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Haplodiploidy and the Evolution of Eusociality: Split Sex Ratios

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ABSTRACT: It is generally accepted that from a theoretical perspective, haplodiploidy should facilitate the evolution of eusociality. However, the “haplodiploidy hypothesis” rests on theoretical arguments that were made before recent advances in our empirical understanding of sex allocation and the route by which eusociality evolved. Here we show that several possible promoters of the haplodiploidy effect would have been unimportant on the route to eusociality, because they involve traits that evolved only after eusociality had become established. We then focus on two biological mechanisms that could have played a role: split sex ratios as a result of either queen virginity or queen replacement. We find that these mechanisms can lead haplodiploidy to facilitating the evolution of helping but that their importance varies from appreciable to negligible, depending on the assumptions. Furthermore, under certain conditions, haplodiploidy can even inhibit the evolution of helping. In contrast, we find that the level of promiscuity has a strong and consistently negative influence on selection for helping. Consequently, from a relatedness perspective, monogamy is likely to have been a more important driver of eusociality than the haplodiploidy effect.

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

Introduction

If a female is fertilized by only one male all the sperm she receives is genetically identical. Thus, although the relationship of a mother to her daughters has the normal value of $1/2$, the relationship between daughters is $3/4$. Consider a species where the female consecutively provisions and oviposits in cell after cell so that she is still at work when the first of her female offspring ecloses, leaves the nest and mates. Our principle tells us that even if this new adult had a nest ready constructed and vacant for her use she would prefer, other things being equal, returning to her mother's and provisioning a cell for

the rearing of an extra sister to provisioning a cell for a daughter of her own. (Hamilton 1964, p. 28–29)

The eusocial societies are dominated by species with haplodiploid genetics, especially the social Hymenoptera—the ants, bees, and wasps. Although eusociality is also found in diploid species, such as termites, its distribution is significantly biased toward haplodiploid families (Crozier 2008). Hamilton (1964, 1972) suggested that this was because haplodiploidy facilitates the evolution of altruistic helping. Altruistic helping behaviors are favored if the benefit of helping relatives outweighs the costs to the altruist and to other relatives, with all costs and benefits weighted by the genetic relatedness of the recipients to the actor (Hamilton 1963, 1964, 1970). Haplodiploidy involves females developing from fertilized (i.e., diploid) eggs and having both a mother and a father, and males developing from unfertilized (i.e., haploid) eggs, and having no father. Hamilton (1964, 1972) suggested that because this leads to a worker being more related to her full sisters (life-for-life relatedness, $R = 3/4$) than to her own daughters ($R = 1/2$), haplodiploidy makes eusociality easier to evolve, even in the absence of efficiency benefits to cooperation.

Trivers and Hare (1976) showed that while Hamilton's “haplodiploidy hypothesis” can work, things are not so simple. Haplodiploidy also leads to a female being less related to her brothers ($R = 1/4$) than to her sons ($R = 1/2$). In the simplest case, with an unbiased sex ratio among reproductives, the relative benefit of rearing sisters is exactly canceled by the relative cost of rearing brothers, and so haplodiploidy has no overall influence (Trivers and Hare 1976). A female-biased sex ratio does not solve this problem, because the benefit of more sisters is exactly counterbalanced by the fact that it increases the average number of mates for each male, making females worth relatively less (Trivers and Hare 1976; Craig 1979). Consequently, in order to make the haplodiploidy hypothesis work, it is required that workers preferentially help sisters but that the population sex ratio is not biased to the same

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Table 1: Split sex ratios and the evolution of eusociality

Reason for split sex ratios	Empirical evidence that this has led to split sex ratios	Could such split sex ratios have occurred on the route to eusociality?
Partially overlapping generations (Seger 1983)	No (West 2009)	Potentially
Worker control of sex allocation in some broods and queen control in others (Trivers and Hare 1976)	No, but would be transient (West 2009)	Potentially (to be analyzed in a companion paper: J. Alpedrinha et al. unpublished manuscript)
Variation across colonies in the relative cost of producing males and females (Grafen 1986)	No (West 2009)	Potentially
Virginity (or any other factor which constrains some queens to produce only males; Taylor 1981; Godfray and Grafen 1988)	Yes, this occurs in solitary and social hymenopteran species, although usually at low (<6%) frequencies (Godfray and Hardy 1992; West 2009)	Yes
Competition for mates between related males (local mate competition, LMC; Frank 1987)	No (West 2009)	Potentially, although LMC is very rare in social Hymenoptera (West et al. 2005)
Synergistic benefits of rearing siblings (Frank and Crespi 1989)	No (West 2009)	Potentially
Variation in response to whether sibmated or not (Greeff 1996; Reece et al. 2004)	No (West 2009)	No evidence for such sex ratio shifts in any organism, and sibmating is rare in social Hymenoptera
Competition between related females for resources (local resource competition; Brown and Keller 2000)	Yes, in ants (West 2009)	No, this occurs in multiple-queen colonies, which only evolved after obligate eusociality was established (Boomsma 2007, 2009; Hughes et al. 2008)
Queen control (Passera et al. 2001)	Yes, in ants and bees (West 2009)	No, this occurs only in obligately eusocial colonies
Relatedness asymmetry due to variation in queen mating frequency (Boomsma and Grafen 1991)	Yes, in ants (Chapuisat and Keller 1999; Meunier et al. 2008; West 2009)	No, multiple mating only evolved after obligate eusociality was established (Boomsma 2007, 2009; Hughes et al. 2008)
Relatedness asymmetry due to variation in queen number (Boomsma and Grafen 1991; Boomsma 1993)	Yes, in ants and wasps (Chapuisat and Keller 1999; Meunier et al. 2008; West 2009)	No, this occurs in multiple-queen colonies, whereas eusociality has only arisen in monogynous species (Boomsma 2007, 2009; Hughes et al. 2008).
Relatedness asymmetry due to queen replacement (Boomsma 1991)	Yes, in bees (Chapuisat and Keller 1999; Meunier et al. 2008; West 2009)	Yes

Note: Although there are many mechanisms that lead to split sex ratios in hymenoptera, only two of these (virginity and queen replacement) are supported by empirical evidence (column 2) and are also likely to have occurred during the transition from solitary to eusocial living (column 3).

extent. Trivers and Hare (1976) suggested that this could happen if workers at some nests gained control of sex allocation and biased this toward sisters. Such sex ratio variation between broods, termed “split sex ratios,” can allow helpers at the relatively female-biased broods to gain the relatedness benefit of rearing sisters, without this being exactly canceled by a reduced reproductive value of females, thanks to the relatively male-biased broods leading to a more even sex ratio at the population level (Seger 1983; Grafen 1986). The idea here is that this favors the initial evolution of helping at some broods and hence

facilitates the spread of genes that lead to more specialized helping en route to eusociality.

Since Trivers and Hare’s (1976) landmark article, a large body of theoretical work has arisen showing that split sex ratios can be favored in response to a multitude of selective forces, with many of these scenarios being supported by the empirical data (table 1). Indeed, work on split sex ratios has even been hailed as one of the most successful and productive areas of evolutionary biology, with a rich interplay between theoretical, observational, and experimental studies (West 2009). Furthermore, subsequent

work has suggested other ways that might allow haplodiploidy to facilitate the evolution of helping, via its impact on relatedness, for example, by selecting for the enforcement of cooperation with worker policing (Ratnieks 1988) or by increasing the benefit of helping siblings in structured populations (Lehmann et al. 2008; Johnstone et al. 2011). Overall, this body of work has led to the general assumption that from a theoretical perspective, the haplodiploidy effect does facilitate the evolution of eusociality (Seger 1991; Krebs and Davies 1993; Bourke and Franks 1995; Crozier and Pamilo 1996; Queller and Strassmann 1998; Alcock 2005).

Here, we reassess the haplodiploidy hypothesis on two grounds. First, empirical progress has clarified the relevant biological scenarios. Eusociality has evolved under specific conditions, with strict lifetime monogamy via the subsocial route, where offspring stay at home to help their parents, and with single queens (Boomsma 2007, 2009; Hughes et al. 2008; Duffy and Macdonald 2010; Bourke 2011). This means that several factors cannot have facilitated the evolution of eusociality, including: (a) the most empirically common causes of split sex ratios, which rely on variation in the number of queens and queen mating frequency and therefore evolved after eusociality was established (table 1); (b) worker policing in response to multiple mating (Ratnieks 1988); and (c) any mechanism that relies on helping siblings to rear offspring (the semisocial route; Lehmann et al. 2008; Johnstone et al. 2011). Furthermore, several other suggested mechanisms for producing split sex ratios are unlikely to be important, such as in response to sib mating or partially overlapping generations, as a recent overview of the literature has shown that there is lack of empirical evidence that they occur (West 2009). Consequently, if the haplodiploidy effect has facilitated the evolution of eusociality, it has done so via split sex ratios, and the potentially important causes of split sex ratios are limited to queen virginity, queen replacement, and partial worker control (table 1).

