

Haplodiploidy and the Evolution of Eusociality: Worker Reproduction

João Alpedrinha,^{1,2} Stuart A. West,¹ and Andy Gardner^{1,3,*}

1. Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom; 2. Instituto Gulbenkian de Ciência, Oeiras, Portugal Rua da Quinta Grande, 6 P-2780-156 Oeiras, Portugal; and Department of Applied Mathematics, University of Western Ontario, 1151 Richmond Street North, London, Ontario N6A 5B7, Canada; 3. Balliol College, University of Oxford, Broad Street, Oxford OX1 3BJ, United Kingdom; and School of Biology, University of St. Andrews, Dyers Brae, St. Andrews KY16 9TH, United Kingdom

Submitted April 6, 2013; Accepted May 15, 2013; Electronically published August 23, 2013

Online enhancement: appendix.

ABSTRACT: Hamilton's haplodiploidy hypothesis suggests that the relatively higher relatedness of full sisters in haplodiploid populations promotes altruistic sib rearing and, consequently, the evolution of eusociality. This haplodiploidy effect works when some broods have a relatively female-biased sex ratio and other broods have a relatively male-biased sex ratio, termed split sex ratios. There is empirical evidence for two scenarios having potentially led to split sex ratios en route to eusociality: unmated queens and queen replacement. A recent analysis of these two scenarios has suggested that haplodiploidy can either promote or inhibit the evolution of eusociality and that the effect is usually small. However, this work made the simplifying assumptions that there is only negligible reproduction by workers and that their offspring have the same sex ratio as those produced by the queen. Here, we relax these assumptions and find that worker reproduction has a negative influence on the evolution of helping, either reducing the extent to which it is promoted or leading to it being inhibited. This is particularly so when workers are unmated and hence constrained to produce only sons, by arrhenotoky. Overall, when parameterized with empirical data, our results suggest that split sex ratios in haplodiploid species have not played an important role in facilitating the evolution of eusociality.

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

Introduction

Eusociality is characterized by the presence of a caste of less reproductive individuals that develops specialized adaptations for helping a caste of more reproductive individuals to reproduce (Crespi and Yanega 1995). Obligate eusociality is characterized by complementary totipotency, such that the presence of both reproductive and nonreproductive castes is required in order for the colony to achieve suc-

cessful reproduction (Michener 1974; Crespi and Yanega 1995; Boomsma 2007, 2009). While elaborated forms of sociality with specialization into castes has emerged in several taxa—soldier aphids (Aoki 1977; Ito 1989), gall-forming thrips (Crespi 1992), snapping shrimps (Duffy 1996), platypodid beetles (Kent and Simpson 1992), and naked mole rats (Jarvis 1981)—obligate eusociality is found only in the social Hymenoptera (bees, ants, and wasps; Wilson 1971; Boomsma 2007, 2009) and the social cockroaches (termites; Thorne 1997; Inward et al. 2007). These groups have achieved remarkable ecological success, with ants and termites together accounting for more than half of all insect biomass (Hölldobler and Wilson 1990).

The problem of eusociality is to explain why individuals altruistically give up their ability to reproduce in order to help others achieve reproductive success (Hamilton 1964a, 1964b, 1972). Hamilton's (1963, 1964a, 1964b, 1970) theory of inclusive fitness reveals that by helping a relative to reproduce, an individual is able to transmit copies of his or her own genes to future generations, albeit indirectly. If this indirect route to genetic success outweighs the loss of direct genetic success via the individual's own reproduction, then altruistic helping is favored by natural selection. Hamilton (1964a, 1964b, 1972) noted that haplodiploid sex determination, whereby fertilized eggs develop into (diploid) females and unfertilized eggs develop into (haploid) males, leads to a female being more related to her full sisters (life-for-life relatedness $R_F = 3/4$, assuming outbreeding and an even sex ratio; table 1) than to her own daughters ($R_D = 1/2$) and suggested that this explains the apparent preponderance of haplodiploidy among eusocial taxa. However, haplodiploidy also leads a female to be less related to her brothers ($R_M = 1/4$) than to her sons ($R_S = 1/2$), which counteracts the inclusive fitness benefit of sib rearing (Hamilton 1964b, 1972). It is easy to see that these two effects of haplodiploidy exactly cancel when there is an even sex ratio,

* Corresponding author; e-mail: andy.gardner@st-andrews.ac.uk.

Table 1: Summary of model notation used in this article

Symbol	Definition
μ	Proportion of colony's offspring derived from workers
u	Proportion of colonies founded by unmated queens (queen virginity model)
a	Relative productive of colonies founded by unmated queens (queen virginity model)
q	Probability of queen survival (queen replacement model)
ϕ	Probability that two maternal sisters share the same father
N_i	Number of individuals from class $i \in \{m, f\}$ in the population
m	Male
f	Female
c_m	Class reproductive value of males
c_f	Class reproductive value of females
v_m	Reproductive value of a male (c_m/\bar{z})
v_f	Reproductive value of a female ($c_f/(1 - \bar{z})$)
p_x	Consanguinity between a focal worker and an individual of role $x \in \{D, S, F, M, Ni, Ne\}$
R_x	Life-for-life relatedness of individual $x \in \{D, S, F, M, Ni, Ne\}$ from the perspective of a focal worker, that is, $(p_i/p) \times (v_i/v_f)$, where $i \in \{m, f\}$ is the individual's sex and p is the consanguinity of the worker to herself
D	Daughter
S	Son
F	Sister
M	Brother
Ni	Niece
Ne	Nephew
w_i	Fitness of individual of sex $i \in \{m, f\}$
\bar{w}_i	Average fitness of individual of sex $i \in \{m, f\}$
z_c	Sex ratio of the focal worker's colony
z_Q	Sex ratio of queen-derived offspring
z_O	Sex ratio of worker-derived offspring
z_M	Sex ratio of queen-derived offspring in mated-queen colonies (queen virginity model)
z_R	Sex ratio of queen-derived offspring in queenright colonies (queen replacement model)
z_L	Sex ratio of queen-derived offspring in queenless colonies (queen replacement model)
\bar{z}	Sex ratio of the population

as here the average relatedness of siblings ($1/2 \times 3/4 + 1/2 \times 1/4 = 1/2$) is the same as the average relatedness of offspring ($1/2 \times 1/2 + 1/2 \times 1/2 = 1/2$; Trivers and Hare 1976). This exact canceling also occurs under female-biased sex allocation (Craig 1979) because the increased genetic similarity to siblings is exactly counteracted by the increased reproductive value of males, owing to their being the rarer sex (Fisher 1930).

One possibility for rescuing the haplodiploidy hypothesis involves split sex ratios, whereby there is a greater female bias among a potential altruist's siblings than in the population as a whole (Trivers and Hare 1976; Seger 1983; Grafen 1986). This allows the potential altruist to enjoy the benefit of close genetic similarity to her siblings (because they are primarily sisters) without the concomitant reduction in the reproductive value of females (because the population sex ratio need not be as biased; Boomsma and Grafen 1990, 1991; Boomsma 1991). Split sex ratios may be favored for a number of reasons and have been found in natural populations (Boomsma 1991;

Mueller 1991; Meunier et al. 2008; West 2009). However, a limited number of mechanisms could have led to split sex ratios during the evolution of eusociality, and previous theoretical work has tended to focus on relatively general models that ask the qualitative question of whether haplodiploidy can promote altruistic sib rearing rather than examining how much haplodiploidy is likely to have mattered (reviewed in Gardner et al. 2012). Consequently, there is a need for more specific models that examine the biologically most relevant scenarios, capturing all the effects of biased sex allocation on the reproductive value of females and males, and that ask the quantitative question of how much haplodiploidy promotes helping.

Gardner et al. (2012) examined the impact of split sex ratios on the origin and elaboration of altruistic helping in haplodiploid populations. Of the possible mechanisms that could lead to split sex ratios, several lack empirical support or have arisen only after advanced eusociality had already evolved (Gardner et al. 2012). Consequently, there are only two mechanisms for stable split sex ratios for

which there is empirical evidence that they could have played a role en route to eusociality: queen virginity and queen replacement (Packer 1986; Godfray 1988; Yanega 1989; Boomsma 1991; Mueller 1991; Godfray and Hardy 1993; Kranz et al. 2000; Gardner et al. 2012). Analyzing these two cases, Gardner et al. (2012) showed that the haplodiploidy effect may promote or inhibit the evolution of altruistic helping, depending on whether helping is facultatively adjusted according to the sex allocation of the individual's colony, and also that the haplodiploidy effect tends to be small.

However, Gardner et al. (2012) examined the best-case scenarios for haplodiploidy to promote the evolution of eusociality and so made two restrictive assumptions. First, they assumed that there is negligible reproduction by workers within the colony. In reality, worker reproduction is significant in haplodiploid species, and conflict over male parentage is almost universal (Ratnieks et al. 2006). In a comparative analysis of 90 species of bees, wasps, and ants, Wenseleers and Ratnieks (2006) found that worker reproduction accounts for 0%–100% of the offspring produced in colonies, with a mean of 12%. This reduces the relatedness of workers to the offspring that they would help to raise (nieces and nephews rather than siblings) and hence would appear to reduce selection for helping. Second, building on the model of Craig (1979), Gardner et al. (2012) assumed that (rare) worker-produced offspring have the same sex ratio as do the offspring produced by the queen. In reality, workers of many species are unmated and hence able to produce only sons (Fletcher and Ross 1985; Bourke 1988; Ratnieks et al. 2006; Wenseleers and Ratnieks 2006). When there is a female-biased sex allocation at the population level, this increases the relative reproductive value of males and hence would appear to also reduce selection for helping.

Here, we extend Gardner et al.'s (2012) analysis to investigate the impact of relaxing these two restrictive assumptions. Specifically, we explore the consequences of allowing worker-produced offspring (1) to represent a significant fraction of the colony's reproductive success and (2) to have a sex ratio different from that of the queen-produced offspring. Following Gardner et al. (2012), we consider that the worker class has already evolved and thus determine the extent to which natural selection favors further elaboration of the helping undertaken by these workers. We consider helping that is either obligately expressed in all colonies in which workers occur or else facultatively adjusted according to the sex ratio of the worker's colony. We examine the two biologically relevant scenarios for stable split sex ratios: queen virginity and queen replacement. In each case we determine the potential for altruistic helping, which we compare with that obtained under dip-

loidy, in order to assess whether, when, and to what extent haplodiploidy promotes eusociality.

General Methods

We consider a newly eclosed female who is choosing between helping her mother rear the colony's juveniles and producing her own offspring within the same colony. We assume that each colony contains one queen who, if mated, produces a cohort of female workers, followed by a cohort of reproductive juveniles of both sexes that the workers help to rear, with successfully reared reproductives leaving the colony to mate at random within the entire population (i.e., no inbreeding). We denote the probability that two maternal sisters share the same father by ϕ . Throughout this article, we present general results that allow for both single and multiple mating ($0 \leq \phi \leq 1$) but give special attention to the predictions for monogamy ($\phi = 1$). We focus on monogamy because (i) there is empirical support for eusociality to have evolved only in monogamous populations (Boomsma 2007, 2009, 2013; Hughes et al. 2008) and (ii) monogamy increases the genetic relatedness between a worker and the juveniles in her colony, constituting a best-case scenario for the evolution of eusociality (Boomsma 2007, 2009, 2013; Hughes et al. 2008). We assume that a proportion μ of the colony's reproductive offspring are derived from the workers and $1 - \mu$ derive from the queen. We assume worker control of the sex ratio of those offspring derived from the queen, and we denote the sex ratio (proportion male) of the queen-derived offspring by z_Q and that of the worker-derived offspring by z_O .

