” From “Notes on Mexican Ants” by Edward Norton (*The American Naturalist*, 1868, 2:57–72).