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Sex-biased dispersal, haplodiploidy and the evolution of helping in social insects

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In his famous haplodiploidy hypothesis, W. D. Hamilton proposed that high sister–sister relatedness facilitates the evolution of kin-selected reproductive altruism among Hymenopteran females. Subsequent analyses, however, suggested that haplodiploidy cannot promote altruism unless altruists capitalize on relatedness asymmetries by helping to raise offspring whose sex ratio is more female-biased than the population at large. Here, we show that haplodiploidy is in fact more favourable than is diploidy to the evolution of reproductive altruism on the part of females, provided only that dispersal is male-biased (no sex-ratio bias or active kin discrimination is required). The effect is strong, and applies to the evolution both of sterile female helpers and of helping among breeding females. Moreover, a review of existing data suggests that female philopatry and non-local mating are widespread among nest-building Hymenoptera. We thus conclude that Hamilton was correct in his claim that 'family relationships in the Hymenoptera are potentially very favourable to the evolution of reproductive altruism'.

Keywords: kin selection; local competition; cooperation; altruism; social insects

1. INTRODUCTION

Bees, wasps and ants (Hymenoptera) have haplodiploid sex determination, whereby males arise from unfertilized eggs and are haploid, whereas females arise from fertilized eggs and are diploid. One consequence of haplodiploidy is that females are more closely related to sisters ($r = 0.75$) than is the case in diploids ($r = 0.5$). W. D. Hamilton suggested that this difference might help to explain the large number of origins of sociality and reproductive altruism among females in the Hymenoptera [1]. More recent work, both theoretical and empirical, cast doubt on this theory. Genetic models suggest that because a female's relatedness to her brothers is lower under haplodiploidy ($r = 0.25$) than under diploidy ($r = 0.5$), haplodiploidy can promote altruism only if altruists help to produce young among whom females are more common than in the general population [2]; although there are conditions under which this may occur, it is questionable how often they are met [3]. In addition, empirical studies have shown that active kin discrimination is rare in the social Hymenoptera [4]. Such findings have led to a shift in focus from genetic to ecological factors favouring hymenopteran eusociality [5], although the two are not necessarily mutually exclusive.

Here, we show that haplodiploidy is in fact favourable to the evolution of reproductive altruism on the part of females, provided only that dispersal is male-biased—it is not necessary to invoke sex-ratio bias or active kin discrimination. Several previous analyses of altruism in viscous populations (with limited dispersal) have considered the impact of haplodiploidy, but none have explored the interaction between haplodiploidy and sex-biased dispersal as we do. In his seminal model of local helping, Taylor [6] explicitly showed that haplodiploidy does not alter the conditions for the evolution of helping among adult breeders, given the assumption that males mate on their natal patch and females then disperse (carrying their partner's genes with them—effectively ensuring identical dispersal rates for both sexes); Queller [7] subsequently suggested that sex-biased dispersal might alter this conclusion, but did not formally analyse this possibility. More recently, Johnstone & Cant [8] showed that sex-biased dispersal can favour helping among adult breeders, but considered only the diploid case. Lastly, Lehmann *et al.* [9] showed that population viscosity can favour the evolution of sterile workers (as opposed to helping among breeders). They explicitly demonstrate, as Taylor [6] did, that haplodiploidy does not affect the conclusions of their model when dispersal is identical for both sexes (and both males and females become workers). Unlike Taylor [6], they also briefly consider the impact of sex differences in dispersal, but do not explore in detail the interaction between sex-biased dispersal and haplodiploidy.

Below, we build on the analyses of Lehmann *et al.* [9] and Johnstone & Cant [8] to show that when dispersal is male-biased, haplodiploidy does favour female reproductive altruism, whether this takes the form of the evolution of sterile female workers or of helping among reproductive females. Since both analyses make very similar assumptions about population structure, we treat them as variants of a single model, distinguished chiefly by their focus on the evolution of sterile female helpers or of helping among adult reproductive females, respectively.