We consider two scenarios for worker reproduction. In the first scenario, we assume that each worker is able to mate and that her offspring have the same sex ratio as do those of the queen ($z_O = z_Q$), under the control of the other workers. In the second scenario, we assume that workers do not mate and thus produce only male offspring ($z_O = 1$). This allows us to investigate the relaxation of Gardner et al.'s (2012) key assumptions—negligible worker reproduction and equal sex ratio for queen-derived and worker-derived offspring—both independently and also in conjunction. Throughout our analysis, we assume that colonies containing workers have them in sufficiently large numbers that from a focal worker's perspective, the colony's reproductive offspring that she may altruistically rear consists of a mixture of siblings and nieces/nephews, with her own sons/daughters comprising only a negligible fraction of these offspring. Relaxing this assumption would promote the evolution of helping, for the simple reason that some of the recipients of helping would be the worker's own offspring.

In both scenarios, workers manipulate the sex ratio of

the queen's offspring but through different mechanisms. In the first scenario, we consider that both queen and workers produce male and female eggs and it is the workers' decision, as a group, that determines the proportion of male and female juveniles that will be raised to adulthood. Thus, the sex ratios of queen-produced and worker-produced offspring are the same as the colony's sex ratio ($z_O = z_Q = z_C$). We model this scenario using a neighbor-modulated (personal) fitness approach (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007) to determine the effect of a gene expressed by workers and controlling the sex ratio of the colony's offspring, z_C . In the second scenario, we consider that workers cannot adjust the sex of their own offspring (they are all males; $z_O = 1$) but that they can manipulate the sex ratio of the queen-produced offspring ($0 \leq z_Q \leq 1$). In this case, we use a neighbor-modulated fitness approach to determine the effect of a gene expressed by workers and controlling for the sex ratio of queen-produced offspring, z_Q . Notice that in this second scenario, workers are producing only sons and thus the sex ratio of the colony's juveniles will be more male biased than the offspring of the queen ($z_C = (1 - \mu)z_Q + \mu \geq z_Q$).

We then take an inclusive fitness approach (Hamilton 1963, 1964a, 1964b, 1970, 1972) to determine the value that a female worker places on her own offspring versus those of her colony. In the first case, the average value of the worker's offspring is $z_O v_m p_s + (1 - z_O) v_f p_D$, where v_f and v_m are the reproductive values of a female and a male (see app. A for derivation), respectively, and p_D and p_s are the consanguinities between a focal worker and her daughters and her sons, respectively (see app. B for derivation). The average value of the colony's offspring can be written as $z_C v_m p_m + (1 - z_C) v_f p_f$, where p_f and p_m are the average consanguinities between a focal worker and a random female juvenile and a random male juvenile, respectively, in their colony. Helping to rear b of the colony's juveniles at a loss of c of her own offspring is favored by natural selection if this increases the worker's inclusive fitness, that is, if $b[z_C v_m p_m + (1 - z_C) v_f p_f] > c[z_O v_m p_s + (1 - z_O) v_f p_D]$. We may rewrite this condition as $c/b < \alpha$, where

$$\alpha = \frac{z_C v_m p_m + (1 - z_C) v_f p_f}{z_O v_m p_s + (1 - z_O) v_f p_D} \quad (1)$$

is the potential for helping and represents the threshold cost/benefit ratio at which the worker is indifferent between helping to rear the colony's juveniles and producing her own offspring (Charnov 1978; Grafen 1986; Gardner et al. 2012). We say that haplodiploidy promotes altruistic helping if $\alpha > 1$ and that haplodiploidy inhibits altruistic helping if $\alpha < 1$, as $\alpha = 1$ represents the best-case scenario for a diploid, outbred, fully monogamous population

(Gardner et al. 2012). This framework holds for both all-or-nothing helping (i.e., all individuals choosing to develop as workers are completely sterile) and a continuum between the extremes of only helping and only reproducing (i.e., individuals choose to help a bit more versus a bit less). We summarize model notation in table 1.

Queen Virginity

In this section, we investigate the impact of haplodiploidy on the potential for altruistic helping in the context of split sex ratios due to queen virginity. We consider a population composed of a large number of colonies, each founded by a single queen. We assume that a proportion u of queens are unmated and hence produce only sons, whereas the remaining proportion $1 - u$ of queens are mated and produce both sons and daughters, including female workers. We denote by z_M the sex ratio of the reproductive offspring produced by mated queens. As unmated-queen colonies do not have workers, we assume that their productivity is a proportion $0 \leq a \leq 1$ of the productivity of the mated-queen colonies (Gardner et al. 2012). As workers are present only in mated-queen colonies and therefore help at only one type of colony, there is no useful distinction between helping that is obligate and helping that is facultative in response to colony type.

Mated Workers

We extend the queen virginity model presented by Gardner et al. (2012) by allowing workers to produce a significant share of the colony's offspring. We assume that workers are mated by unrelated males from their fathers' generation and that their offspring have the same sex ratio as the queen-derived offspring in their colony ($z_O = z_M = z_C$).

We find that the convergence stable sex ratio strategy (Taylor 1996; Taylor and Frank 1996) for colonies with workers is given by

$$\bar{z}_C = \frac{4 - \mu[\mu - 2(2 + \mu)\phi] - \mu[2a(2 - \mu)(1 + 2\phi) + (2 + \mu)[2 - \mu(1 - 2\phi)]]}{4(1 - u)[2 - \mu + [2 - (1 - \mu)\mu]\phi]} \quad (2a)$$

if $u \leq \{(2 + \mu)[2 - \mu(1 - 2\phi)]\}/\{2a(2 - \mu)(1 + 2\phi) + (2 + \mu)[2 - \mu(1 - 2\phi)]\}$ and

$$\bar{z}_C = 0 \quad (2b)$$

if $u \geq \{(2 + \mu)[2 - \mu(1 - 2\phi)]\}/\{2a(2 - \mu)(1 + 2\phi) + (2 + \mu)[2 - \mu(1 - 2\phi)]\}$ (see app. C for derivation). This solution can be used to calculate the population sex ratio, $\bar{z} = [ua + (1 - u)\bar{z}_C]/[ua + (1 - u)]$. In agreement with Gardner et al. (2012), we find that as the proportion of unmated queens increases in the population and hence

reproductive females become rarer, the workers are favored to produce a lower proportion of males (\bar{z}_C ; fig. 1).

We find that worker reproduction leads to workers favoring higher \bar{z}_C (fig. 1A). In the absence of worker reproduction, males may make genetic contributions to the next generation of reproductive females but do not contribute to the next generation of reproductive males. However, when workers reproduce, males make larger contributions to the next generation of reproductive females (by mating with workers, who then produce daughters) and are also able to contribute to the next generation of reproductive males (by fathering workers, who then produce sons; fig. 2). As a consequence, worker reproduction increases the class reproductive value of males and hence leads selection to favor a higher proportion of males.

In this scenario, the average value that a worker places on one of her colony's offspring is $\bar{z}_C v_m [(1 - \mu) p_M + \mu p_{Ne}] + (1 - \bar{z}_C) v_f [(1 - \mu) p_F + \mu p_{Ni}]$, where p_{Ne} is her consanguinity to a nephew and p_{Ni} is her consanguinity to a niece. As workers produce offspring with the same sex ratio as their colony, the average value they place on one of their own offspring is $\bar{z}_C v_m p_S + (1 - \bar{z}_C) v_f p_D$. Hence, the potential for helping is $\alpha = \{\bar{z}_C v_m [(1 - \mu) p_M + \mu p_{Ne}] + (1 - \bar{z}_C) v_f [(1 - \mu) p_F + \mu p_{Ni}]\} / \{\bar{z}_C v_m p_S + (1 - \bar{z}_C) v_f p_D\}$. We substitute the appropriate reproductive values, consanguinity coefficients, and sex ratios, giving

$$\alpha = \frac{(1 - u)\{2 - \mu + [2 - (1 - \mu)\mu]\phi\}[2 - \mu(1 - 2\phi)]}{4(1 - u)(2 - \mu) - 8[au(1 - \mu) - \mu(1 - u)]\phi} \tag{3a}$$

if $u \leq \{(2 + \mu)[2 - \mu(1 - 2\phi)]\} / \{2a(2 - \mu)(1 + 2\phi) + (2 + \mu)[2 - \mu(1 - 2\phi)]\}$ and

$$\alpha = \frac{(2 - \mu)(1 + 2\phi)}{4} \tag{3b}$$

if $u \geq \{(2 + \mu)[2 - \mu(1 - 2\phi)]\} / \{2a(2 - \mu)(1 + 2\phi) + (2 + \mu)[2 - \mu(1 - 2\phi)]\}$.

In the special case where there is no worker reproduction ($\mu = 0$), equation (3) simplifies to equation (5) of Gardner et al. (2012), and we find that haplodiploidy promotes altruistic helping in the context of split sex ratios due to queen virginity and that this effect increases with the proportion of unmated queens ($\alpha > 1$ and $d\alpha/du \geq 0$, when $\mu = 0$; fig. 3A). Colonies with mated queens are favored to produce an excess of females (fig. 1A), resulting in split sex ratios between mated-queen colonies and unmated-queens colonies (which produce only males). Consequently, all workers occur only in mated-queen colonies and are able to gain a relatedness advantage of having a higher proportion of sisters without this being completely canceled by an equivalent female bias at the population level.

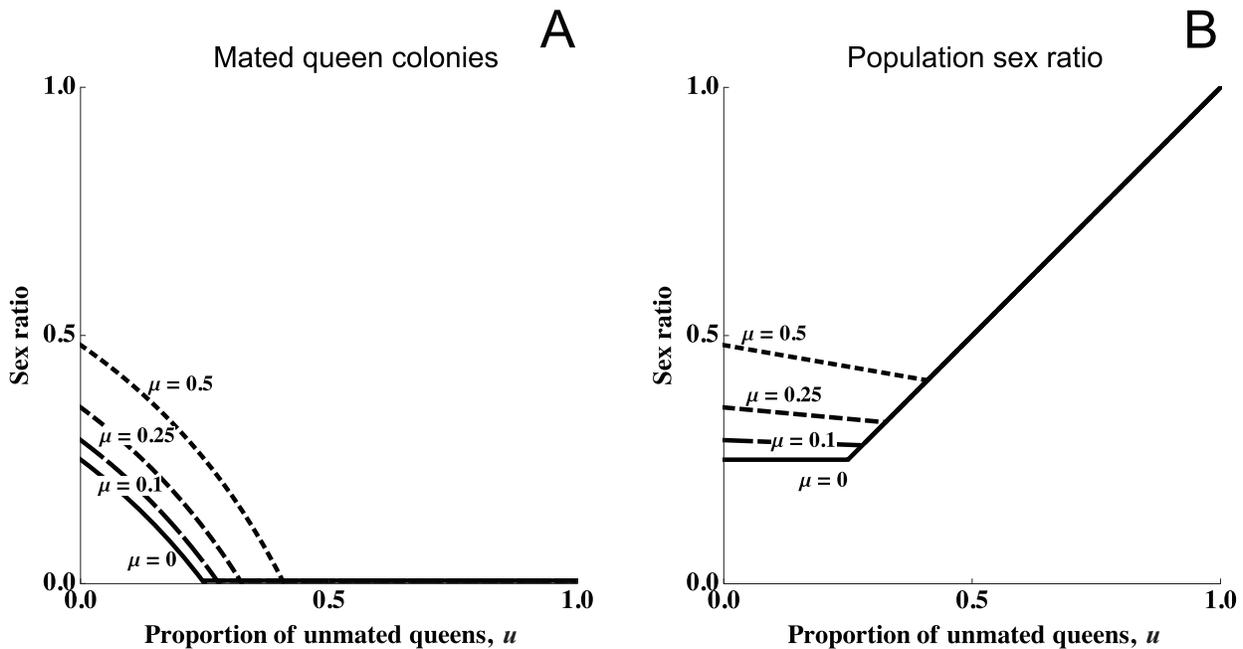


Figure 1: Split sex ratios due to queen virginity. The sex ratio (proportion males) is plotted against the proportion of unmated queens (u), assuming that workers are mated and produce offspring with the same sex ratio as the queen's offspring ($z_o = z_q$) and that a proportion μ of offspring are produced by workers. The figures show the sex ratio in colonies with mated queens (A; z_c) and the population sex ratio (B; \bar{z}).