Second, haplodiploidy can have different influences at different stages of the evolution of eusociality and for different types of helping trait. One issue is whether we are considering facultative helping at a fraction of broods or obligate helping in all broods. Previous split sex ratio arguments have been relatively heuristic, showing how selection for facultative helping can be increased at relatively female-biased broods. However, at relatively male-biased broods, potential helpers will be less related to the young that they could help to raise, which disfavors helping. While this will not matter for facultative helping traits, which are only expressed at female-biased broods, it will have to be taken into account when considering obligate helping traits, such as those committing the individual to permanent sterility relatively early in her life and before she

is able to assess the sex ratio of the brood that she would help to rear. Another issue is whether we are examining the initial evolution (origin) of helping, or the subsequent elaboration (maintenance) of helping (Charnov 1978). In the former, a potential worker must decide whether to stay at her mother's nest and rear siblings or disperse away to found her own nest, whereas in the latter, a potential worker must decide how much to invest in rearing the queen's offspring versus selfishly pursuing her own reproduction within the same nest.

Our aim in this article is to determine, from a theoretical perspective, the extent to which the haplodiploidy effect can facilitate the evolution of eusociality. In order to provide an illustrative overview, we first consider a population divided into colonies that may vary in their sex allocation but not in any other respect. We then construct models for two specific scenarios that the empirical data suggest could have played a role on the route to eusociality: queen virginity and queen replacement (table 1). Our aim with these models is not just to show whether haplodiploidy and split sex ratios can facilitate the evolution of eusociality but also to parameterize the models with empirical data and hence quantify their possible importance. Although it seems reasonable that both mechanisms could facilitate the evolution of helping, we do not know whether the effect is large or negligible. Quantification requires specific models because factors such as queen replacement that lead to split sex ratios can cause variation in the relatedness structure within colonies, which may also mediate selection for helping. For each of the situations that we consider, we examine (when relevant) how the impact of haplodiploidy varies along the route to eusociality (i.e., initial evolution versus later elaboration of helping), and for different types of trait (facultative vs. obligate helping). We consider a third possible cause of split sex ratios, Trivers and Hare's (1976) idea of partial worker control of sex allocation, alongside the role of male production by workers, in a separate article (J. Alpedrinha et al., unpublished manuscript), because it leads to only transient split sex ratios and hence is not amenable to the equilibrium analysis approach that we take in this study.

Split Sex Ratios and the Evolution of Helping

We examine how haplodiploidy influences selection for helping when the sex ratio (proportion of reproductives that are male) may vary between broods (Grafen 1986). We perform an inclusive fitness analysis (Hamilton 1963, 1964, 1970, 1972), weighing the b extra siblings that the female could rear if she were more helpful against the c extra offspring that she could rear if she were less helpful, with the valuation of each relative being given by the prod-

Table 2: A summary of model notation used in the main text

Symbol	Definition
α	Potential for helping
α_{OBL}	Potential for obligate helping
α_{FAC}	Potential for facultative helping
v_f	Reproductive value of a juvenile female
v_m	Reproductive value of a juvenile male
p_d	Consanguinity of a female to her daughter
p_s	Consanguinity of a female to her son
p_f	Consanguinity of a female to a queen-derived juvenile female
p_m	Consanguinity of a female to a queen-derived juvenile male
ϕ	Degree of monogamy (probability that maternal sisters are paternal sisters)
a	Relative productivity of workerless colonies (virginity model)
u	Frequency of unmated queens (virginity model)
q	Frequency of queenright colonies (queen replacement model)
z	Colony sex ratio
\bar{z}	Population sex ratio
\bar{z}_M	Sex ratio of mated-queen colonies (virginity model)
\bar{z}_U	Sex ratio of unmated-queen colonies (virginity model)
\bar{z}_R	Sex ratio of queenright colonies (queen replacement model)
\bar{z}_L	Sex ratio of queenless colonies (queen replacement model)

uct of its reproductive value v and its consanguinity p to the focal female (app. A; Hamilton 1964, 1970; Taylor and Frank 1996; Frank 1998; Rousset 2004; Grafen 2006a, 2006b). We compute the threshold ratio c/b , below which helping is favored and above which helping is disfavored, and denote this α . This is the “efficiency ratio” of Charnov (1978) and Grafen (1986), and the “potential for altruism” of Gardner (2010). A higher value of α corresponds to a scenario where helping is more readily favored. In particular, $\alpha > 1$ indicates that helping is more readily favored under the given scenario than it is under the assumption of diploidy with full monogamy (Grafen 1986). Model notation is summarized in table 2.

Origin of Helping

We assume an otherwise solitary species, and examine the inclusive fitness consequences for a female (the “worker”) who chooses to stay with her mother (the “queen”) and rear siblings rather than dispersing and rearing her own brood in her own nest. We allow the sex ratio z of the queen’s offspring to depart from the population average \bar{z} . The expected sex ratio of the worker’s own offspring, should she disperse and raise her own brood, is simply the population average \bar{z} . Thus, the inclusive fitness valuation that the worker places on queen-derived offspring is $z v_m p_m + (1 - z) v_f p_f$ and the inclusive fitness valuation that she places on her own offspring is $\bar{z} v_m p_s + (1 - \bar{z}) v_f p_d$, where p_m and p_f are the consanguinities of the worker to the queen’s sons and queen’s daughters, respectively; p_s and p_d are the consanguinities of the worker

to her own sons and daughters, respectively; and v_f and v_m are the reproductive values of a female and a male, respectively. If the worker is trading b of the queen’s offspring against c of her own offspring, then she increases her inclusive fitness by helping to rear the queen’s offspring if $b[z v_m p_m + (1 - z) v_f p_f] > c[\bar{z} v_m p_s + (1 - \bar{z}) v_f p_d]$. Rearranging this condition into the form $c/b < \alpha$ obtains the potential for helping α , and this is given by dividing the valuation of the queen’s offspring by the valuation of the worker’s own offspring.

If the focal female knows the sex ratio of her mother’s brood and adjusts her helping accordingly, we obtain a potential for facultative helping of $\alpha_{\text{FAC}} = [z v_m p_m + (1 - z) v_f p_f] / [\bar{z} v_m p_s + (1 - \bar{z}) v_f p_d]$. Substituting in the appropriate reproductive values and consanguinity coefficients (app. B), this is

$$\alpha_{\text{FAC}} = \frac{1}{4} \left[\frac{1 - z}{1 - \bar{z}} (1 + 2\phi) + \frac{z}{\bar{z}} \right], \quad (1)$$

where ϕ is probability that two given maternal sisters are also paternal sisters. In figures 1–3, we assume $\phi = 1$ because eusociality has evolved only in monogamous species. The corresponding result for diploidy is $\alpha = (1 + \phi)/2$ (app. B), so haplodiploidy promotes facultative helping when the right-hand side (RHS) of equation (1) exceeds $(1 + \phi)/2$, and haplodiploidy inhibits facultative helping when the RHS of equation (1) is less than $(1 + \phi)/2$. If $\bar{z} > 1/[2(1 + \phi)]$ (i.e., $\bar{z} > 1/4$, under full monogamy), then haplodiploidy promotes the origin of facultative helping in relatively female-biased broods ($z < \bar{z}$)