2. MODEL

We focus on an infinite, sexually reproducing population divided into discrete groups or colonies, each comprising n breeding females or queens, possibly assisted by a

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variable number of sterile female workers. The population cycles through a series of steps: queens in a colony (with the assistance of local workers) each produce a large number of offspring. Some fraction of female young develop as sterile workers; the remaining females and all males are reproductively capable, with a primary sex ratio of f reproductive female to $(1-f)$ reproductive male young. Reproductively capable female and male offspring then disperse with probability $(1-h_{\mathrm{f}})$ and $(1-h_{\mathrm{m}})$; we assume that workers always remain in their natal colony. Dispersal is followed by random mating among reproductively capable offspring present in a patch (if a female remains in her natal colony with probability h_{f}, then with probability h_{m} she mates with a male from the same colony who has not dispersed; otherwise, she mates with a non-local male). Following mating, all queens and workers of the parental generation die, as do reproductively capable males of the offspring generation. Lastly, queens of the offspring generation compete for breeding spots vacated by the death of queens of the parental generation. Those queens who fail to obtain a breeding position die, while those that survive will, with the assistance of local workers, go on to produce a new generation of young.

We consider the evolution of two forms of altruism. First, following Lehmann *et al.* [9], we focus on an allele of small effect that causes a slight increase of c in the proportion of female offspring that become sterile workers (assuming that development as a worker or as a reproductive is under offspring control). This entails a reduction of c in the fraction of female offspring bearing the allele that become reproductively capable, but the additional workers are assumed later to increase the number of reproductively capable offspring produced by their colony by a fraction b.

Second, following Johnstone & Cant [8] (an extension of Taylor [6]), we consider an allele that causes a queen bearing it to engage (after dispersal and mating, just before reproduction) in helping behaviour, which again entails a proportional reduction of c in the number of reproductively capable young she produces, but confers an immediate proportional fecundity gain of b on other queens in the same colony.

3. ANALYSIS

To derive the inclusive fitness effects of helping alleles, we adopt the terminology of Lehmann *et al.* [9], and will write Q_i for the probability of identity between two homologous genes randomly sampled with replacement from the same individual of sex i, Q_{ij} for the probability of identity between a gene sampled in a reproductive adult of sex i and another homologous gene randomly sampled from a distinct reproductive adult of sex j in the same colony (immediately after dispersal), and $Q_{ii}^{\mathrm{R}} = (1/n)Q_i + (1-(1/n))Q_{ii}$ for the probability of identity between two genes sampled with replacement from same-sex reproductive individuals in the same colony at the adult stage. We will also write Q_{ij}^{J} for the probability of identity between a gene sampled in a juvenile of sex i and another homologous gene randomly sampled from a distinct juvenile of sex j in the same colony (immediately prior to dispersal), and Q_{ij}^{W} for the probability of identity between a gene sampled in an adult worker of sex i and another homologous gene randomly sampled from a reproductive adult of sex j in the same colony (immediately after dispersal). Given our assumptions above, it is straightforward to determine these probabilities of genetic identity under either diploidy or haplodiploidy (see appendix A). We can then use these values to determine the inclusive fitness effects of the alleles with which we are concerned. Our analysis follows the direct fitness method of Taylor & Frank [10] and Rousset [11], whereby we focus on the effect of all actors expressing a mutant helping allele on the fitness of a focal adult bearing the allele in question (including the effect of the focal adult on itself).

Table 1. Inclusive fitness effects of female worker allele.

	offspring number	weight
through daughters:	$-c$	$v_{\mathrm{f}}(t_{\mathrm{ff}}Q_{\mathrm{f}} + t_{\mathrm{fm}}Q_{\mathrm{f}})$
	ch_{f}^2	$v_{\mathrm{f}}(t_{\mathrm{ff}}Q_{\mathrm{ff}}^{\mathrm{J}} + t_{\mathrm{fm}}Q_{\mathrm{ff}}^{\mathrm{J}})$
	fb	$v_{\mathrm{f}}(t_{\mathrm{ff}}Q_{\mathrm{ff}}^{\mathrm{W}} + t_{\mathrm{fm}}Q_{\mathrm{fm}}^{\mathrm{W}})$
	$-fbh_{\mathrm{f}}^2$	$v_{\mathrm{f}}(t_{\mathrm{ff}}Q_{\mathrm{ff}}^{\mathrm{W}} + t_{\mathrm{fm}}Q_{\mathrm{fm}}^{\mathrm{W}})$
through sons:	fb	$v_{\mathrm{m}}(t_{\mathrm{mf}}Q_{\mathrm{ff}}^{\mathrm{W}} + t_{\mathrm{mm}}Q_{\mathrm{fm}}^{\mathrm{W}})$
	$-fbh_{\mathrm{m}}^2$	$v_{\mathrm{m}}(t_{\mathrm{mf}}Q_{\mathrm{ff}}^{\mathrm{W}} + t_{\mathrm{mm}}Q_{\mathrm{fm}}^{\mathrm{W}})$