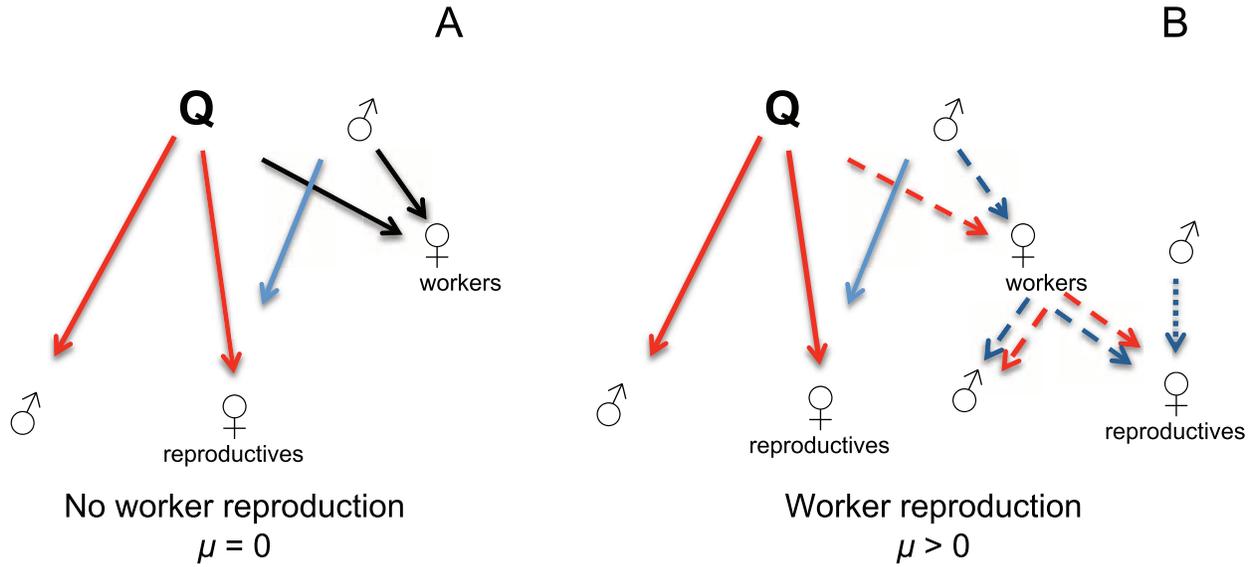


Figure 2: Worker reproduction and reproductive value. *A*, In the absence of worker reproduction, a male contributes half the genes of his diploid daughters but no genes to the haploid males produced by the queen. Thus, the genetic contribution of females to future generations is twice the contribution of males. *B*, If workers produce offspring, a male may contribute to the next generation of males through his grandsons (dashed blue lines). Consequently, worker reproduction increases the relative genetic contribution of males to future generations. The relative genetic contribution of males to future generations is further increased if the males also mate with workers.

However, when worker reproduction is considered ($\mu > 0$), we find that the potential for helping decreases with increasing worker reproduction ($d\alpha/d\mu \leq 0$; fig. 3A). As the proportion of worker reproduction increases in the population, the increased reproductive value of males drives an increase in the colony's sex ratio (fig. 3A). This results in a decrease in the relatedness between a worker and the offspring in her colony, which reduces the potential for helping. If the rate of worker reproduction is sufficiently high and queen unmatedness is sufficiently low, then this can even result in haplodiploidy inhibiting the evolution of altruistic helping. Specifically, $\alpha < 1$ when $u < \{2 + \mu - \phi[2 - \mu(1 - \mu)]\}[2 - \mu(1 - 2\phi)] / (4 - \mu^2 - \phi\{4 - 8a(1 - \mu) - \mu[8 - \mu(1 - \mu)]\} - 2\mu\phi^2[2 - \mu(1 - \mu)])$.

The empirical data on levels of virginity in outbreeding haplodiploid species, consistent with the expected breeding system of species en route to eusociality, show a range of $0.00 < u < 0.06$ with a mode of $u = 0$ (Godfray and Hardy 1993; West 2009). Within this range, the potential for helping is maximized when $u = 0.06$. Focusing on the best-case scenario of $u = 0.06$ and $a = 1$, we find that haplodiploidy actually inhibits the evolution of altruistic helping if the extent of worker reproduction exceeds $\mu \approx 0.11$ (fig. 3A). However, we might expect levels of virginity to be lower in social species (lower u) because there will be selection to avoid the large cost associated with not being able to produce workers. Workerless colonies are also expected to have lower productivity (lower

a). Both effects will act to further decrease the potential for altruistic helping.

Unmated Workers

We now assume that workers are unmated. In this case, the workers produce a proportion μ of the colony's offspring, and these worker-derived offspring are all males ($z_o = 1$). The remaining proportion $1 - \mu$ of the colony's offspring are queen derived, and the workers set the sex ratio of these offspring to z_M . Thus, from the point of view of a random worker, the colony offspring is composed of $(1 - \mu)z_M$ brothers, $(1 - \mu)(1 - z_M)$ sisters, and μ nephews (recall that each worker's own offspring represents a negligible fraction of the colony's brood).

We find that the convergence stable sex ratio strategy of workers for the queen-derived offspring within colonies with workers is given by

$$\bar{z}_M = \frac{(2 - 3\mu - 2\mu\phi)(1 - u) - 2au(1 + 2\phi)}{4(1 - u)(1 - \mu)(1 + \phi)} \quad (4a)$$

if $u \leq [2 - \mu(3 + 2\phi)] / [2 + 2a(1 + 2\phi) - \mu(3 + 2\phi)]$ and

$$\bar{z}_M = 0 \quad (4b)$$

if $u \geq [2 - \mu(3 + 2\phi)] / [2 + 2a(1 + 2\phi) - \mu(3 + 2\phi)]$ (see app. C for derivation). This solution can be used to calculate the colony's sex ratio $\bar{z}_C = \mu + (1 - \mu)\bar{z}_M$ and the

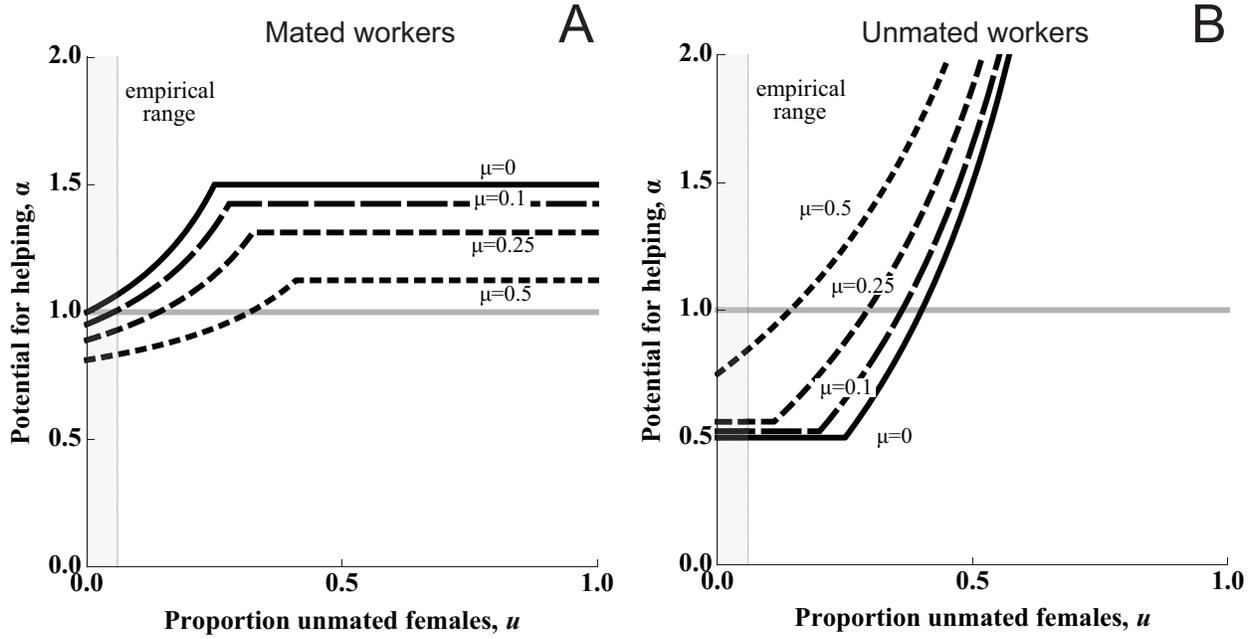


Figure 3: Potential for helping with queen virginity. The potential for helping (α) is plotted against the proportion of unmated queens (u), assuming that a proportion μ of offspring are produced by workers. The figures show the scenarios where workers are mated and produce offspring with the same sex ratio as the queen's offspring (A; $z_o = z_Q$) and workers are unmated and produce only sons (B; $z_o = 1$). In both cases we consider the best-case scenario of equal productivity among colonies ($a = 1$) and strict monogamy ($\phi = 1$). The shaded area shows the empirical range found for the rate of unmated queens in natural populations ($0 < u < 0.06$).

population sex ratio $\bar{z} = [au + (1 - u)z_M(1 - \mu) + \mu]/[1 - (1 - a)u]$. Both queen virginity and unmated worker reproduction increase the proportion of males in the population, and, as a result, workers are favored to bias the sex ratio of queen-derived offspring toward females ($d\bar{z}_M/du \leq 0$ and $d\bar{z}_M/d\mu \leq 0$; fig. E1; figs. E1, E2 available online).

In this scenario, the average value that a worker places on one of the colony's offspring is $\bar{\mu}v_m p_{Nc} + (1 - \mu)[\bar{z}_M v_m p_M + (1 - \bar{z}_M)v_f p_F]$. As workers are unmated, they may produce only sons ($z_o = 1$) and so the value the worker places on one of her own offspring is $v_m p_s$. Hence, the potential for helping is $\alpha = \{\mu v_m p_{Nc} + (1 - \mu)[\bar{z}_M v_m p_M + (1 - \bar{z}_M)v_f p_F]\}/v_m p_s$. Substituting the appropriate reproductive values, consanguinity coefficients, and sex ratios, this is

$$\alpha = \frac{2 - \mu(1 - 2\phi)}{4} \quad (5a)$$

if $u \leq [2 - \mu(3 + 2\phi)]/[2 + 2a(1 + 2\phi) - \mu(3 + 2\phi)]$ and

$$\alpha = \frac{[au + \mu(1 - u)](1 + 2\phi)}{2(1 - u)} \quad (5b)$$

if $u \geq [2 - \mu(3 + 2\phi)]/[2 + 2a(1 + 2\phi) - \mu(3 + 2\phi)]$.

We find that when workers are unmated and hence

constrained to produce only male offspring ($z_o = 1$), haplodiploidy inhibits the evolution of eusociality at low to medium rates of queen virginity, even when worker reproduction is negligible (fig. 3B). Specifically, $\alpha < 1$ when $u < [2 - \mu(1 + 2\phi)]/[2 - \mu(1 + 2\phi) + a(1 + 2\phi)]$ (fig. 3B). This is because the overall population sex ratio is female biased, which increases the reproductive value of males relative to that of females. Consequently, this leads to scenarios where sons are worth more to a worker than a female-biased mixture of siblings ($\alpha < 1$).

We also find that higher rates of worker reproduction promote the evolution of helping ($d\alpha/d\mu \geq 0$; fig. 3B). This is in the direction opposite to what we found when workers produced offspring of both sexes (fig. 3A). The reason for this difference is that an increase in the rate of worker reproduction increases the population sex ratio when workers can produce only sons, which increases the reproductive value of females. This increases the value of a mixture of sisters, brothers, and nephews relative to that of sons.

As the rates of worker reproduction (μ) and queen virginity (u) increase, this eventually leads to a male-biased population sex ratio, which decreases the value of sons, such that their relative value drops below that of a mixture of siblings and nephews. When this happens, haplodiploidy acts to promote the evolution of helping ($\alpha > 0$; fig. 1B).