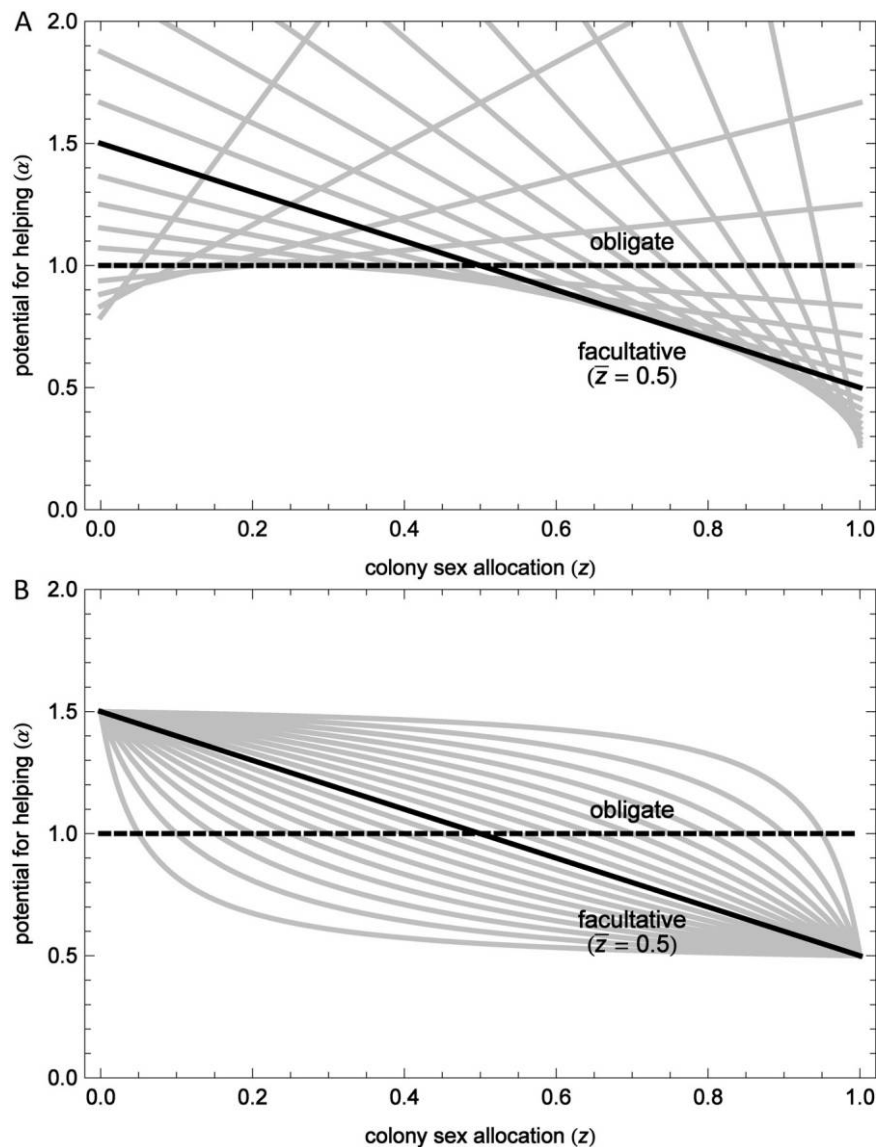


Figure 1: Potential for helping in a generic model of split sex ratios, assuming full monogamy ($\phi = 1$). *A*, In the context of the origin of helping, haplodiploidy does not promote obligate helping ($\alpha_{\text{OBL}} = 1$, dashed black line), but it promotes facultative helping in colonies that have relatively female-biased sex ratios ($z < \bar{z}$ when $\bar{z} > 1/4$) and inhibits facultative helping in colonies that have relatively male-biased sex ratios ($z > \bar{z}$ when $\bar{z} > 1/4$). The solid black line indicates facultative helping when the population sex ratio is $\bar{z} = 0.5$, and the solid gray lines indicate facultative helping for other population sex ratios, with all lines intersecting $\alpha = 1$ at $z = \bar{z}$. *B*, In the context of the elaboration of helping, haplodiploidy does not promote obligate helping ($\alpha_{\text{OBL}} = 1$, dashed black line), but it promotes facultative helping in colonies that have relatively female-biased sex ratios ($z < \bar{z}$) and inhibits facultative helping in colonies that have relatively male-biased sex ratios ($z > \bar{z}$). The solid black line indicates facultative helping when the population sex ratio is $\bar{z} = 0.5$, and the solid gray lines indicate facultative helping for other population sex ratios, with all lines intersecting $\alpha = 1$ at $z = \bar{z}$.

and inhibits the origin of facultative helping in relatively male-biased broods ($z > \bar{z}$). If $\bar{z} < 1/[2(1 + \phi)]$ (i.e., $\bar{z} < 1/4$, under full monogamy), then the opposite is true (fig. 1A) because in such strongly female-biased populations, brothers are more valuable than sisters (Trivers and Hare 1976). In the absence of split sex ratios ($z = \bar{z}$ for every

brood), haplodiploidy neither promotes nor inhibits the origin of facultative helping, irrespective of the population sex ratio, because the increased relatedness to siblings is exactly balanced by the decreased reproductive value of daughters (Craig 1979).

If the focal female does not know the sex ratio of her

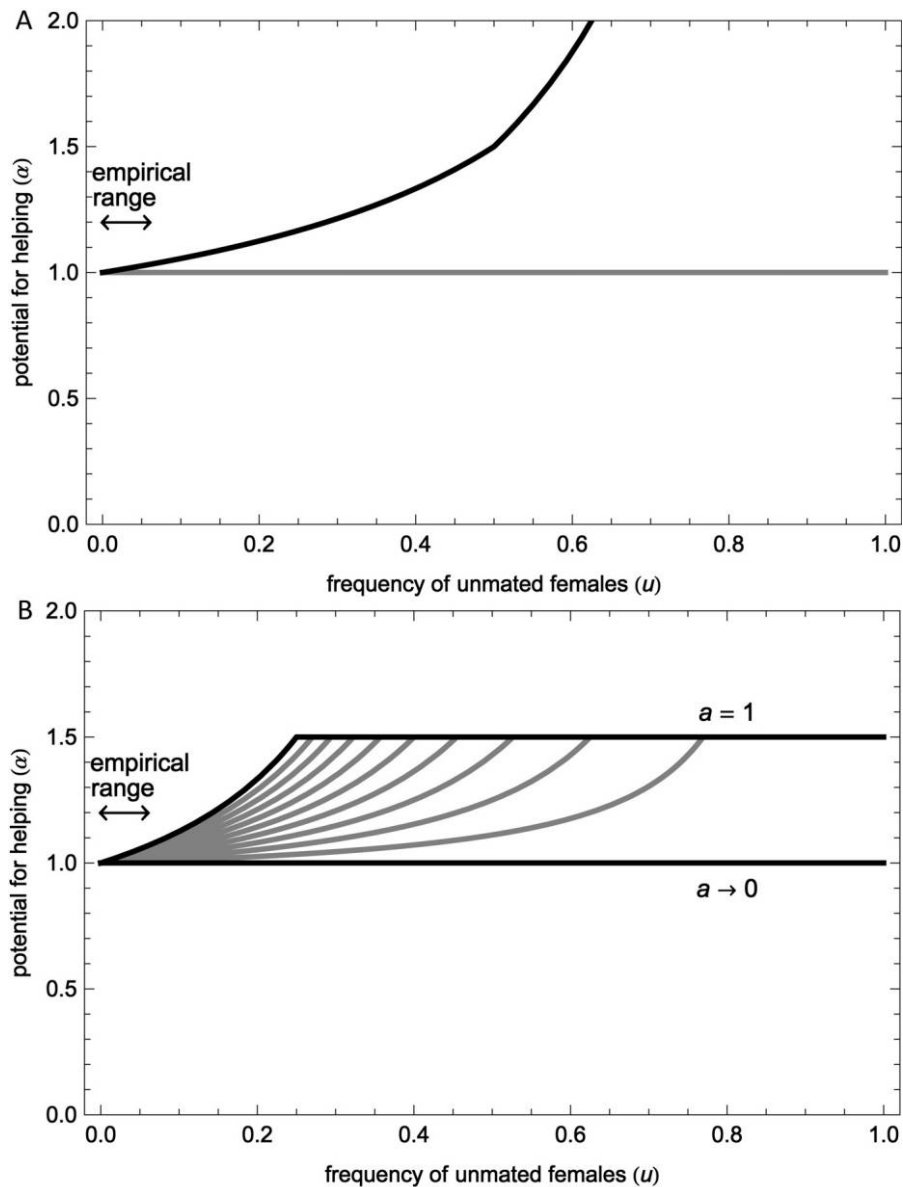


Figure 2: Potential for helping in a model of split sex ratios owing to virginity, assuming full monogamy ($\phi = 1$). A, In the context of the origin of helping, haplodiploidy always promotes helping. As the rate of unmatedness is generally $<6\%$, this suggests the potential for helping is $\alpha < 1.03$. B, In the context of the elaboration of helping, haplodiploidy always promotes helping. Again, as the rate of unmatedness is generally $<6\%$, the potential for helping is $\alpha < 1.07$. Furthermore, it is predicted to be lower if workerless colonies suffer reduced productivity ($a < 1$; with $\alpha \rightarrow 1$ as $a \rightarrow 0$), as will be the case when helping is selected for.

mother's brood, the decision as to whether or not she should help must be made by taking an average over this uncertainty, and this is equivalent to evaluating the right-hand side of equation (1) at $z = \bar{z}$. This obtains $\alpha_{\text{OBL}} = (1 + \phi)/2$, which is identical to the condition for obligate helping under diploidy, so haplodiploidy neither promotes nor inhibits the origin of obligate helping (fig. 1A).