Table 1 summarizes the inclusive fitness effects of an allele that increases the proportion of female offspring who become workers. This is equivalent to table 3 of Lehmann *et al.* [9], but differs for three reasons: (i) we have assumed that only female offspring become workers; (ii) we have assumed that workers do not disperse; and (iii) we have allowed for different rates of female and male dispersal among reproductively capable young; we have also partitioned terms slightly differently. The table lists inclusive fitness effects through daughters and through sons, the four rows in the former case corresponding to (i) the immediate loss of reproductive daughters due to a greater proportion of them becoming workers, (ii) the gain in reproductive daughters attributable to reduced local competition caused by the former loss, (iii) the gain in reproductive daughters owing to the positive impact of increased worker numbers on colony productivity and, lastly, (iv) the loss of reproductive daughters attributable to increased local competition caused by this greater productivity. Since the worker allele is not expressed in males, there are only two rows for effects through sons, corresponding to (i) the gain in reproductive sons owing to the positive impact of increased worker numbers on colony productivity and (ii) the loss of reproductive sons attributable to increased local competition caused by this greater productivity. These fitness effects are calculated taking into account the possibility that the focal helping allele may reside in an adult male or queen, with the sexes weighted according to t_{ij}, the probability that a gene randomly taken in an individual of sex i descends from an individual of sex j; effects through sons and daughters are also weighted according to the reproductive value v_i of an individual of sex i (see appendix A).

Lehmann *et al.* [9] observe, in their analysis, that the population female-to-male sex ratio f (among reproductive young) does not affect the evolution of the helping

Table 2. Inclusive fitness effects of adult female helping allele.

	offspring number	weight
through daughters:	$-c$	$v_\mathrm{f}(t_\mathrm{ff}Q_\mathrm{f} + t_\mathrm{fm}Q_\mathrm{fm})$
	ch_f^2	$v_\mathrm{f}(t_\mathrm{ff}Q_\mathrm{ff}^\mathrm{R} + t_\mathrm{fm}Q_\mathrm{fm})$
	b	$v_\mathrm{f}(t_\mathrm{ff}Q_\mathrm{ff} + t_\mathrm{fm}Q_\mathrm{fm})$
	$-bh_\mathrm{f}^2$	$v_\mathrm{f}(t_\mathrm{ff}Q_\mathrm{ff}^\mathrm{R} + t_\mathrm{fm}Q_\mathrm{fm})$
through sons:	$-c$	$v_\mathrm{m}(t_\mathrm{mf}Q_\mathrm{f} + t_\mathrm{mm}Q_\mathrm{fm})$
	ch_m^2	$v_\mathrm{m}(t_\mathrm{mf}Q_\mathrm{ff}^\mathrm{R} + t_\mathrm{mm}Q_\mathrm{fm})$
	b	$v_\mathrm{m}(t_\mathrm{mf}Q_\mathrm{ff} + t_\mathrm{mm}Q_\mathrm{fm})$
	$-bh_\mathrm{m}^2$	$v_\mathrm{m}(t_\mathrm{mf}Q_\mathrm{ff}^\mathrm{R} + t_\mathrm{mm}Q_\mathrm{fm})$

allele (see also [6,8]), because the relative expected reproductive success of individual females compared with males is inversely proportional to the female-to-male sex ratio, so that a queen obtains equal reproductive success through sons and daughters regardless of the value of f. In our case, however, it is only females that become workers, as in the social Hymenoptera. Under these circumstances, although a queen's loss of fitness owing to a given proportion of her daughters becoming workers is unaffected by f, the absolute number of workers produced as a result, and the benefit to colony productivity they provide, is proportional to f. Consequently, the population sex ratio does affect the fate of a sex-specific worker allele.

Table 2 summarizes, in a similar way to table 1, the inclusive fitness effects of an allele that promotes helping by adult queens. These are equivalent to the effective costs and benefits derived in Johnstone & Cant [8]; for ease of comparison, we have split them into similar components as in table 1, and expressed them in a more general form valid for both diploids and haplodiploids, using the notation of Lehmann *et al.* [9].