If we consider the high end of the observed empirical range, with 6% virgin queens ($u = 0.06$), we find that haplodiploidy promotes the evolution of altruistic helping only if the extent of worker reproduction exceeds $\mu \approx 0.60$ (fig. 1B), which is much higher than the mean observed in empirical studies ($\mu \approx 0.12$; Wenseleers and Ratnieks 2006).

Queen Replacement

We now investigate the impact of haplodiploidy on the potential for altruistic helping in the context of split sex ratios due to queen replacement. We consider a population composed of a large number of colonies, each founded by a single queen. We assume that a proportion q of colonies are headed by their original queen (“queenright”), whose reproductive offspring have a sex ratio of z_R . The remaining proportion $1 - q$ of colonies are headed by a replacement queen (“queenless”), who is a daughter of the original queen and a sister of the colony’s workers and whose offspring have a sex ratio of z_L .

In this model, workers may find themselves in two different types of colony—queenless versus queenright—so we may usefully draw a distinction between obligate helping, which is expressed at the same level in both colonies, and facultative helping, which is restricted to one type of colony only. If helping is facultative, it is more likely to be favored in queenright colonies, as these will tend to have a relatively greater female bias in their sex ratios (Gardner et al. 2012). Hence, when considering facultative helping, we will restrict attention to helping in queenright colonies.

Mated Workers

We extend the queen replacement model presented by Gardner et al. (2012) by allowing workers to produce a significant share of the colony offspring. We assume that workers are mated by unrelated males from their fathers’ generation and that their offspring have the same sex ratio as the queen-derived offspring in their colony ($z_o = z_c$). We find that the joint convergence sex ratios for queenright (\bar{z}_R) and queenless (\bar{z}_L) colonies are

$$(\bar{z}_R, \bar{z}_L) = \left(0, \frac{3 - q(1 - u)}{4(1 - q)} \right) \quad (6a)$$

if $q \leq 1/(3 + \mu)$,

$$(\bar{z}_R, \bar{z}_L) = (0, 1) \quad (6b)$$

if $1/(3 + \mu) \leq q \leq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$, and

$$(\bar{z}_R, \bar{z}_L) = \left(\frac{(2 - \mu)[1 - q(3 + \mu)] - 2[2 - \mu - q[2 + (1 + \mu)\mu]\phi]}{4q[2 - \mu + [2 - (1 - \mu)\mu]\phi]}, 1 \right) \quad (6c)$$

if $q \geq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$ (see app. D for derivation). This solution can be used to calculate the population sex ratio $\bar{z} = q\bar{z}_R + (1 - q)\bar{z}_L$, with worker reproduction leading again to a higher proportion of males (fig. 4).

If helping is a facultative trait, expressed only in queenright colonies, the average value that a worker places on one of the queenright colony’s offspring is $\bar{z}_R v_m [\mu p_{Nc} + (1 - \mu)p_M] + (1 - \bar{z}_R) v_i [\mu p_{Ni} + (1 - \mu)p_F]$, and the average value she places on one of her own offspring is $\bar{z}_R v_m p_S + (1 - \bar{z}_R) v_i p_D$. The potential for helping is $\alpha = \{\bar{z}_R v_m [\mu p_{Nc} + (1 - \mu)p_M] + (1 - \bar{z}_R) v_i [\mu p_{Ni} + (1 - \mu)p_F]\} / [\bar{z}_R v_m p_S + (1 - \bar{z}_R) v_i p_D]$. Substituting the appropriate reproductive values, consanguinity coefficients, and sex ratios, this gives

$$\alpha = \frac{(2 - \mu)(1 + 2\phi)}{4} \quad (7a)$$

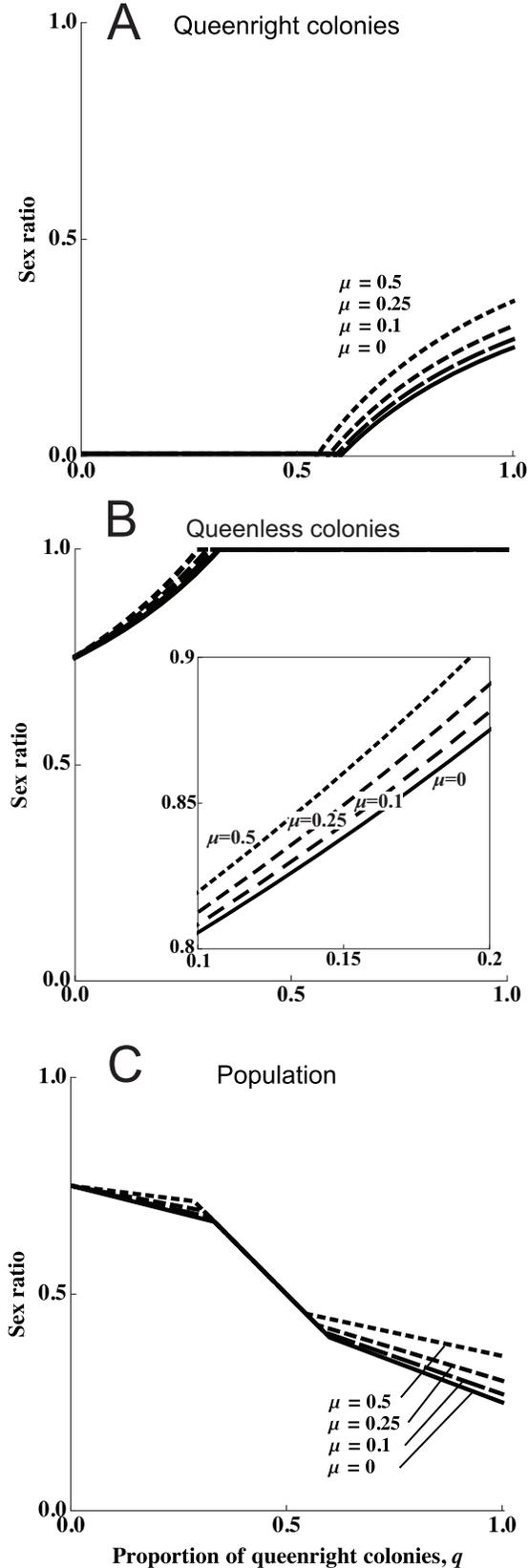
if $q \leq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$ and

$$\alpha = \frac{q[2 - \mu + [2 - (1 - \mu)\mu]\phi][2 - \mu(1 - 2\phi)]}{4q[2 - \mu(1 - \phi) + \phi] - 4(1 - \mu)\phi} \quad (7b)$$

if $q \geq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$.

Considering the facultative helping scenario with negligible worker reproduction ($\mu = 0$), we recover Gardner et al.’s (2012) result that haplodiploidy always promotes facultative helping. However, as we increase the level of worker reproduction, we find that this decreases the extent to which facultative helping is promoted ($d\alpha/d\mu \leq 0$) and even leads to facultative helping being inhibited ($\alpha < 1$; fig. 5A). The reason for this is that worker reproduction (1) increases the relative reproductive value of males (fig. 2) and (2) decreases the relative relatedness of the workers to the mixture of siblings and nephews that they could help to rear. Both of these factors reduce the value of helping relative to rearing their own offspring.

The potential for facultative helping also increases with the proportion of colonies where the queen is replaced ($d\alpha/dq \leq 0$). Specifically, for relatively lower frequency of queen replacement (if $q > [(2 - \mu)(1 + 2\phi)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$), helping can be promoted by haplodiploidy (if $\mu < 2(2\phi - 1)/(1 + 2\phi)$). The reason for this is that queenless colonies produce a relatively male-biased sex ratio, which increases the relative reproductive value of females and hence increases the value of a female-biased brood of siblings in the queenright colonies. If the frequency of queen replacement is higher (if $q < [(2 -$



$\mu)(1 + 2\phi)/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$, it no longer affects the potential for helping (α), which decreases with worker reproduction ($\alpha > 1$ if $\mu < 2(2\phi - 1)/(1 + 2\phi)$).

A small number of empirical studies on primitive eusocial bees have estimated that levels of queen replacement are between 20% and 40% ($0.6 \leq q \leq 0.8$, $n = 3$) in species with split sex ratios due to queen replacement (Packer 1986; Yanega 1989; Mueller 1991). However, at low rates of queen replacement, it could be hard to observe both queen replacement and the subsequent split sex ratios, and so we consider the range of 0%–40% queen replacement ($0.6 \leq q \leq 1$; Chapuisat and Keller 1999; Meunier et al. 2008; West 2009). In the best-case scenario for the evolution of eusociality, with queen replacement at 40% ($q = 0.6$), we find that haplodiploidy inhibits the evolution of facultative altruistic helping whenever the extent of worker reproduction exceeds $\mu \approx 0.4$ (fig. 5A).

We now consider the evolution of obligate helping, expressed equally by workers in queenright and queenless workers. In this case, the average value that a worker places on one of her colony's offspring is $q\{\bar{z}_R v_m[\mu p_{Nc} + (1 - \mu)p_M] + (1 - \bar{z}_R)v_f[\mu p_{Ni} + (1 - \mu)p_F]\} + (1 - q)[\bar{z}_L v_m p_{Nc} + (1 - \bar{z}_L)v_f p_{Ni}]$, and the average value she places on one of her own offspring is $q[\bar{z}_R v_m p_S + (1 - \bar{z}_R)v_f p_D] + (1 - q)[\bar{z}_L v_m p_S + (1 - \bar{z}_L)v_f p_D]$. Thus, the potential for helping is $\alpha = (q\{\bar{z}_R v_m[\mu p_{Nc} + (1 - \mu)p_M] + (1 - \bar{z}_R)v_f[\mu p_{Ni} + (1 - \mu)p_F]\} + (1 - q)[\bar{z}_L v_m p_{Nc} + (1 - \bar{z}_L)v_f p_{Ni}]) / \{q[\bar{z}_R v_m p_S + (1 - \bar{z}_R)v_f p_D] + (1 - q)[\bar{z}_L v_m p_S + (1 - \bar{z}_L)v_f p_D]\}$. Substituting the appropriate reproductive values, consanguinity coefficients, and sex ratios, this gives

$$\alpha = \frac{[1 + q(1 - \mu)](1 + 2\phi)}{4} \quad (8a)$$

if $q \leq 1/(3 + \mu)$,

$$\alpha = \frac{1 + 2\phi}{3 + \mu} \quad (8b)$$

if $1/(3 + \mu) \leq q \leq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$, and

$$\alpha = \frac{\{2 - \mu + [2 - (1 - \mu)\mu]\phi\}[1 + 2\phi + q(1 - \mu)(1 - 2\phi)]}{4\{2 - \mu(1 - \mu\phi) + [1 - q(1 - \mu)^2]\phi\}} \quad (8c)$$

if $q \geq [(1 + 2\phi)(2 - \mu)]/[6 + 4\phi - \mu(1 + \mu)(1 - 2\phi)]$.

In the case of no worker reproduction ($\mu = 0$), we

Figure 4: Split sex ratios due to queen replacement. The sex ratio (proportion males) is plotted against the proportion of queenright colonies (q), assuming that workers are mated and produce offspring with the same sex ratio as the queen's offspring ($z_o = z_q$) and that a proportion μ of offspring are produced by workers. The figures show the sex ratios in queenright colonies (A; z_R), queenless colonies (B; z_L), and the overall population (C; \bar{z}).