Elaboration of Helping

We next consider the evolutionary elaboration of helping in a social haplodiploid species, by examining the inclusive fitness consequences for a newly eclosed female (the "worker") who chooses to help her mother (the "queen") to rear siblings rather than selfishly rearing her own offspring within the same colony. We imagine that the sex

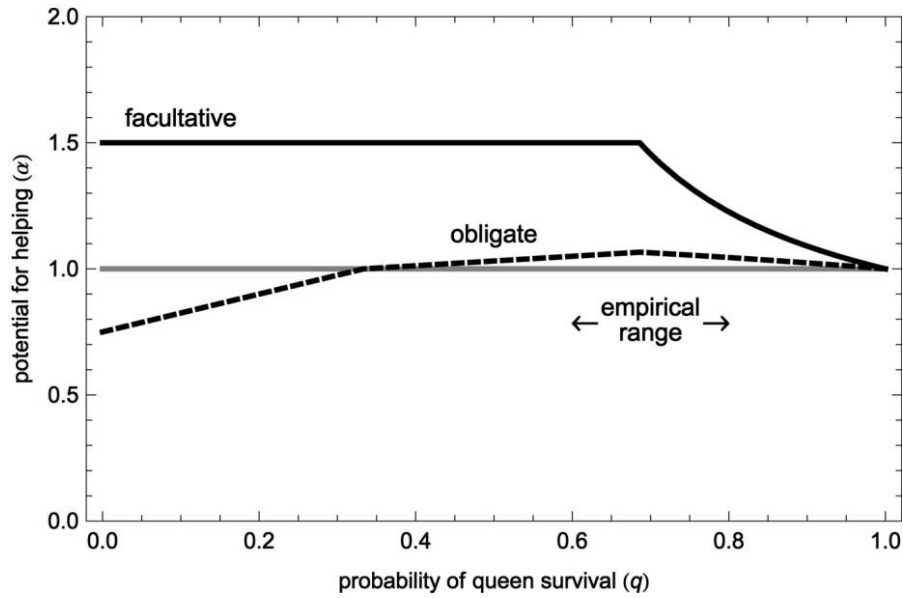


Figure 3: Potential for helping in a model of split sex ratios owing to queen replacement, assuming full monogamy ($\phi = 1$). In the context of the elaboration of helping, haplodiploidy can promote or inhibit obligate helping (dashed black line). Over the empirically estimated range of queen survival ($0.6 < q < 0.8$), haplodiploidy has a promoting effect, with maximum potential for obligate helping at $\alpha_{\text{OBL}} \approx 1.07$ when $q \approx 0.69$. Moreover, haplodiploidy always promotes facultative helping in relatively female-biased (i.e., queenright) colonies (solid black line). The maximum potential for facultative helping is at $\alpha_{\text{FAC}} \approx 1.50$, for a range of empirically valid rates of queen survival.

ratio of the colony is controlled by its cohort of workers, and we allow the sex ratio z among the queen’s offspring to depart from the population average \bar{z} . We assume that the expected sex ratio of the worker’s own offspring, should she choose to reproduce, is also z (this assumption is relaxed by J. Alpedrinha et al., unpublished manuscript). Thus, the inclusive fitness valuation that the worker places on queen-derived offspring is $z v_m p_m + (1 - z) v_f p_p$, and the inclusive fitness valuation that she places on her own offspring is $z v_m p_s + (1 - z) v_f p_d$. We assume that worker reproduction is sufficiently rare to be considered negligible for the purpose of calculating reproductive values (this assumption is relaxed by J. Alpedrinha et al., unpublished manuscript).

If the focal female knows the sex ratio of her mother’s brood, and adjusts her helping accordingly, we obtain a potential for facultative helping of $\alpha_{\text{FAC}} = [z v_m p_m + (1 - z) v_f p_p] / [z v_m p_s + (1 - z) v_f p_d]$. Substituting in the appropriate reproductive values and consanguinity coefficients (app. B), this is

$$\alpha_{\text{FAC}} = \frac{1}{2} + \phi \frac{\bar{z}(1 - z)}{z(1 - \bar{z}) + \bar{z}(1 - z)}. \quad (2)$$

Again, haplodiploidy promotes facultative helping when the RHS of equation (2) exceeds $(1 + \phi)/2$ and haplodiploidy inhibits facultative helping when the RHS of equation

(2) is less than $(1 + \phi)/2$. That is, haplodiploidy promotes the elaboration of facultative helping in relatively female-biased broods ($z < \bar{z}$) and inhibits the elaboration of facultative helping in relatively male-biased broods ($z > \bar{z}$), irrespective of the actual population sex ratio (fig. 1B). In the absence of split sex ratios ($z = \bar{z}$ for every brood), haplodiploidy neither promotes nor inhibits the elaboration of facultative helping, irrespective of the population sex ratio (Craig 1979).

If the focal female does not know the sex ratio of her mother’s brood, the decision as to whether she should help must be made by taking an average over this uncertainty, and this is equivalent to evaluating the RHS of equation (2) at $z = \bar{z}$. This obtains $\alpha_{\text{OBL}} = (1 + \phi)/2$, which is identical to the condition for obligate helping under diploidy, so haplodiploidy neither promotes nor inhibits the maintenance of obligate helping (fig. 1B).

Split Sex Ratios Owing to Virginity

Virginity can lead to split sex ratios because unmated females cannot produce daughters but can produce sons (Taylor 1981; Godfray and Grafen 1988). Hence, colonies founded by unmated queens cannot produce workers or female reproductives and so specialize in male reproduc-

tion, whereas colonies founded by mated queens can produce workers and reproductives of either sex.

Origin of Helping

We consider the evolutionary origin of helping in an otherwise solitary haplodiploid species, by examining the inclusive fitness consequences for a newly eclosed female (the “worker”) who chooses to stay with her mother (the “queen”) and rear siblings rather than dispersing and rearing her own brood. We assume that a fraction $1 - u$ of queens are mated and are able to exhibit any sex allocation strategy $0 \leq z_M \leq 1$, whereas a fraction u of queens are unmated (or by some other constraint are able to produce only sons; Godfray 1990) and are constrained to exhibit a sex allocation strategy of $z_U = 1$. We assume that a mated queen controls her own sex allocation, and we find that her convergence stable strategy (Taylor 1996) is

$$\bar{z}_M = \begin{cases} \frac{1 - 2u}{2(1 - u)} & \text{if } u \leq \frac{1}{2} \\ 0 & \text{if } u \geq \frac{1}{2} \end{cases} \quad (3)$$

(see app. C for derivation). The population sex ratio is given by $\bar{z} = u + (1 - u)\bar{z}_M$, or

$$\bar{z} = \begin{cases} \frac{1}{2} & \text{if } u \leq \frac{1}{2} \\ u & \text{if } u \geq \frac{1}{2} \end{cases} \quad (4)$$

Only mated queens can produce daughters, so the focal worker must be at the nest of a mated queen, and hence, there is no sense in discriminating facultative versus obligate helping. The expected sex ratio of the worker’s own offspring, should she disperse and raise her own brood, is simply the population average \bar{z} , as she could be either a mated or an unmated queen. Thus, the inclusive fitness valuation that the worker places on queen-derived offspring is $\bar{z}_M v_m p_m + (1 - \bar{z}_M) v_f p_f$ and the inclusive fitness valuation that she places on her own offspring is $\bar{z} v_m p_s + (1 - \bar{z}) v_f p_d$. The potential for helping is $\alpha = [\bar{z}_M v_m p_m + (1 - \bar{z}_M) v_f p_f] / (\bar{z} v_m p_s + (1 - \bar{z}) v_f p_d)$ and, substituting in the appropriate reproductive values, consanguinity coefficients, and sex ratios, this obtains

$$\alpha = \begin{cases} \frac{1 - u + \phi}{2(1 - u)} & \text{if } u \leq \frac{1}{2} \\ \frac{1 + 2\phi}{4(1 - u)} & \text{if } u \geq \frac{1}{2} \end{cases} \quad (5)$$

Again, haplodiploidy promotes helping, relative to diploidy, when $\alpha > (1 + \phi)/2$, which is true for all $u > 0$ (fig. 2A). Hence, haplodiploidy always promotes the origin of

helping under split sex ratios caused by queen virginity. Empirical estimates of the frequency of unmatedness suggest that it is usually low in outbreeding species, in the range $0.00 < u < 0.06$ (with a mode of 0.00; Godfray and Hardy 1992). Assuming full monogamy ($\phi = 1$), this would lead to the potential for helping in the range $1.00 < \alpha < 1.03$ (with a mode of ~ 1.00), which even in the best case scenario is only marginally greater than the corresponding value for diploidy ($\alpha = 1$; fig. 2A). That is, it is only for species in which the cost/benefit ratio lies within the narrow range $1.00 < c/b < 1.03$ that the haplodiploidy effect can matter. Below this range, helping is disfavored in both diploids and haplodiploids, and above this range, helping is favored in both diploids and haplodiploids. Higher levels of virginity are observed in species with local mate competition, where males do not disperse, but this does not occur on the route to eusociality (West et al. 1997).