Summing up the elements of table 1 or table 2, and inserting the equilibrium values for the relevant probabilities of identity derived in the appendix, we obtain conditions for invasion of alleles that cause an increased proportion of female offspring to become workers, or that promote helping by adult reproductive females, in diploids or haplodiploids.

4. RESULTS: WORKER EVOLUTION

We consider first the conditions for the invasion of an allele that leads to an increased proportion of female offspring becoming workers. When $h_\mathrm{f} = h_\mathrm{m}$, implying that there is no sex-bias in dispersal, we find (as did Taylor [6] and Lehmann *et al.* [9]) that haplodiploidy does not influence the conditions for invasion; in both diploids and haplodiploids the allele can invade when

$$\frac{fh}{n} b > c,$$

where h denotes the frequency of philopatry for both females and males, which we assume is less than 1, so that there is some dispersal linking patches in a metapopulation (given that there is no sex-bias in dispersal, a single parameter suffices to specify the frequency of philopatry for both sexes). Note that the critical ratio of c to b below which invasion is possible differs from that given in eqn (2.5) of Lehmann *et al.* [9] by a factor of h (equivalent to $1 - m$ in their notation) because we have assumed that workers do not disperse (and hence are on average more closely related to the individuals that they help). In addition, because we have assumed that only female offspring become workers, the ratio is proportional to the fraction of offspring that are female (this was not the case in Lehmann *et al.*'s analysis, because it was based on the assumption that both sexes become workers).

Now consider the impact of sex-biased dispersal. When $h_\mathrm{f} = 1$ and $h_\mathrm{m} = 0$, implying that males all disperse to mate while females all remain on their natal patch, the invasion conditions are $(f/(3n-1))b > c$ for diploids and $(3f/(6n-4))b > c$ for haplodiploids. The critical ratio of c to b below which invasion is possible (a simple measure of the strength of selection for helping) is thus (for any positive value of f) three times greater in haplodiploids than in diploids when there is a single breeding queen per colony (i.e. when $n = 1$), as is often the case in social Hymenoptera. As the number of queens per colony, n, increases, the relative strength of selection under haplodiploidy compared with diploidy declines, but always remains substantial, tending to precisely 50 per cent greater in haplodiploids than in diploids as n becomes large. By contrast, when $h_\mathrm{f} = 0$ and $h_\mathrm{m} = 1$, implying that it is females who disperse and males who stay put, the invasion conditions are $(f/(3n+1))b > c$ for diploids and $(f/4n)b > c$ for haplodiploids. In this case, the critical ratio of c to b below which invasion is possible is (for any positive value of f) smaller for haplodiploids than for diploids, tending to 25 per cent smaller as n becomes large. To sum up, haplodiploidy favours the evolution of helping when dispersal is completely male-biased, but is unfavourable when dispersal is completely female-biased.

Figure 1 shows the relative strength of selection for female workers in haplodiploids compared with diploids, for the full range of values of h_f and h_m (for the illustrative case of $n = 5$ breeding queens per colony; other values of n yield qualitatively similar results, although the effects are more pronounced with fewer queens per colony); as above, the relative strength of selection for workers under haplodiploidy compared with diploidy is independent of the population sex ratio. The graph confirms the general pattern suggested by the extreme cases considered above. Haplodiploidy generally favours the evolution of female workers when dispersal is male-biased (and inhibits the evolution of female workers when dispersal is female-biased), and does so more strongly the greater the degree of bias.

Although the relative strength of selection for female workers under haplodiploidy compared with diploidy does not change with the sex ratio, the absolute strength of selection under either genetic system does change. Moreover, the stable sex ratio itself changes according to the extent of sex-difference in dispersal. To illustrate this effect, figure 2 shows the absolute strength of selection for female workers in haplodiploids and in diploids, as female and male dispersal vary in opposition to one another, assuming that the sex ratio has evolved to its stable value (under maternal control) given the rates of