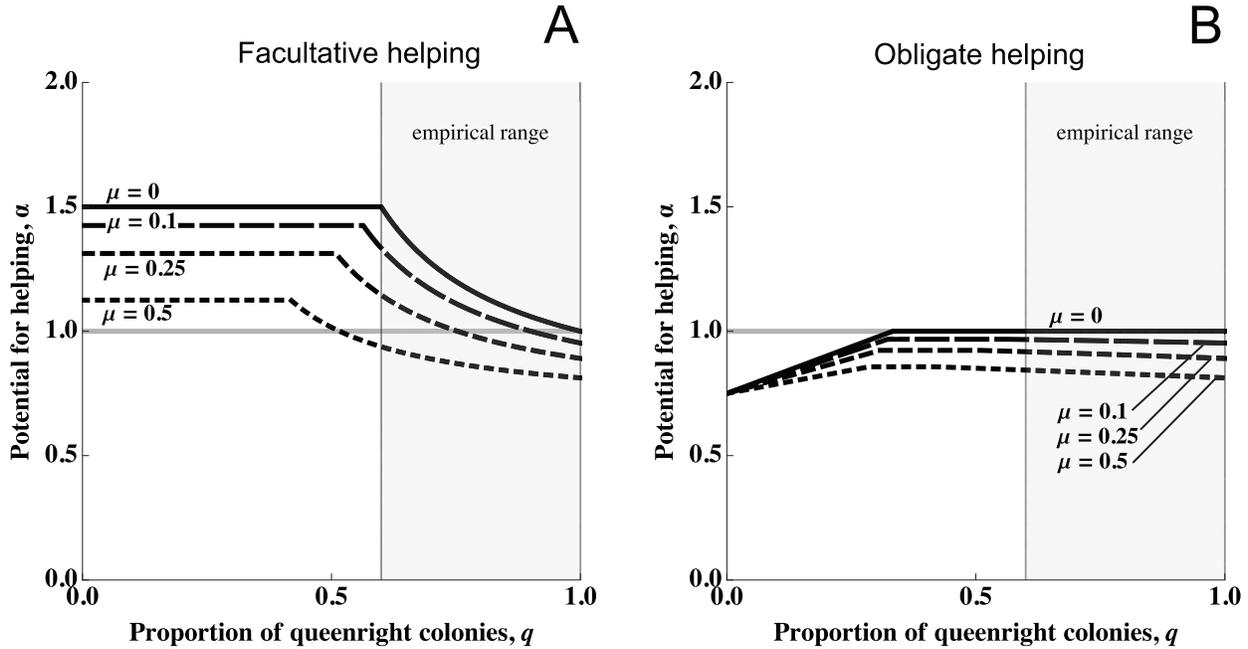


Figure 5: Potential for helping in the queen replacement model with mated workers. The potential for helping (α) is plotted against the proportion of queenright colonies (q), assuming that workers are mated and produce offspring with the same sex ratio as the queen’s offspring ($z_o = z_q$) and that a proportion μ of offspring are produced by workers. The figures show the potential for facultative helping given only in queenright colonies (A) and obligate helping given at both queenright and queenless colonies (B). The shaded area shows the empirical range observed in natural populations ($0.6 < q < 1$).

recover Gardner et al.’s (2012) result that haplodiploidy has no influence on the evolution of obligate helping ($\alpha = 1$) when the rate of queen replacement is low ($q > 0.67$) and inhibits the evolution of obligate helping ($\alpha < 1$) at higher levels of queen replacement ($q < 0.67$; fig. 5B). As the rate of worker reproduction increases ($\mu > 0$), this increases the relative reproductive value of males (fig. 2) and leads to workers rearing a higher proportion of worker-derived offspring. Both of these factors increase the sex ratio among the offspring that the workers help to rear (fig. 4). All of these factors decrease the average relatedness between a worker and her colony’s offspring and hence decrease the potential for helping (fig. 5B).

As worker reproduction increases, this decreases the extent to which haplodiploidy promotes the evolution of obligate helping ($d\alpha/d\mu \leq 0$; fig. 5B). Indeed, if worker reproduction is nonnegligible, then obligate helping is always inhibited by haplodiploidy ($\alpha < 1$ if $\mu > 0$; fig. 5B). The reason for this, as discussed above, is that worker reproduction increases the relative reproductive value of males and hence decreases the relative relatedness to the offspring (siblings and nephews) that the worker could help to rear.

Unmated Workers

We now consider the consequences of reproductive workers being unmated. All our assumptions are the same as in the worker reproduction model, except that the worker-derived offspring are all males ($z_o = 1$). We find that the joint convergence stable sex ratio strategy for queenright (\bar{z}_R) and queenless (\bar{z}_L) colonies is given by

$$(\bar{z}_R, \bar{z}_L) = \begin{cases} \left(0, \frac{3 - q(1 - \mu) - 4\mu}{4(1 - q)(1 - \mu)}\right) & q \leq \frac{1}{3(1 - \mu)} \\ (0, 1) & \text{if } \frac{1}{3(1 - \mu)} \leq q \leq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \\ \left(\frac{q(1 - \mu)(3 + 2\phi) - 2\phi - 1}{4q(1 - \mu)(1 + \phi)}, 1\right) & q \geq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \end{cases} \quad (9a)$$

when $\mu \leq (3 - q)/(4 - q)$ and by

$$(\bar{z}_R, \bar{z}_L) = (0, 0) \quad (9b)$$

when $\mu \geq (3 - q)/(4 - q)$ (see app. D for derivation). This solution can be used to calculate the population sex ratio $\bar{z} = \mu + (1 - \mu)[q\bar{z}_R + (1 - q)\bar{z}_L]$. Both queen replacement and worker reproduction increase the population sex ratio. As a result, workers from both queenright and queenless colonies are selected to bias the sex ratio of queen-derived

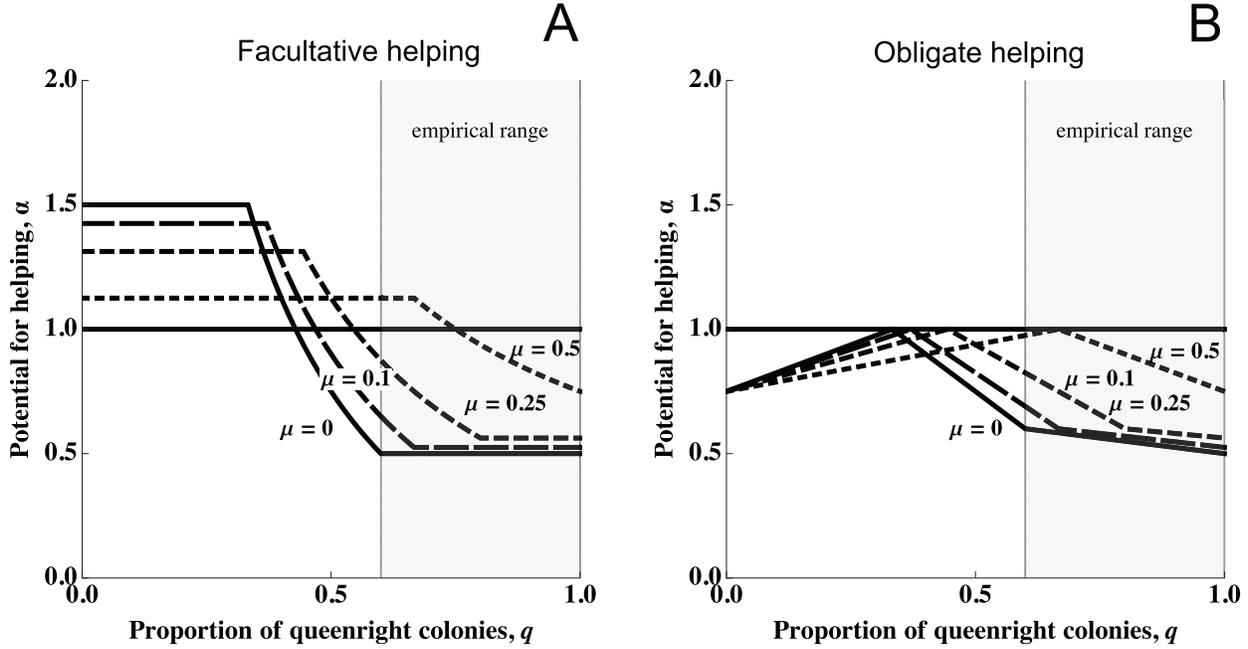


Figure 6: Potential for helping in the queen replacement model with unmated workers. The potential for helping (α) is plotted against the proportion of queenright colonies (q), assuming that workers are unmated and produce only sons ($z_{\text{O}} = 1$) and that a proportion μ of offspring are produced by workers. The figures show the potential for facultative helping given only in queenright colonies (A) and obligate helping given at both queenright and queenless colonies (B). The shaded area shows the empirical range observed in natural populations ($0.6 < q < 1$).

offspring toward the production of females ($d\bar{z}_R/dq \geq 0$ and $d\bar{z}_R/d\mu \leq 0$ and $d\bar{z}_L/du \leq 0$; fig. E2).

If helping is a facultative trait, expressed only in queenright colonies, the average value that a worker places on one of the colony's offspring is $\mu v_m p_{Nc} + (1 - \mu)[\bar{z}_R v_m p_M + (1 - \bar{z}_R) v_f p_F]$, and the average value that she places on one of her own offspring is $v_m p_S$. Thus, the potential for helping is $\alpha = \{\bar{z}_R v_m [\mu p_{Nc} + (1 - \mu) p_M] + (1 - \bar{z}_R) v_f [\mu p_{Ni} + (1 - \mu) p_F]\} / [\bar{z}_R v_m p_S + (1 - \bar{z}_R) v_f p_D]$. Substituting the appropriate reproductive values, consanguinity coefficients, and sex ratios, we obtain

$$\alpha = \begin{cases} \frac{(2 - \mu)(1 + 2\phi)}{4} & q \leq \frac{1}{3(1 - \mu)} \\ \frac{[1 - q(1 - 2\mu)](1 + 2\phi)}{4q} & \text{if } \frac{1}{3(1 - \mu)} \leq q \leq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \\ \frac{2 - \mu(1 + 2\phi)}{4} & q \geq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \end{cases} \quad (10a)$$

when $\mu \leq (3 - q)/(4 - q)$ and

$$\alpha = \frac{(5 - q)\mu(1 + 2\phi)}{4(3 - q)} \quad (10b)$$

when $\mu \geq (3 - q)/(4 - q)$. If the extent of worker repro-

duction is negligible ($\mu \approx 0$), haplodiploidy promotes facultative helping only if the frequency of queen replacement is sufficiently high ($q < (1 + 2\phi)/(5 + 2\phi)$; fig. 6A). This result differs from that of Gardner et al. (2012), who showed that haplodiploidy always promotes facultative helping. This difference stems from us considering that workers produce only sons rather than a mixture of sons and daughters in the same ratio as the offspring of the queen. In a population where workers control colony sex ratio and the proportion of queenright colonies is high (large q), the population sex ratio is female biased, which increases the reproductive value of males. Consequently, sons are worth more than a mixture of sons and daughters. If we consider a monogamous population and the empirically estimated range of rates of queen replacement ($0.6 \leq q \leq 1$), helping is never promoted in this scenario (fig. 6A).

As the rate of worker reproduction increases, the parameter range over which facultative helping is promoted by haplodiploidy becomes larger (fig. 6A; $\alpha > 1$ if $q < (1 + 2\phi)/[5 - 2\mu(1 + 2\phi) + 2\phi]$ and $0 < \mu < (3 - q)/(4 - q)$). The reason for this is that worker reproduction decreases the relative reproductive value of males (fig. 2) and hence reduces the relative value of producing sons. As the proportion of worker-derived offspring increases to very high levels ($\mu > (3 - q)/(4 - q)$), the population sex ratio

becomes increasingly male biased and the rare-sex effect means that the inclusive fitness value of a worker's own offspring (a son) is lower than that of a random juvenile in the worker's colony (which is composed of both male and female offspring). Thus, helping is promoted by haplodiploidy, with the potential for helping increasing with both the proportion of queen survival and the proportion of worker reproduction ($\alpha > 1$ if $q > [12 - 5\mu(1 + 2\phi)]/[4 - \mu(1 + 2\phi)]$). Considering the best-case scenario of $q = 0.6$, facultative helping is promoted if the proportion of worker reproduction exceeds $\mu \approx 0.33$ (fig. 3A).