Elaboration of Helping

We next consider the evolutionary elaboration of helping in a situation where helping is already common, by examining the inclusive fitness consequences for a newly eclosed female (the “worker”) who chooses to help her mother (the “queen”) to rear siblings rather than selfishly rearing her own offspring within the same colony. We consider that colonies founded by unmated queens have a fraction $0 < a < 1$ of the productivity (i.e., number of reproductive offspring) enjoyed by colonies founded by mated queens, owing to the absence of workers in the former. Also, we now assume that the workers control sex allocation in the mated-queen colonies, and we find that their convergence stable sex allocation strategy is

$$\bar{z}_M = \begin{cases} \frac{1 - [1 + (1 + 2\phi)a]u}{2(1 + \phi)(1 - u)} & \text{if } u \leq \frac{1}{1 + (1 + 2\phi)a} \\ 0 & \text{if } u \geq \frac{1}{1 + (1 + 2\phi)a} \end{cases} \quad (6)$$

(see app. C for derivation). The population sex ratio is given by $\bar{z} = [ua + (1 - u)z_M] / [1 - (1 - a)u]$, or

$$\bar{z} = \begin{cases} \frac{1}{2(1 + \phi)} & \text{if } u \leq \frac{1}{1 + (1 + 2\phi)a} \\ \frac{ua}{1 - (1 - a)u} & \text{if } u \geq \frac{1}{1 + (1 + 2\phi)a} \end{cases} \quad (7)$$

The inclusive fitness valuation that the worker places on queen-derived offspring is $\bar{z}_M v_m p_m + (1 - \bar{z}_M) v_f p_f$ and the inclusive fitness valuation that she places on her own

offspring is $\bar{z}_M v_m p_s + (1 - \bar{z}_M) v_f p_d$. Assuming that worker reproduction is sufficiently rare to be considered negligible for the purpose of calculating reproductive value, the potential for helping is $\alpha = [\bar{z}_M v_m p_m + (1 - \bar{z}_M) v_f p_f] / [\bar{z}_M v_m p_s + (1 - \bar{z}_M) v_f p_d]$ and, substituting in the appropriate reproductive values, consanguinity coefficients, and sex ratios, this obtains

$$\alpha = \begin{cases} \frac{(1-u)(1+\phi)}{2[1-u(1+\phi a)]} & \text{if } u \leq \frac{1}{1+(1+2\phi)a} \\ \frac{1+2\phi}{2} & \text{if } u \geq \frac{1}{1+(1+2\phi)a} \end{cases} \tag{8}$$

Haplodiploidy promotes helping, relative to diploidy, when $\alpha > (1 + \phi)/2$, which is true for all $u > 0$ (fig. 2B). However, the empirical estimate of $0.00 < u < 0.06$ indicates a maximum potential for helping of only $\alpha \approx 1.07$ under full monogamy ($\phi = 1$), which is only marginally greater than the corresponding value for diploids ($\alpha = 1$; fig. 2B). Again, this means that the haplodiploidy hypothesis has explanatory power only insofar as ancestral taxa fell into the cost/benefit range defined by $1.00 < c/b < 1.07$. Moreover, the potential for helping can be substantially lower if workerless colonies suffer a productivity penalty relative to colonies that contain workers ($a < 1$), with the haplodiploidy effect vanishing in the limit of low productivity of workerless colonies ($\alpha \rightarrow [1 + \phi]/2$ as $a \rightarrow 0$; fig. 2B). Overall, this suggests that as helping spreads through the population, and becomes more efficient, the benefit of haplodiploidy will be removed.

Split Sex Ratios Owing to Queen Replacement

We next consider the scenario where split sex ratios evolve owing to queen replacement, when the queen is lost from some colonies and replaced by a mated daughter. Assuming haplodiploidy then, in colonies where the original queen is still present (“queenright” colonies), the workers are more related to the queen’s daughters (sisters, $r = 3/4$) than to her sons (brothers, $r = 1/2$). In contrast, in colonies where the original queen has been replaced by one of her daughters (“queenless” colonies), the workers are more related to the new queen’s sons (nephews, $r = 3/4$) than they are to her daughters (nieces, $r = 3/8$). This favors workers to bias the colony sex ratio toward females in queenright colonies, and toward males in queenless colonies, as has been observed and experimentally demonstrated in cooperative bees (Boomsma 1991; Mueller 1991; Packer and Owen 1994). In contrast, under diploidy, queen replacement does not drive split sex ratios, owing to the symmetry of male and female inheritance. This mechanism applies only to the elaboration of helping,

in already social species where workers have seized control of the colony sex ratio, as queen-controlled sex allocation does not give rise to split sex ratios.

We consider a model that is identical to the generic model of split sex ratios presented above, except that we now assume that only a proportion q of colonies are headed by their original queen, and that a proportion $1 - q$ of colonies are headed by one the original queen’s daughters. One consequence of queen replacement is that males gain extra reproductive value, owing to their ability to father and mate with replacement queens (Trivers and Hare 1976; app. D). We assume that colony sex allocation is controlled by workers, and we find that the convergence stable state of the population, in terms of the sex allocation of queenright (\bar{z}_R) and queenless (\bar{z}_L) colonies, is given by

$$(\bar{z}_R, \bar{z}_L) = \begin{cases} \left[0, \frac{3-q}{4(1-q)} \right] & \text{if } q \leq \frac{1}{3} \\ (0, 1) & \text{if } \frac{1}{3} \leq q \leq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \\ \left[\frac{3q - 1 - 2(1-q^2)\phi}{2q[2 + (1+q)\phi]}, 1 \right] & \text{if } q \geq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \end{cases} \tag{9}$$

(see app. D for derivation). This solution can be used to calculate the population sex ratio $\bar{z} = q\bar{z}_R + (1 - q)\bar{z}_L$.

If the focal female knows the status of her natal colony when deciding whether or not to help, and facultatively adjusts her helping according to this information, then she may be expected to help more in colonies where the sex ratio is more female biased, that is, queenright colonies. Here, the sex ratio among the queen’s offspring is \bar{z}_R . We assume that the expected sex ratio of the worker’s offspring, should she choose to reproduce, is also \bar{z}_R . Thus, the inclusive fitness valuation that the worker places on queen-derived offspring is $\bar{z}_R v_m p_{mR} + (1 - \bar{z}_R) v_f p_{fR}$, and the inclusive fitness valuation that she places on her own offspring is her own offspring is $\bar{z}_R v_m p_s + (1 - \bar{z}_R) v_f p_d$. Thus, the potential for helping is $\alpha_{FAC} = [\bar{z}_R v_m p_{mR} + (1 - \bar{z}_R) v_f p_{fR}] / [\bar{z}_R v_m p_s + (1 - \bar{z}_R) v_f p_d]$. Substituting in the appropriate reproductive values, consanguinity coefficients and sex ratios, we obtain:

$$\alpha_{FAC} = \begin{cases} \frac{1+2\phi}{2} & \text{if } q \leq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \\ \frac{q[2 + (1+q)\phi]}{4q - 2(1-q^2)\phi} & \text{if } q \geq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \end{cases} \tag{10}$$

Since $\alpha > (1 + \phi)/2$ is true for all $q < 1$, haplodiploidy promotes the maintenance of facultative helping in queen-right colonies, under split sex ratios caused by queen replacement (fig. 3). This effect of haplodiploidy is substantial: assuming full monogamy ($\phi = 1$), the potential for facultative helping can be as great as $\alpha_{\text{FAC}} = 1.50$. In natural populations, the empirically observed range of queen survival rates is $0.6 < q < 0.8$, which would give $1.23 \leq \alpha_{\text{FAC}} \leq 1.50$ (fig. 3)

If the decision to help rear the queen's offspring versus own offspring is taken without reference to whether the queen is original or a replacement, then the inclusive fitness value of queen offspring and own offspring must be taken as an expectation over this uncertainty. Hence, the potential for obligate helping is given by $\alpha_{\text{OBL}} = \{q[\bar{z}_R v_m p_{mR} + (1 - \bar{z}_R) v_i p_{fR}] + (1 - q)[\bar{z}_L v_m p_{mL} + (1 - \bar{z}_L) v_i p_{fL}]\} / \{q[\bar{z}_R v_m p_s + (1 - \bar{z}_R) v_i p_d] + (1 - q)[\bar{z}_L v_m p_s + (1 - \bar{z}_L) v_i p_d]\}$. Substituting in the appropriate reproductive values, consanguinity coefficients and sex ratios, this obtains

$$\alpha_{\text{OBL}} = \begin{cases} \frac{(1+q)(1+2\phi)}{4} & \text{if } q \leq \frac{1}{3} \\ \frac{(5+q)(1+2\phi)}{16} & \text{if } \frac{1}{3} \leq q \leq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \\ \frac{[1+q+2(1-q)\phi][2+(1+q)\phi]}{8} & \text{if } q \geq \frac{-3 + \sqrt{9 + 8\phi(1+2\phi)}}{4\phi} \end{cases} \quad (11)$$