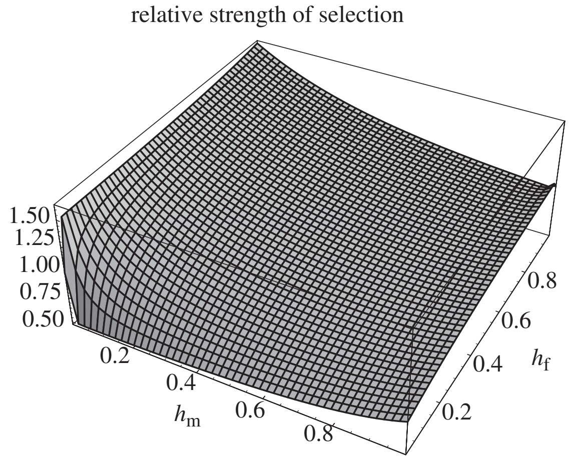

Figure 1. Relative strength of selection for female workers under haplodiploidy compared with diploidy. Strength of selection is measured as the critical ratio of c/b below which selection favours an allele that causes an increased proportion of female offspring to become workers. Results are shown as a function of the levels of male philopatry (h_m) and of female philopatry (h_f). In all cases, $n = 5$ breeding queens per colony (other values of n yield qualitatively similar results, with haplodipoidy becoming relatively more favourable to the evolution of female workers under male-biased dispersal for smaller values of n); note that the relative strength of selection for female workers under haplodiploidy compared with diploidy is independent of the population sex ratio (i.e. is unaffected by the proportion of female offspring f).

female and male dispersal. Results are shown for four different values of n, the number of breeding queens per colony ($n = 1$, 2, 4 and 8). It is constructive to compare these results with those previously shown. As figure 1 revealed, the relative strength of selection for helping under haplodiploidy, compared with under diploidy, is greatest when dispersal is completely male-biased (i.e. when $h_m = 0$ and $h_f = 1$). By contrast, figure 2 shows that the absolute strength of selection for helping under haplodiploidy attains a maximum when dispersal is somewhat (but not completely) male-biased. This is because an extreme male-bias in dispersal selects for a male-biased sex ratio, which tends to reduce the strength of selection for female helping. The effect is most pronounced when there is a single breeding female per colony (i.e. when $n = 1$), because the lack of female–female competition within a colony means that strongly male-biased dispersal can then favour a very skewed sex ratio, leading to a collapse in the strength of selection for female helping to zero as dispersal approaches the extreme of complete male-bias. Nevertheless, despite the effects of sex-ratio evolution, helping always evolves more easily under haplodiploidy than under diploidy when dispersal is female-biased, and the maximum strength of selection for helping (as one ranges from female- to male-biased philopatry) is greater under haplodiploidy than under diploidy.

5. RESULTS: HELPING BY ADULT FEMALES

When $h_f = h_m = h$, implying that there is no sex-bias in dispersal, an allele for adult female helping cannot invade (assuming $c > 0$) under either diploidy or haplodiploidy—this is simply a restatement of Taylor's [6] seminal result. However, when $h_f = 1$ and $h_m = 0$, implying that males all disperse to mate while females all remain on their natal patch, the invasion conditions are

$$-\frac{n-1}{6n^2 - 3n + 1} b > c$$

for diploids and

$$\frac{1}{4n-2} b > c$$

for haplodiploids. In this case, selection on diploids (as shown by Johnstone & Cant [8]) actually favours 'harming' behaviour, such that the allele in question cannot invade unless $b < 0$ (implying that queens bearing it exert a negative effect on the fecundity of others in their colony); in haplodiploids, by contrast, selection can favour helping behaviour, provided that the ratio of c to b is sufficiently low. When $h_f = 0$ and $h_m = 1$, implying that it is females who disperse and males who stay put, the invasion condition is

$$-\frac{1}{2n-1} b > c$$

for both diploids and haplodiploids. In this case, selection favours harming behaviour on the part of adult females (the dispersing sex) regardless of the genetic system.

Figure 3 shows the strength of selection for adult female helping and/or harming in haplodiploids and in diploids, over the full range of h_f (the frequency of female philopatry), for different degrees of male-bias in dispersal (i.e. for different ratios of h_m to h_f; the figure uses the illustrative case of $n = 5$ breeding queens per colony; other values of n yield very similar results); note that because selection sometimes favours helping and sometimes harming, the results are more complex than was the case in our analysis of a worker allele, and we cannot simply present the strength of selection for female helping in haplodiploids compared with diploids in a single graph as we did in figure 1. Nevertheless, the figure demonstrates that selection will only favour helping among adult queens when dispersal is male-biased, and that it is generally more likely to do so, and to do so more strongly, in haplodiploids than in diploids.