If helping is an obligate trait, expressed equally by workers in queenright and queenless colonies, the average value a worker places on one of the colony's offspring is $\mu v_m p_{Ne} + (1 - \mu)\{q[\bar{z}_R v_m p_M + (1 - \bar{z}_R) v_f p_F] + (1 - q)[\bar{z}_L v_m p_{Ne} + (1 - \bar{z}_L) v_f p_{Ni}]\}$, and the average value she places on her own offspring is $v_m p_S$. Thus, the potential for helping is $\alpha = (\mu v_m p_{Ne} + (1 - \mu)\{q[\bar{z}_R v_m p_M + (1 - \bar{z}_R) v_f p_F] + (1 - q)[\bar{z}_L v_m p_{Ne} + (1 - \bar{z}_L) v_f p_{Ni}]\})/(v_m p_S)$. Substituting the appropriate reproductive values, consanguinity coefficients, and sex ratios, this gives

$$\alpha = \begin{cases} \frac{[1 + q(1 - \mu)(1 + 2\phi)]}{4} & q \leq \frac{1}{3(1 - \mu)} \\ \frac{[1 - q(1 - \mu)(1 + 2\phi)]}{2} & \text{if } \frac{1}{3(1 - \mu)} \leq q \leq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \\ \frac{1 + 2\phi + q(1 - \mu)(1 - 2\phi)}{4} & q \geq \frac{1 + 2\phi}{(1 - \mu)(3 + 2\phi)} \end{cases} \quad (11a)$$

when $\mu \leq (3 - q)/(4 - q)$ and

$$\alpha = \frac{\mu(1 + 2\phi)}{3 - q} \quad (11b)$$

when $\mu \geq (3 - q)/(4 - q)$. We find that obligate helping is inhibited by haplodiploidy ($\alpha < 1$), except when the frequency of worker reproduction is very high ($\alpha > 1$ when $q > 3 - \mu(1 + 2\phi)$; fig. 6B). Again, this corresponds to a male bias in sex allocation at the population level, which decreases the relative reproductive of males and hence reduces the value of producing sons. For example, assuming $q = 0.8$, obligate helping is promoted by haplodiploidy only if the proportion of worker-laid offspring exceeds $\mu \approx 0.73$.

Discussion

We have quantified the effect of haplodiploidy on the evolution of helping, in the context of split sex ratios that arise owing to queen virginity or queen replacement. We have found that worker reproduction, especially when workers are constrained to produce only sons, has a negative influence on the evolution of helping (lower α), ei-

ther reducing the extent to which it is promoted or even leading to it being inhibited. Considering queen virginity, we expect the influence of haplodiploidy on the evolution of helping to be a slight promotion, a slight inhibition, or a strong inhibition ($0.5 < \alpha < 1.068$; fig. 3). Considering queen replacement, we expect the influence of haplodiploidy on the evolution of helping to be (a) positive or negative for facultative helping ($0.5 < \alpha < 1.5$; figs. 5A, 6A) or (b) slightly or strongly inhibitive for obligate helping ($0.5 < \alpha < 1$; figs. 5B, 6B).

Worker Reproduction and Unmated Workers

We found that increasing the level of worker reproduction tends to reduce the extent to which haplodiploidy promotes the evolution of helping and can even lead to haplodiploidy inhibiting the evolution of helping (figs. 3, 5, 6). This arises for two reasons. First, because brothers and sisters are replaced with nephews and nieces, this decreases the relatedness between workers and the offspring that they could help to raise in their colony. Second, the increased reproductive value of males (fig. 2; Trivers and Hare 1976; Pamilo 1991; Gardner et al. 2012) and equal relatedness to nephews and nieces both lead to workers being favored to bring about a higher proportion of males in the brood that they help to raise (higher z_C). This also reduces the relatedness between potential workers and the offspring that they could help to raise. Empirical data from the social Hymenoptera suggest that the proportion of offspring produced by workers ranges from 0% to 100%, with an average of 12% (Ratnieks et al. 2006; Wenseleers and Ratnieks 2006).

We found that constraining workers to produce only male offspring leads to haplodiploidy having a strong inhibitory affect on the evolution of helping. The reason for this is that when workers control the sex allocation of their colonies, the population sex ratio tends to be female biased (figs. 1, 4, E1, E2), which increases the relative reproductive value of males. Consequently, helping is relatively inhibited when the offspring of workers contain a higher proportion of males. Worker reproduction being constrained to only males also means that workers would be helping to rear only nephews within a colony and not nieces, which has implications for relatedness and reproductive value, but these effects are smaller. Empirical data from the social hymenoptera suggest that in many of the cases where workers reproduce, they are constrained to produce only males (Ratnieks et al. 2006; Wenseleers and Ratnieks 2006). Whenever this is the case, we predict that haplodiploidy will inhibit the evolution of helping and that this affect will be relatively strong, with $\alpha \approx 0.5$ (figs. 3B, 6).

Haplodiploidy and the Evolution of Eusociality

We have shown that there are only two scenarios that could have possibly led to nontransient split sex ratios en route to eusociality: queen virginity and queen replacement (Gardner et al. 2012). In the above sections and figures 3, 5, and 6, we have used the empirical data to parameterize these models and estimate the range of possible consequences. We now condense this information to provide an overall estimate of the influence of these two scenarios. Considering queen virginity, levels of unmatedness in outbreeding Hymenoptera species are in the range 0%–6%, with a mode of 0%. Assuming a virginity rate of 3% ($u = 0.03$) and that workers produce 12% of offspring ($\mu = 0.12$), we predict that haplodiploidy will inhibit rather than promote the evolution of helping. This inhibition will be weak when workers produce both sons and daughters ($\alpha \approx 0.97$) and strong when workers are constrained to produce only sons ($\alpha \approx 0.53$). These predictions assume that colonies without helpers are as productive as colonies with helpers ($a = 1$). If colonies without helpers are less productive ($a < 1$), then this effectively reduces the extent to which sex ratios are split and leads to a lower potential for helping (lower α ; Gardner et al. 2012).

Queen replacement occurs in 0%–40% of colonies (Packer 1986; Yanega 1989; Mueller 1991). Assuming a replacement rate of 20% ($q = 0.8$) and that workers produce 12% of offspring, we predict that haplodiploidy will inhibit the evolution of obligate helping but will either slightly promote or slightly or strongly inhibit the evolution of facultative helping. Facultative helping will be slightly promoted when workers produce sons and daughters ($\alpha \approx 1.05$) but strongly inhibited when workers are constrained to produce only sons ($\alpha \approx 0.5$). Obligate helping will be slightly inhibited when workers produce sons and daughters ($\alpha \approx 0.95$) but strongly inhibited when workers are constrained to produce only sons ($\alpha \approx 0.5$).

Overall, our results suggest that split sex ratios are unlikely to have led to haplodiploidy promoting the evolution of eusociality. Our empirically parameterized predictions suggest that the influence of split sex ratios is likely to have been minor and may have actually inhibited rather than promoted the evolution of eusociality. Furthermore, split sex ratios due to either queen virginity or queen replacement are very rare. Consequently, the most common scenario is that in which neither occurs ($u \approx 0$, $q \approx 1$), in which case haplodiploidy has no effect ($\alpha \approx 1$ or $\alpha < 1$ with worker reproduction) if workers can produce sons and daughters or is strongly inhibitory if workers are constrained to produce only sons ($\alpha \approx 0.5$). Trivers and Hare (1976) also suggested that split sex ratios could arise transiently as worker control spreads through the population. We have analyzed this scenario elsewhere and

concluded that it is unlikely to have had a major influence on the evolution of eusociality (J. Alpedrinha, A. Gardner, and S. A. West, unpublished manuscript).

More generally, our results support the argument that from the perspective of how relatedness influences the evolution of eusociality, the most important factor is monogamy and not haplodiploidy (Boomsma 2007, 2009; Hughes et al. 2008; West and Gardner 2010). In species with strict lifetime monogamy, potential helpers are as related to the siblings that they could help to raise as they are to their own offspring. Consequently, only a small economic (ecological) benefit to cooperation is required for helping to be favored (Boomsma 2007). Consistent with this, eusociality has evolved only in species with strict lifetime monogamy (Hughes et al. 2008; Cornwallis et al. 2010) and where there is some ecological benefit to cooperation, which tends to be associated with extended parental care or fortress defence (Queller and Strassmann 1998; Davies et al. 2012).

Acknowledgments

Our work on haplodiploidy and the evolution of eusociality was inspired by questions from J. Boomsma at the “Evolution of Societies” meeting held by the Royal Society in 2009. We thank A. Grafen, I. Pen, and two reviewers for comments on the manuscript and the European Research Council, the Royal Society, and Balliol College for funding.

APPENDIX A**Reproductive Value**

Reproductive value describes the expected contribution of genes made by an individual or class of individuals to a generation in the distant future (Fisher 1930; Taylor 1996; Gardner et al. 2012). Reproductive value may first be calculated for a class and then shared equally by all the individuals of that class, that is, $v_j = c_j/N_j$, where v_j is the individual reproductive value, c_j the class reproductive value, and N_j the number of individuals from that class in the population. More generally, we may scale individual class reproductive values by any constant, without impacting our key predictions. In our models, we define two classes of reproductive (as opposed to worker) individuals: males and females. Male class reproductive value, c_m , is the probability that a gene picked at random in a distant generation descends from a male ancestor in the present generation. If we multiply all individual reproductive val-

ues by the total number of individuals in the population, we obtain $v_m = c_m/\bar{z}$, where \bar{z} is the population sex ratio. Similarly, we define female class reproductive value as $v_f = c_f/(1 - \bar{z})$.

We now derive the class reproductive values for males and females for a haplodiploid population, allowing for worker reproduction and queen replacement. We census the population at the moment that reproductive offspring are produced and following sex allocation decision (for details on sex allocation decision, see apps. C, D). Only reproductive larvae are included in the census (all other individuals in the population are adults at this time). The proportion of genes in female larvae at the time of census that derive from the females at the last census is $\mathcal{P}_{f \leftarrow f} = (1/2)\zeta_{Q,f} + (1/4)\zeta_{W,f}$ where $\zeta_{Q,f}$ is the probability of picking at random from the whole female population a larvae that is queen derived and $\zeta_{W,f}$ is the probability of picking at random from the whole female population a larvae that is worker derived (notice that $\zeta_{Q,f} = 1 - \zeta_{W,f}$). That is, with probability $\zeta_{Q,f}$ the larva is queen derived and hence a proportion 1/2 of her genes descend from a female from the previous census (i.e., her mother, the queen), and with probability $\zeta_{W,f}$ the larva is worker derived and hence a proportion 1/4 of her genes descend from a female from the previous census (i.e., half derive from her mother, a worker, who derives half of her genes from the queen). Thus, the proportion of genes in female larvae at the time of census that derive from males in the previous census is $\mathcal{P}_{f \leftarrow m} = 1 - \mathcal{P}_{f \leftarrow f}$. The proportion of genes in male larvae at the time of census that derived from females in the previous census is $\mathcal{P}_{m \leftarrow f} = \zeta_{Q,m} + (1/2)\zeta_{W,m}$, where $\zeta_{Q,m}$ is the probability of picking at random from the whole population a queen-derived male and $\zeta_{W,m}$ is the probability of picking at random from the whole population a worker-derived male. Thus, the proportion of genes in male larvae at the time of census that derived from males in the previous census is $\mathcal{P}_{m \leftarrow m} = 1 - \mathcal{P}_{m \leftarrow f}$.

The class reproductive values are given by the dominant left eigenvector of the gene-flow matrix, that is, the solution to $(c_f \ c_m) = (c_f \ c_m) \cdot \mathbf{M}$ (Taylor 1996; Frank 1998), where \mathbf{M} is

$$\mathbf{M} = \begin{bmatrix} \mathcal{P}_{f \leftarrow f} & \mathcal{P}_{f \leftarrow m} \\ \mathcal{P}_{m \leftarrow f} & \mathcal{P}_{m \leftarrow m} \end{bmatrix}. \quad (\text{A1})$$

Thus, we solve the system of equations $c_f = \mathcal{P}_{f \leftarrow f}c_f + \mathcal{P}_{m \leftarrow f}c_m$ and $c_m = \mathcal{P}_{f \leftarrow m}c_f + \mathcal{P}_{m \leftarrow m}c_m$.