Here, $\alpha_{\text{OBL}} > (1 + \phi)/2$ is not always satisfied. Thus, haplodiploidy sometimes promotes and sometimes inhibits the maintenance of obligate helping if there is queen replacement, relative to the basic model of diploidy (fig. 3). Assuming full monogamy ($\phi = 1$), then $0.75 < \alpha_{\text{OBL}} < 1.07$. Considering the empirically observed range of queen survival rates ($0.6 < q < 0.8$), then $1.05 < \alpha_{\text{OBL}} < 1.07$, with the greatest potential for obligate helping being $\alpha_{\text{OBL}} \approx 1.07$ at $q \approx 0.69$. Note that the potential for obligate helping under diploidy is actually lower than $(1 + \phi)/2$ with queen replacement, owing to the reduced relatedness of a worker to the offspring of her queen. However, it is not meaningful to compare the potential for obligate helping under haplodiploidy with this lower value: all that we learn is that queen replacement inhibits helping more under diploidy than under haplodiploidy.

Discussion

We have shown that: (1) many of the proposed consequences of haplodiploidy are unlikely to have been im-

portant for the evolution of eusociality, because they rely on biological assumptions that the comparative data suggest did not occur en route to eusociality, such as multiple mating or associations between same-generation breeders (the "semisocial route"); (2) the most plausible route by which the haplodiploidy hypothesis could work is with split sex ratios, building on Trivers and Hare (1976); (3) although split sex ratios can be favored for many reasons, there are only two mechanisms that have both been observed empirically and are consistent with the biology of primitively social hymenopterans—virginity and queen replacement; and (4) while these two mechanisms can lead to haplodiploidy favoring eusociality, the overall effect is likely to be small and can even be negative.

Split Sex Ratios

We have examined two specific mechanisms that could have led to evolutionarily stable split sex ratios. First, unmated queens are constrained to produce only sons, whereas mated queens may produce both sons and daughters (Godfray and Grafen 1988). Hence, workers—who are female and therefore necessarily born into mated-queen colonies—have the option of rearing a cohort of siblings with a sex ratio that is female biased relative to the average for the population, which favors helping in haplodiploids. However, under the empirically plausible range of unmatedness rates (0%–6%, with a mode of 0%), the potential for helping is boosted by only 0%–3% when considering the origin of helping and only 0%–7% when considering the subsequent elaboration of helping. Moreover, this effect is predicted to be substantially lower if colonies with mated queens and workers have increased productivity, because this reduces the extent to which their offspring are female biased relative to the population average. That is, the situation that is most conducive to the evolution of helping (i.e., when helping leads to a large increase in the colony's productivity) is precisely the situation that erodes the impact of haplodiploidy on the potential for helping.

Second, split sex ratios may evolve in response to when queens die and are replaced by their daughters (Boomsma 1991). In colonies that retain the original queen (the mother of the workers), the workers are more related to the female (sisters) than the male (brothers) reproductives and so are favored to produce a relatively female-biased sex ratio. In contrast, in colonies where the original queen has died and has been replaced by one of her daughters (sister of the workers), the workers are less related to the female (nieces) than the male (nephews) reproductives and so are favored to produce a relatively male-biased sex ratio. We have found that this can lead to selection for helping being either promoted or inhibited by haplodiploidy, de-

Table 3: Empirical objections to the haplodiploidy hypothesis and their current status

Potential problem	Current status
If queens mate multiply, this removes the relatedness advantage of helping to raise siblings (Bourke and Franks 1995; Queller and Strassmann 1998)	Irrelevant, as multiple mating only evolved after obligate eusociality was established (Boomsma 2007, 2009; Hughes et al. 2008)
Assumes subsocial route, where offspring help mothers, and does not work with semisocial route where sisters cooperate (Bourke and Franks 1995)	Irrelevant, as phylogenetic evidence provides no evidence for eusociality ever evolving by the semisocial route (Boomsma 2007, 2009; Hughes et al. 2008)
Requires sex ratio manipulation with worker control (Charnov 1978; Stubblefield and Charnov 1986)	Not a problem, as considerable evidence for worker control of sex allocation, including prior to the evolution of permanent eusociality (Mueller 1991; West 2009)
There are alternative explanations for why eusociality is common in the Hymenoptera, such as extended parental care (Stubblefield and Charnov 1986; Queller and Strassmann 1998) and monogamy (Boomsma 2007, 2009)	True, but does not exclude a role of haplodiploidy
Given more recent discoveries of eusociality (albeit facultative, not obligate) in other taxa (Aoki 1977; Jarvis 1981; Crespi 1992; Kent and Simpson 1992; Duffy 1996), has haplodiploidy really evolved more often in haplodiploids?	Valid question, but it does not exclude a role of haplodiploidy. Crozier (2008) has shown that eusociality is significantly more common in haplodiploid families, but this does not allow for fact that families are not phylogenetically independent. There has been no phylogenetic study testing whether the rate of transition to eusociality is significantly higher in haplodiploids.

pending on: (a) the incidence of queenright colonies; and (b) whether the workers can facultatively adjust their helping behavior according to the queenright/queenless status of the colony, or are obliged to help equally in both types of colonies. However, under the empirically supported range of probabilities of queen survival (60%–80%), haplodiploidy always promotes helping, with the potential for facultative helping boosted by up to 50% and the potential for obligate helping boosted to up to 7%. The overall importance of this mechanism will depend on how frequently queen replacement leads to split sex ratios: to date, it has been found only in some cooperative bees, suggesting it is not a general factor on the route to eusociality (Boomsma 1991; Mueller 1991; Packer and Owen 1994).

Furthermore, our analyses are likely to have overestimated the extent to which haplodiploidy favors eusociality via queen replacement. We followed previous analyses in assuming that when workers selfishly produce their own offspring within the queen's nest, these offspring will exhibit the same sex ratio as the queen-derived juveniles (Craig 1979). However, the female bias in the population sex ratio means that males have higher reproductive value than females, so that when workers are reproductive they will be favored to produce sons rather than daughters. This would tend to decrease the potential for facultative helping in queenright colonies and obligate helping in both colony types. We consider this effect, and the consequences of reproduction by workers more generally, elsewhere (J. Alpedrinha et al., unpublished manuscript).

Our emphasis in this article has been different to most

previous work on the haplodiploidy hypothesis. Most previous articles have examined whether the haplodiploidy hypothesis can be made to work (e.g., Trivers and Hare 1976; Seger 1983; Grafen 1986; Stubblefield and Charnov 1986; Godfray and Grafen 1988). In contrast, our aim has been to quantify the extent to which the haplodiploidy effect favors the evolution of eusociality. We have focused on those scenarios that are biologically most plausible (table 3), and found that the extent to which haplodiploidy favors eusociality will be either: (a) small (unmated females); or (b) small to medium but not widespread (queen replacement). In addition, we have clarified the distinction between selection on facultative versus obligate helping. The latter is less aided by haplodiploidy, because the increased relatedness to siblings when helping at female-biased colonies is negated by the decreased relatedness when helping at male-biased colonies. This means that haplodiploidy will be less likely to favor helping if females must choose whether to help before they know which type of colony they will be helping in, especially with regard to commitments to expressing helping adaptations that are made relatively early in development; for example, preclosure. Overall, our results suggest that, for the scenarios we consider here, haplodiploidy would have had only a minor influence on the evolution of eusociality.

Manipulation, Maternal Care, and Monogamy

In this final section, we briefly consider other factors that may have influenced the evolution of eusociality. First,

parental manipulation or parasitism may have helped the evolution of eusociality, by enforcing cooperation on workers (Alexander 1974; Charnov 1978). However, the extent to which workers will be favored to resist versus acquiesce to their queen depends on their relatedness to (and the reproductive value of) the different types of offspring, just as when considering cases with split sex ratios (Crozier 2008). Consequently, it is wrong to think of parental manipulation and kin selection as competing hypotheses for the evolution of eusociality (Crozier 2008). Furthermore, explicit theory has shown that queen manipulation is equally likely to occur in diploids and haplodiploids, and so it will not lead to haplodiploids being predisposed to eusociality (Charnov 1978).

Second, it is possible that haplodiploidy has predisposed certain taxa to eusociality, for reasons that are separate from Hamilton's (1964, 1972) suggestion concerning the asymmetry in relatedness to sisters versus daughters. Wade (2001; Linksvayer and Wade 2005) has suggested that maternal care—a prerequisite for eusociality—evolves more readily in haplodiploids than in diploids. Reeve (1993; Reeve and Shellman-Reeve 1997) has suggested that, even when helping genes experience the same systematic selection pressure under diploidy and haplodiploidy, they may be better protected from stochastic loss under haplodiploidy. Fromhage and Kokko (2011) have suggested that haplodiploidy can enhance synergistic interaction between genes for helping. However, these three ideas require restrictive assumptions, which make them unlikely to be of general importance. Specifically, they require that maternal care genes have particular, deleterious pleiotropic effects (Wade 2001); helping genes are overdominant (Reeve 1993); or that the worker phenotype is controlled by a single allele of large effect (Fromhage and Kokko 2011). More generally, we emphasize the importance of constructing realistic models of specific scenarios that are led by and parameterized with empirical data.

Third, both theory and data suggest that monogamy has played a key role in the evolution of eusociality. Strict lifetime monogamy leads to a worker being equally related to her own offspring and to the offspring of her mother and hence to a potential for helping of $\alpha = 1$ (Boomsma 2007, 2009). In this case, any small efficiency benefit from rearing siblings ($b/c > 1$) would lead to helping being favored by natural selection (i.e., $b/c > 1/\alpha$). Multiple mating reduces the relatedness of siblings and decreases selection for any form of cooperation (Charnov 1981). For example, if females mate with two or three males, this reduces the potential for helping to $\alpha = 3/4$ or $2/3$, respectively, and so substantial efficiency benefits to cooperation would be required ($b/c > 4/3$ or $3/2$, respectively). Consistent with this, obligate eusociality has evolved only in lineages where strict monogamy is the ancestral state (Boomsma 2007,

2009; Hughes et al. 2008), and the evolution of facultative cooperative breeding is more common in species with lower rates of promiscuity (Cornwallis et al. 2010). Consequently, the hunt to find a way for haplodiploidy to push the potential for helping higher than unity ($\alpha > 1$) may have been misguided. Instead, a more important factor may have been the need for monogamy to keep the potential for helping at unity ($\alpha = 1$), and some small efficiency benefit for rearing siblings over one's own offspring ($b/c > 1$). Efficiency benefits appear to arise from the life insurance of allowing helpers to complete parental care after the death of the mother, or the fortress-defense benefits of protecting a common nest (Hamilton 1964, 1972; Queller 1989, 1994; Foster 1990; Gadagkar 1991; Queller and Strassmann 1998; Field et al. 2000; Strassmann and Queller 2007).

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APPENDIX A

Reproductive Value and Relatedness

Inclusive fitness is gained by sending copies of one's genes into future generations. Hence, an actor is predicted to behave as if she values the reproductive success of her relatives, as they may carry copies of her genes and pass them on to their descendants (Hamilton 1964). Specifically, the value that she places on a relative is given by the product of the relative's reproductive value (v ; i.e., how well they transmit copies of their own genes into future generations; Fisher 1930) and the consanguinity of the relative to the actor (p ; i.e., the probability the relative's and actor's genes are identical by descent; Bulmer 1994).

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 1990; Grafen 2006b). Typically, reproductive value is first calculated for a class, and then the class's reproductive value is shared equally over all individuals in that class. For example, in diploids, the probability that a gene picked at random from a distant future generation descends from

a male ancestor in the present generation is $1/2$. Hence, the class reproductive value of males is $c_m = 1/2$, and the reproductive value of an individual male is $v_m = c_m/N_m$, where N_m is the number of males in the population. Alternatively, reproductive values may be scaled by any arbitrary constant, to make the quantities more manageable. For example, multiplying all individual reproductive values by the total number of individuals in the population, we have $v_m = c_m/\bar{z} = 1/[2(1 - \bar{z})]$ and $v_f = c_f/(1 - \bar{z}) = 1/[2(1 - \bar{z})]$, where \bar{z} is the proportion of reproductive individuals who are male.

Consanguinity is defined as the probability that two genes picked at random from two given individuals are identical by descent (Bulmer 1994). Thus, the probability of drawing a given allele from the recipient given that it has already been drawn from the actor is $x' = p + (1 - p)\bar{x}$, where p is the consanguinity of the actor and recipient and \bar{x} is the frequency of the allele in the whole population. This allows a regression interpretation for consanguinity: rearranging, we have $p = (x' - \bar{x})/(1 - \bar{x})$, that is, consanguinity measures the concentration of the actor's genes in the recipient.

It is often natural to seek a measure of relative genetic similarity such that the similarity to oneself is 1. This is obtained by dividing consanguinity between actor and recipient by the consanguinity of actor to self, that is, $r = p/p_{\text{self}}$. This is the regression coefficient of relatedness (Hamilton 1970; Michod and Hamilton 1980; Pamilo and Crozier 1982; Grafen 1985) and, for outbred diploids, this takes the familiar values of $r = 1$ for self, $r = 1/2$ for full sibs, $r = 1/4$ for half sibs, and $r = 1/8$ for cousins. More generally, since throughout our analysis we will assume outbreeding and diploid actors (i.e., females), the consanguinity to self for the actor is always $p_{\text{self}} = 1/2$, and hence the regression coefficient of relatedness is $r = 2p$.

The regression relatedness values for a female to her son and to her brother under haplodiploidy are $r = 1$ and $r = 1/2$, respectively. Many readers will be more familiar with values of $1/2$ and $1/4$, respectively. The latter values refer to "life-for-life" relatedness coefficients, which were commonly used in the kin selection literature on haplodiploids to account for both genetic similarity and reproductive value effects in a single coefficient (Hamilton 1972; Trivers and Hare 1976; Grafen 1986). Assuming an even sex ratio and vanishingly rare worker reproduction, these life-for-life relatedness coefficients can be recovered by simply multiplying the regression coefficient of relatedness by individual reproductive value, that is, $R = r \times v$ (Hamilton 1972; Bulmer 1994), and scaling all reproductive values such that the reproductive value of a female is $v_f = 1$. Thus, the life-for-life relatedness of a female to her son is $R = 1 \times 1/2 = 1/2$ and to her brother is $R = 1/2 \times 1/2 = 1/4$. Sometimes, life-for-life relatedness

coefficients have been defined as the probability that a gene picked at random from the actor is identical by descent with any gene in the recipient (Trivers and Hare 1976; Charlesworth 1980). If the recipient is haploid this is simply the consanguinity of the actor and recipient, whereas if the recipient is diploid this is twice the consanguinity of the actor and recipient. This corrects for reproductive value but only owing to a mathematical coincidence: in both diploids and haplodiploids, the ratio of female to male ploidies is equal to the ratio of female to male individual reproductive values (under the assumption of vanishingly rare worker reproduction and an even sex ratio). This correction does not work more generally, for example, under certain hypothetical haplotriploid modes of inheritance (Grafen 1986) or, more importantly, when worker reproduction is common and/or sex ratios are biased (see apps. B–D).

APPENDIX B

Split Sex Ratios and the Evolution of Helping

For the purpose of calculating reproductive value, we census the population at the moment of production of offspring. The proportion of genes in female larvae at the time of census that derive from the females of the last census is $\phi_{f \leftarrow f} = 1/2$ and hence the proportion of genes in female larvae that derive from the males of the last census is $\phi_{f \leftarrow m} = 1 - \phi_{f \leftarrow f} = 1/2$. The proportion of genes in male larvae at the time of census that derive from the females of the last census is $\phi_{m \leftarrow f} = 1$, and hence the proportion of genes in male larvae that derive from the males of the last census is $\phi_{m \leftarrow m} = 1 - \phi_{m \leftarrow f} = 0$. These quantities can be summarized in a gene flow matrix:

$$\mathbf{M} = \begin{bmatrix} \phi_{f \leftarrow f} & \phi_{f \leftarrow m} \\ \phi_{m \leftarrow f} & \phi_{m \leftarrow m} \end{bmatrix}. \quad (\text{B1})$$

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). This yields $c_f = 2/3$ for females and $c_m = 1/3$ (Price 1970; Taylor 1996). Individual reproductive values can be expressed as the class reproductive value divided by the proportion of the population that belongs to that class, that is, $v_m = c_m/\bar{z}$ for males and $v_f = c_f/(1 - \bar{z})$ for females (Taylor 1996).

The consanguinity of a female to her brothers and sisters is $p_m = 1/4$ and $p_f = (1 + 2\phi)/8$, respectively, where ϕ is the consanguinity of two random sperm that fertilize the eggs of the same female. The consanguinity of a female to her sons and daughters is $p_s = 1/2$ and $p_d = 1/4$, respectively.