Queen Virginity

If we pick a male at random from the population after the sex allocation culling, the probability that his mother

was a queen rather than a worker is $\zeta_{Q,m} = [ua + (1 - u)(1 - \mu)z_M]/[ua + (1 - u)(1 - \mu)z_M + (1 - u)z_O]$. If we pick a female at random from the population after the sex allocation culling, the probability that her mother was a queen rather than a worker is $\zeta_{Q,f} = (1 - u)(1 - \mu)(1 - z_M)/\{(1 - u)(1 - \mu)(1 - z_M) + \mu(1 - z_O)\}$. If we pick a male at random from the population after the sex allocation culling, the probability that his mother was a worker rather than a queen is $\zeta_{W,m} = 1 - \zeta_{Q,m}$, and if we pick a female at random from the population after the sex allocation culling, the probability that her mother was a worker rather than a queen is $\zeta_{W,f} = 1 - \zeta_{Q,f}$.

Substituting these in matrix \mathbf{M} and solving $(c_f \ c_m) = (c_f \ c_m) \cdot \mathbf{M}$ gives the class reproductive values

$$c_f = \frac{1}{\Psi} (2[1 - z_M(1 - \mu) - z_O\mu] \times \{2au + (1 - u)[2z_M(1 - \mu) + z_O\mu]\}), \quad (\text{A2})$$

$$c_m = \frac{1}{\Psi} [2 - 2z_M(1 - \mu) + \mu(1 - 3z_O)] \times \{au + (1 - u)[z_M(1 - \mu) + z_O\mu]\}, \quad (\text{A3})$$

where $\Psi = au(6[1 - z_M(1 - \mu) + \mu(1 - 7z_O)] - (1 - u)[6z_M^2(1 - \mu)^2 - z_O\mu(4 + \mu - 5z_O\mu)] - z_M(1 - \mu)(6 + \mu - 11z_O\mu))$.

Queen Replacement

If we pick a male at random from the population after the sex allocation culling, the probability that his mother was a queen rather than a worker is $\zeta_{Q,m} = (1 - \mu)qz_R/\{(1 - \mu)[qz_R + (1 - q)z_L] + \mu z_O\}$. If we pick a female at random from the population after the sex allocation culling, the probability that her mother was a queen rather than a worker is $\zeta_{Q,f} = (1 - \mu)q(1 - z_R)/\{(1 - \mu)[q(1 - z_R) + (1 - q)(1 - z_L)]\}$. If we pick a male at random from the population after the sex allocation culling, the probability that his mother was a worker rather than a queen is $\zeta_{W,m} = 1 - \zeta_{Q,m}$, and if we pick a female at random from the population after the sex allocation culling, the probability that her mother was a worker rather than a queen is $\zeta_{W,f} = 1 - \zeta_{Q,f}$.

Substituting these in matrix \mathbf{M} and solving $(c_f \ c_m) = (c_f \ c_m) \cdot \mathbf{M}$ gives the class reproductive values

$$c_f = \frac{1}{\Omega} (2\{[(1 - q)z_L + 2qz_R](1 - \mu) + z_O\mu\} \times [(1 - q)z_L + qz_R](1 - \mu) + z_O\mu - 1), \quad (\text{A4})$$

$$c_m = \frac{1}{\Omega} (\{3z_L + q(1 - 3z_L + 2z_R)(1 - \mu) + 3(z_O - z_L)\mu - 3\} \times \{qz_R(1 - \mu) + z_O\mu + z_L[1 - q(1 - \mu)]\}), \quad (\text{A5})$$

where $\Omega = 5(1 - q)^2 z_L^2 (1 - \mu)^2 + q^2 z_R (1 - 6z_R)(1 - \mu)^2 - (1 - q)z_L(1 - \mu)[5 - q(1 + 11z_R)(1 - \mu) - 10z_O\mu] - 5z_O\mu(1 - z_O\mu) - q(1 - \mu)(7z_R - z_O\mu - 11z_Oz_R\mu)$.

APPENDIX B

Genetic Associations

Consanguinity

The coefficient of consanguinity p_{ij} between two individuals, i and j , describes the probability that a gene drawn at random from individual i is identical by descent to a gene drawn at random from individual j (Bulmer 1994). Due to the haplodiploid genetics, the consanguinity of a male to himself is different from the consanguinity of a female to herself. Assuming outbreeding, the consanguinity of a (diploid) female to herself is $p_{FF} = 1/2$. The consanguinity of a (haploid) male to himself is $p_{MM} = 1$. The consanguinity of two maternal sisters is given by the probability $1/4$ of drawing their two maternal genes, times the consanguinity $1/2$ of their mother to herself, plus the probability $1/4$ of drawing their two paternal genes, times the probability ϕ that they share the same father, times the consanguinity 1 of their father to himself, that is, $p_F = (1 + 2\phi)/8$. The consanguinity between opposite-sex siblings is the probability $1/2$ of drawing their two maternal genes times the consanguinity $1/2$ of the mother to herself, that is, $p_M = 1/4$. The consanguinity between mother and daughter is given by the probability $1/2$ of drawing the maternal gene from the daughter times the consanguinity $1/2$ of the mother to herself, that is, $p_D = 1/4$. The consanguinity between mother and son is given by the probability 1 of drawing the maternal gene from the son times the consanguinity $1/2$ of the mother to herself, that is, $p_S = 1/2$. The consanguinity between aunt and niece is given by the consanguinity $(1 + 2\phi)/8$ between two maternal sisters times the probability $1/2$ of drawing the maternal gene from the niece, that is, $p_{Ni} = (1 + 2\phi)/16$. Equally, the consanguinity between aunt and nephew is given by the consanguinity $(1 + 2\phi)/8$ between two maternal sisters times the probability 1 of drawing the maternal gene from the nephew, that is, $p_{Ne} = (1 + 2\phi)/8$.

APPENDIX C

Queen Virginity

Here we derive the convergence stable sex ratio strategies (Taylor 1996) for the queen virginity models.

Mated Workers

We determine sex allocation the following way: we assume that the queen produces $N(1 - \mu)$ sons and $N(1 - \mu)$ daughters and the workers decide which half of these to raise, giving $N(1 - \mu)$ queen-derived offspring in total, with sex ratio z_M . Thus, there will be $(1 - \mu)Nz_M$ male and $(1 - \mu)N(1 - z_M)$ female queen-derived offspring developing to reproductive maturity, where μ is the proportion of worker reproduction in the colony and z_M is the sex ratio followed for queen-derived offspring. If workers are limited to produce sons, then they produce μN males. If they produce offspring of both sexes, we assume that they produce N sons and N daughters, of which only μN survive. Hence, there will be μNz_O male and $\mu N(1 - z_O)$ female worker-derived offspring developing to reproductive maturity, where z_W is the sex ratio followed for worker-derived offspring. We assume that workers are limited to produce the same sex ratio as queen-derived offspring, and thus $z_O = z_M$.

The fitness of a queen-derived female is the probability that she will be reared to maturity, which is $(1 - \mu)(1 - z_M)$; the average fitness of her class is $(1 - \mu)(1 - \bar{z}_M)$; and, thus, her relative fitness is $W_f = [(1 - \mu)(1 - z_M)]/[(1 - \mu)(1 - \bar{z}_M)]$. The probability of survival of a male is found in a similar way, and the relative fitness of a male egg is $W_r = [(1 - u)(1 - \mu)z_M + ua]/[(1 - u)(1 - \mu)\bar{z}_M + ua]$. Natural selection favors the increase of a trait in the population if individuals carrying genes for that trait are on average fitter than the population average. If we consider that a gene G with genic value g affects the sex allocation strategy of the individuals carrying it, G is favored if $dW/dg > 0$. Hence, the marginal fitness of G is given by

$$\begin{aligned} \frac{dW}{dg} &= c_f \frac{dW_f}{dg} + c_m \frac{dW_m}{dg} \\ &= c_f \frac{\partial W_f}{\partial z_M} \frac{dz_M}{d\hat{g}} \frac{d\hat{g}}{dg_f} + c_m \frac{\partial W_m}{\partial z_M} \frac{dz_M}{d\hat{g}} \frac{d\hat{g}}{dg_m}, \end{aligned} \quad (C1)$$

where $dz_M/d\hat{g} = 1$ is the genotype-phenotype map, $d\hat{g}/dg_f = \mu p_{Ni} + (1 - \mu)p_F$ is the coefficient of consanguinity between a worker and an average female juvenile in the colony, and $d\hat{g}/dg_m = \mu p_{Ne} + (1 - \mu)p_M$ is the average consanguinity coefficient between a worker and a random male juvenile in the colony. Replacing these expressions with the model parameters allows us to find the convergence stable sex ratio strategy z_M^* for mated-queen colonies.

Unmated Workers

We consider that workers contribute a proportion μ of offspring, and these are all male. They also decide the sex

ratio of the $1 - \mu$ queen offspring. Thus, there will be $N(1 - \mu)$ queen sons and $N(1 - \mu)$ queen daughters, from which workers choose to raise half, given by sex ratio z_M . Thus, the colony's offspring are composed of $N(1 - \mu)z_M$ queen's sons, $N(1 - \mu)(1 - z_M)$ queen's daughters, and $N\mu$ workers' sons.

The fitness of a juvenile female in the population is given by the probability that she will be reared to maturity, which is $(1 - u)(1 - z_M)$. The average fitness of her class is $(1 - u)(1 - \bar{z}_M)$, and thus, her relative fitness is $W_f = [(1 - u)(1 - z_M)]/[(1 - u)(1 - \bar{z}_M)]$. The probability of survival of a male is found in a similar way, and the relative fitness of a male egg is $W_m = \{(1 - u)[(1 - \mu)z_M + \mu] + ua\}/\{(1 - u)[(1 - \mu)\bar{z}_M + ua]\}$. Natural selection favors the increase of a trait in the population if individuals carrying that trait are on average fitter than the population average. If we consider that a gene G with genic value g affects the sex allocation strategy of the individuals carrying it, G is favored if $dW/dg > 0$. We use the procedure described by equation (C2) to find the marginal fitness equation of z_M , where $d\hat{g}/dg_f = p_f$ is the coefficient of consanguinity between sisters and $d\hat{g}/dg_m = p_m$ is the average coefficient of consanguinity between a random male juvenile in the colony and a worker. Replacing these expressions by the model parameters allows us to find the convergence stable sex ratio strategy for mated-queen colonies.

APPENDIX D

Queen Replacement

Mated Workers

The fitness of a juvenile queenright colony male is defined as the probability of a male to survive, that is, $(1 - \mu)[qz_R + (1 - q)z_L] + \mu\bar{z}_O$. The average fitness of a male is $(1 - \mu)[q\bar{z}_R + (1 - q)\bar{z}_L] + \mu\bar{z}_O$; thus, the relative fitness of a male is $W_m = \{(1 - \mu)[qz_R + (1 - q)z_L] + \mu\bar{z}_O\}/\{(1 - \mu)[q\bar{z}_R + (1 - q)\bar{z}_L] + \mu\bar{z}_O\}$. Equally, the fitness of a juvenile female is $(1 - \mu)[q(1 - z_R) + (1 - q)(1 - z_L)] + \mu(1 - \bar{z}_O)$, the average fitness of a female is $(1 - \mu)[q(1 - \bar{z}_R) + (1 - q)(1 - \bar{z}_L)] + \mu(1 - \bar{z}_O)$, and, thus, her relative fitness is $W_f = [(1 - \mu)[q(1 - z_R) + (1 - q)(1 - z_L)] + \mu(1 - \bar{z}_O)]/[(1 - \mu)[q(1 - \bar{z}_R) + (1 - q)(1 - \bar{z}_L)] + \mu(1 - \bar{z}_O)]$. Following the same reasoning as in the previous section, the average fitness of an individual is $W = c_f W_f + c_m W_m$, where c_m and c_f are the male and the female class reproductive values, respectively, derived in appendix A (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Consider a gene H with genic value h controlling sex allocation in queenright colonies. Natural selection favors an increase of frequency of

this trait in the population if $dW/dg > 0$. Thus, the marginal fitness of H is given by

$$\begin{aligned} \frac{dW}{dh} &= c_f \frac{dW_f}{dh} + c_m \frac{dW_m}{dh} \\ &= c_f \frac{\partial W_f}{\partial z_R} \frac{dz_R}{dh} \frac{d\hat{h}}{dh_f} + c_m \frac{\partial W_m}{\partial z_R} \frac{dz_R}{dh} \frac{d\hat{h}}{dh_m}, \end{aligned} \quad (D1)$$

where $d\hat{g}/dg_f = \mu p_{Ni} + (1 - \mu)p_f$ is the average consanguinity between a worker and a juvenile female in the colony and $d\hat{g}/dg_m = \mu p_{Ne} + (1 - \mu)p_m$ is the average consanguinity between a worker and a juvenile male in the colony.

We use the same rationale to model the action of natural selection on the sex allocation strategy in queenless colonies. In this case, we consider a gene K with genic value k controlling sex allocation in queenless colonies. Through natural selection, this trait increases its value in the population if $dW/dk > 0$. Hence, the marginal fitness of K is given by

$$\begin{aligned} \frac{dW}{dk} &= c_f \frac{dW_f}{dk} + c_m \frac{dW_m}{dk} \\ &= c_f \frac{\partial W_f}{\partial z_L} \frac{dz_L}{dk} \frac{d\hat{k}}{dk_f} + c_m \frac{\partial W_m}{\partial z_L} \frac{dz_L}{dk} \frac{d\hat{k}}{dk_m}, \end{aligned} \quad (D2)$$

where $d\hat{h}/dh_f = p_{Ni}$ and $d\hat{h}/dh_m = p_{Ne}$ are the coefficients of consanguinity between a worker and her niece and her nephew, respectively. By replacing in equations (D1) and (D2) expressions with the model parameters, we find the joint convergence stable sex ratio strategy for queen-derived and worker-derived offspring in mated-queen colonies.

Unmated Workers

We consider that workers produce male offspring by replacing μ of the queen-derived offspring, in both queenless and queenright colonies. The fitness of a juvenile queenright colony male is defined as the probability of a male to survive, that is, $qz_R + (1 - q)z_L$. The average fitness of a male is $q\bar{z}_R + (1 - q)\bar{z}_L$; thus, the relative fitness of a male is $W_m = \{(1 - \mu)[qz_R + (1 - q)z_L] + \mu\}/\{(1 - \mu)[q\bar{z}_R + (1 - q)\bar{z}_L] + \mu\}$. Equally, the fitness of a juvenile female is $q(1 - z_R) + (1 - q)(1 - z_L)$, the average fitness of a female is $q(1 - \bar{z}_R) + (1 - q)(1 - \bar{z}_L)$, and thus, her relative fitness is $W_f = [q(1 - z_R) + (1 - q)(1 - z_L)]/[q(1 - \bar{z}_R) + (1 - q)(1 - \bar{z}_L)]$. Following the same reasoning as in the previous section, the average fitness of an individual is $W = c_f W_f + c_m W_m$, where c_m and c_f are the male and the female class reproductive values, respectively, derived in appendix A (Taylor 1996; Taylor and Frank

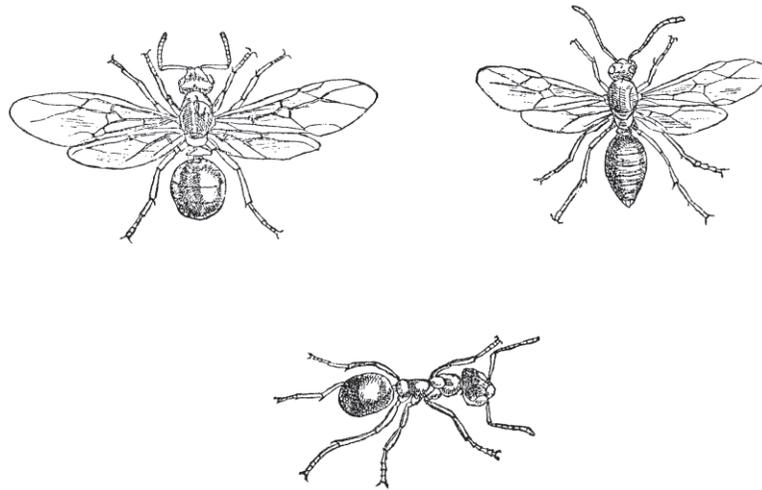
1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Consider a gene G with genic value g controlling sex allocation in queenright colonies. Natural selection favors an increase of frequency of this trait in the population if $dW/dg > 0$. We use the procedure described by equations (D1) and (D2) to find the marginal fitness equations for z_R and z_L . Substituting model parameters in this system of equations allows us to determine the joint convergence stable sex ratio strategies. These expressions by the model parameters allow us to find the convergence stable sex ratio strategy for mated-queen colonies.

Literature Cited

- Aoki, S. 1977. *Colophina clematis* (Homoptera: Pemphigidae) and aphid species with soldiers. *Kontyu* 45:276–282.
- Boomsma, J. J. 1991. Adaptive colony sex ratios in primitively eusocial bees. *Trends in Ecology and Evolution* 6:92–95.
- . 2007. Kin selection versus sexual selection: why the ends do not meet. *Current Biology* 17:R673–R683.
- . 2009. Lifetime monogamy and the evolution of eusociality. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3191–3208.
- . 2013. Beyond promiscuity: mate-choice commitments in social breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:20120050, doi:10.1098/rstb.2012.0050.
- Boomsma, J. J., and A. Grafen. 1990. Intraspecific variation in ant sex ratios and the Trivers-Hare hypothesis. *Evolution* 44:1026–1034.
- . 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. *Journal of Evolutionary Biology* 4:383–407.
- Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. *Quarterly Review of Biology* 63:291–311.
- Bulmer, M. 1994. *Theoretical evolutionary ecology*. Sinauer, Sunderland, MA.
- Chapuisat, M., and L. Keller. 1999. Testing kin selection with sex allocation data in eusocial Hymenoptera. *Heredity* 82:473–478.
- Charnov, E. L. 1978. Evolution of eusocial behavior: offspring choice or parental parasitism? *Journal of Theoretical Biology* 75:451–465.
- Cornwallis, C., S. A. West, K. E. Davies, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466:969–972.
- Craig, R. 1979. Parental manipulation, kin selection, and the evolution of altruism. *Evolution* 33:319–334.
- Crespi, B. J. 1992. Eusociality in Australian gall thrips. *Nature* 359:724–726.
- Crespi, B. J., and D. Yanega. 1995. The definition of eusociality. *Behavioral Ecology* 6:109–115.
- Davies, N. B., J. R. Krebs, and S. A. West. 2012. *An introduction to behavioural ecology*. Wiley, Oxford.
- Duffy, J. E. 1996. Eusociality in a coral-reef shrimp. *Nature* 381:512–514.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Fletcher, D. J. C., and K. G. Ross. 1985. Regulation of reproduction in eusocial Hymenoptera. *Annual Review of Entomology* 30:319–343.
- Frank, S. A. 1997. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. *Journal of Theoretical Biology* 189:307–316.
- . 1998. *Foundations of social evolution*. Princeton University Press, Princeton, NJ.
- Gardner, A., J. Alpedrinha, and S. A. West. 2012. Haplodiploidy and the evolution of eusociality: split sex ratios. *American Naturalist* 179:240–256 (correction, *American Naturalist* 179:554–555).
- Godfray, H. C. J. 1988. Virginity in haplodiploid populations: a study on fig wasps. *Ecological Entomology* 13:283–291.
- Godfray, H. C. J., and I. C. W. Hardy. 1993. Sex ratio and virginity in haplodiploid insects. Pages 404–417 in D. L. Wrensch and M. Ebbert, eds. *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, New York.
- Grafen, A. 1986. Split sex ratios and the evolutionary origins of eusociality. *Journal of Theoretical Biology* 122:95–121.
- Hamilton, W. D. 1963. The evolution of altruistic behaviour. *American Naturalist* 97:354–356.
- . 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1–16.
- . 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17–52.
- . 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220.
- . 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3:193–232.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, MA.
- Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral monogamy shows kin selection is the key to the evolution of eusociality. *Science* 320:1213–1216.
- Inward, D., G. Beccaloni, and P. Eggleton. 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters* 3:331–335.
- Ito, Y. 1989. The evolutionary biology of sterile soldiers in aphids. *Trends in Ecology and Evolution* 4:69–73.
- Jarvis, J. U. M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* 212:571–573.
- Kent, D. S., and J. A. Simpson. 1992. Eusociality in the beetle *Austroplatypus incompertus* (Coleoptera: Curculionidae). *Naturwissenschaften* 79:86–87.
- Kranz, B. D., M. P. Schwartz, L. C. Giles, and B. J. Crespi. 2000. Split sex ratios and virginity in a gall-inducing thrips. *Journal of Evolutionary Biology* 13:700–706.
- Meunier, J., S. A. West, and M. Chapuisat. 2008. Split sex ratios in the social Hymenoptera: a meta-analysis. *Behavioral Ecology* 19:382–390.
- Michener, C. D. 1974. *The social behavior of the bees*. Harvard University Press, Cambridge, MA.
- Mueller, U. G. 1991. Haplodiploidy and the evolution of facultative sex ratios in a primitively eusocial bee. *Science* 254:442–444.
- Packer, L. 1986. The social organization of *Halictus ligatus* (Hymenoptera, Halictidae) in southern Ontario. *Canadian Journal of Zoology* 64:2317–2324.
- Pamilo, P. 1991. Evolution of colony characteristics in social insects. I. Sex allocation. *American Naturalist* 137:83–107.
- Queller, D. C., and J. E. Strassmann. 1998. Kin selection and social insects. *BioScience* 48:165–175.
- Ratnieks, F. L. W., K. R. Foster, and T. Wenseleers. 2006. Conflict resolution in insect societies. *Annual Review of Entomology* 51:581–608.

- Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton University Press, Princeton, NJ.
- Seger, J. 1983. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* 301:59–62.
- Taylor, P. D. 1996. Inclusive fitness arguments in genetic models of behaviour. *Journal of Mathematical Biology* 34:654–674.
- Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *Journal of Theoretical Biology* 180:27–37.
- Taylor, P. D., G. Wild, and A. Gardner. 2007. Direct fitness or inclusive fitness: how shall we model kin selection. *Journal of Evolutionary Biology* 20:301–309.
- Thorne, B. L. 1997. Evolution of eusociality in termites. *Annual Review of Ecology, Evolution, and Systematics* 28:27–54.
- Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of the social insects. *Science* 191:249–263.
- Wenseleers, T., and F. L. W. Ratnieks. 2006. Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory. *American Naturalist* 168:E163–E179.
- West, S. A. 2009. Sex allocation. Princeton University Press, Princeton, NJ.
- West, S. A., and A. Gardner. 2010. Altruism, spite, and greenbeards. *Science* 327:1341–1344.
- Wilson, E. O. 1971. The insect societies. Belknap Press of Harvard University Press, Cambridge, MA.
- Yanega, D. 1989. Caste determination and differential diapause within the first brood of *Halictus rubicundus* in New York (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* 24:97–107.

Associate Editor: Peter D. Taylor
 Editor: Troy Day



“The females [left] closely resemble the workers-major [bottom], but are larger, more robust, and in the virgin state are winged. The males [right] are winged, [and] are smaller than the females, from whom they are further readily distinguished by the smaller head, an additional segment to the abdomen and the different form of the same. ... [T]hey are referred to in the following notes as *Formica exsectoides* Forel, a new American ally of *F. exsecta*.” From “Mound-Making Ants of the Alleghenies” by Henry C. McCook (*American Naturalist*, 1878, 12:431–445).