APPENDIX C

Split Sex Ratios Owing to Virginity

Origin of Helping

Here we derive the queen's convergence stable sex allocation strategy. We model this by assuming that she produces fertilized (female) and unfertilized (male) eggs in equal numbers but has resources to raise only half of these eggs to maturity, so by choosing which individuals to raise, she determines the sex ratio of her offspring. The expected fitness of a female egg laid by a mated queen, before the enactment of the sex allocation decision, is therefore $1 - z_M$, that is, the probability that she will be reared to reproductive maturity. The average fitness of her class is $1 - \bar{z}_M$, and hence her relative fitness is $W_f = (1 - z_M)/(1 - \bar{z}_M)$. Similarly, the relative fitness of a male egg, expressed relative to the average for all males, is $W_m = [u + (1 - u)z_M]/[u + (1 - u)\bar{z}_M]$. Natural selection favors an increase in the population average value of any trait if individuals carrying genes for this trait are fitter on average. In a class structured population, fitness is averaged using class reproductive values as weights, that is, $W = c_f W_f + c_m W_m$ (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). If a gene affecting the trait of interest has genic value g , then the condition for natural selection to favor an increase in the population average value of this trait is $dW/dg > 0$. Hence, the direction of selection acting on the sex ratio of mated queens is given by

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

where $\partial W_f/\partial z_M = -1/(1 - \bar{z}_M)$ and $\partial W_m/\partial z_M = (1 - u)/[u + (1 - u)\bar{z}_M]$ are the fitness effects of the queen's sex allocation decision on female and male eggs, respectively; \bar{g} is the queen's genetic value for her sex allocation trait; $dz_M/d\bar{g} = 1$ is the genotype-phenotype map; and $d\bar{g}/dg_{fM} = p_d = 1/4$ and $d\bar{g}/dg_{mM} = p_s = 1/2$ are the coefficients of consanguinity between mother and daughter and between mother and son, respectively (Taylor 1990, 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Substituting in the class reproductive values obtains a condition for increase in sex ratio strategy employed by mated queens $dW/dg > 0$ in terms of model parameters, and we use this to obtain equation (3) in the main text.

Elaboration of Helping

Here we derive the workers' convergence stable sex allocation strategy. This is modeled by assuming that the queen produces fertilized (female) and unfertilized (male) eggs in equal numbers, and the workers choose which half of these are to be raised to reproductive maturity. The expected fitness of a female egg in a mated-queen colony, before the enactment of the worker sex allocation decision, is therefore $1 - z_M$, that is, the probability that she will be reared to reproductive maturity. The average fitness of her class is $1 - \bar{z}_M$, and hence her relative fitness is $W_f = (1 - z_M)/(1 - \bar{z}_M)$. Similarly, the relative fitness of a male egg, expressed relative to the average for all males, is $W_m = [ua + (1 - u)z_M]/[ua + (1 - u)\bar{z}_M]$. As before, the direction of selection acting on the sex ratio of mated-queen colonies is given by equation (C1), where $\partial W_f/\partial z_M = -1/(1 - \bar{z}_M)$ and $\partial W_m/\partial z_M = (1 - u)/[ua + (1 - u)\bar{z}_M]$ are the fitness effects of the worker sex allocation decision on female and male eggs, respectively; \bar{g} is the average of the workers' genetic values for their sex allocation trait; $dz_M/d\bar{g} = 1$ is the genotype-phenotype map; and $d\bar{g}/dg_{fM} = p_f = 3/8$ and $d\bar{g}/dg_{mM} = p_m = 1/4$ are the coefficients of consanguinity between worker and queen's female offspring and between worker and queen's male offspring, respectively (Taylor 1990, 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Substituting in the class reproductive values obtains a condition for increase in sex ratio of mated-queen colonies $dW/dg > 0$ in terms of model parameters, and we use this to obtain equation (6) in the main text.

APPENDIX D

Split Sex Ratios Owing to Queen Replacement

One consequence of queen replacement is that males gain extra reproductive value, owing to their ability to father and mate with replacement queens. Again, for the purpose of calculating reproductive value, we census the population at the moment of production of reproductive offspring. The proportion of genes in female larvae at the time of census that derive from the females of the last census is $\wp_{f \leftarrow f} = q/2 + (1 - q)/4 = (1 + q)/4$, and hence the proportion of genes in female larvae that derive from the males of the last census is $\wp_{f \leftarrow m} = 1 - \wp_{f \leftarrow f} = (3 - q)/4$. The proportion of genes in male larvae at the time of census that derive from the females of the last census is $\wp_{m \leftarrow f} = q + (1 - q)/2 = (1 + q)/2$, and hence the proportion of genes in male larvae that derive from the males of the last census is $\wp_{m \leftarrow m} = 1 - \wp_{m \leftarrow f} = (3 - q)/2$. Using the procedure outlined in appendix B, the class reproductive values are $c_f = (2 + 2q)/(5 + q)$ and $c_m = (3 -$

$q)/(5 + q)$. It is useful to define four classes of young reproductives, according to their sex and the colony type from which they were reared. So, the class reproductive value of queenright females is $c_{fR} = [q(1 - \bar{z}_R)/(1 - \bar{z})]c_P$, that of queenright males is $c_{mR} = [q\bar{z}_R/\bar{z}]c_m$, that of queenless females is $c_{fL} = [(1 - q)(1 - \bar{z}_L)/(1 - \bar{z})]c_P$ and that of queenless males is $c_{mL} = [(1 - q)\bar{z}_L/\bar{z}]c_m$, where \bar{z}_R and \bar{z}_L are the average sex ratios of queenright colonies and queenless colonies, respectively.

The sex allocation decision of the workers is modelled in the usual way. An equal number of male and female larvae are produced, and the workers choose which of these to rear. The expected fitness of a female egg in a queenright colony, prior to the enactment of the worker sex allocation decision, is therefore $1 - z_R$, that is, the probability that she will be reared to reproductive maturity. The average fitness of her class is $1 - \bar{z}_R$, and hence her relative fitness is $W_{fR} = (1 - z_R)/(1 - \bar{z}_R)$. Similarly, the relative fitness of a queenright male is $W_{mR} = z_R/\bar{z}_R$, that of a queenless female is $W_{fL} = (1 - z_L)/(1 - \bar{z}_L)$, and that of a queenless male is $W_{mL} = z_L/\bar{z}_L$. Thus, natural selection maximizes the quantity $W = c_{fR}W_{fR} + c_{mR}W_{mR} + c_{fL}W_{fL} + c_{mL}W_{mL}$ (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Hence, the direction of selection acting on the sex ratio of queenright colonies is given by

$$\begin{aligned} \frac{dW}{dg} &= c_{fR} \frac{dW_{fR}}{dg_{fR}} + c_{mR} \frac{dW_{mR}}{dg_{mR}}, \\ &= c_{fR} \frac{\partial W_{fR}}{\partial z_R} \frac{dz_R}{d\tilde{g}} \frac{d\tilde{g}}{dg_{fR}} + c_{mR} \frac{\partial W_{mR}}{\partial z_R} \frac{dz_R}{d\tilde{g}} \frac{d\tilde{g}}{dg_{mR}}, \quad (D1) \end{aligned}$$

where $\partial W_{fR}/\partial z_R = -1/(1 - \bar{z}_R)$ and $\partial W_{mR}/\partial z_R = 1/\bar{z}_R$ are the fitness effects of the worker sex allocation decision on female and male eggs, respectively, in a queenright colony; \tilde{g} is the average of the workers' genetic values for their sex allocation trait; $dz_R/d\tilde{g} = 1$ is the genotype-phenotype map; and $d\tilde{g}/dg_{fR} = p_{fR}$ and $d\tilde{g}/dg_{mR} = p_{mR}$ are the coefficients of consanguinity between worker and queen's female offspring and between worker and queen's male offspring, respectively, in a queenright colony (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). Since the queen's offspring are the worker's siblings, these are $p_{fR} = 3/8$ and $p_{mR} = 1/4$. Substituting in the class reproductive values obtains a condition for increase in sex ratio of queenright colonies $dW/dg > 0$ in terms of model parameters. We consider the action of selection on the sex ratio of queenless colonies in exactly the same way, deriving a condition for increase. In this case, the coefficients of consanguinity to female and male eggs are those for nieces and nephews, that is, $p_{fL} = 3/16$ and $p_{mL} = 3/8$. We use these conditions to

identify the convergence stable state of the population (Taylor 1996). This obtains equation (9) in the main text.

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A queen ant (*Formica truncorum*) preparing for her nuptial flight. Photograph by L. Sundström.