6. DISCUSSION

Our analysis suggests that haplodiploidy is favourable to the evolution of female helping, when combined with male-biased dispersal. This applies both to the evolution of helping by adult, breeding females and to the evolution of a sterile caste of worker females. In the former case, haplodiploidy can lead to selection for helping where harming would be favoured in diploids, while in the latter it simply leads to stronger selection for helping. The quantitative effect of haplodiploidy is pronounced—in the case of worker production, the critical ratio of c to b below which invasion is possible is more than 50 per cent greater in haplodiploids than in diploids, and rises, as the number of queens per colony falls, to three times greater in haplodiploids than in diploids for a single breeding queen per colony.

Why does haplodiploidy favour helping when dispersal is male-biased? Philopatry leads to positive local relatedness among females on a patch, which can potentially favour

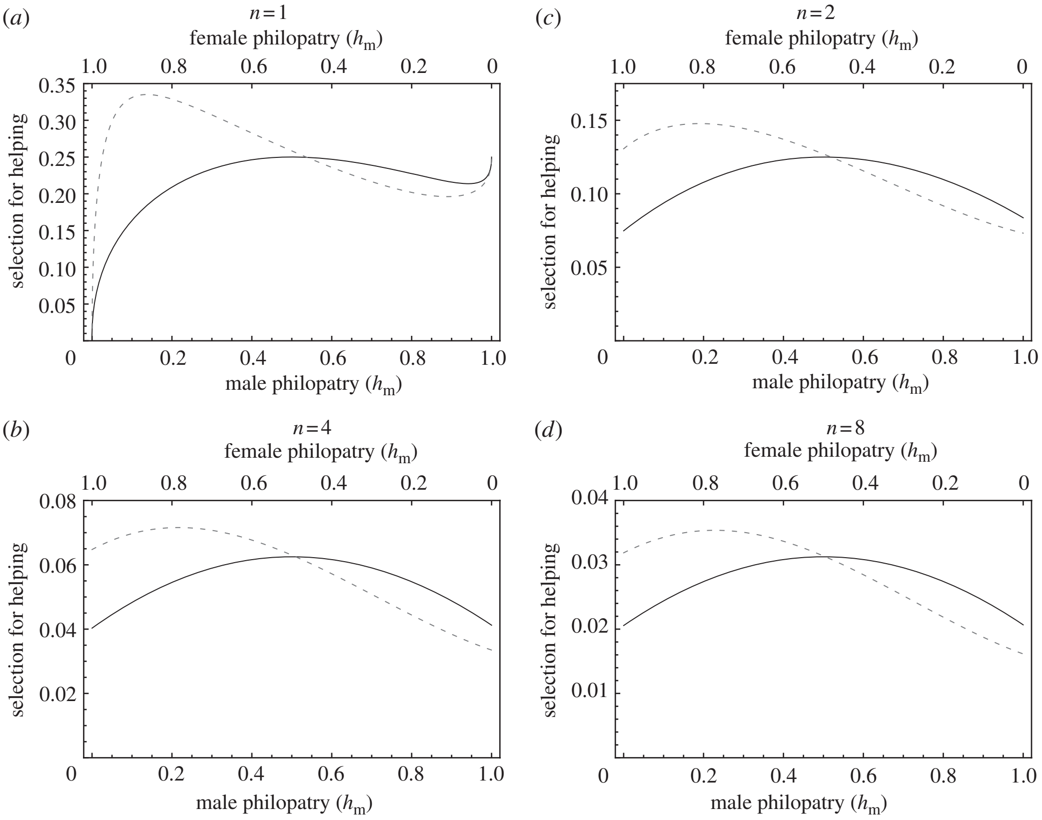

Figure 2. Absolute strength of selection for female workers under haplodiploidy and under diploidy, given a stable sex ratio. Strength of selection (under haplodiploidy, dashed line; under under diploidy, solid line) is measured as the critical ratio of *c*/*b* below which selection favours an allele that causes an increased proportion of female offspring to become workers. Results are shown as a function of the levels of male philopatry (h_m) and of female philopatry (h_f), assuming that these vary in opposition to one another (i.e. that $h_m = 1 - h_f$); thus, the left-hand side of each graph corresponds to female philopatry and male dispersal ($h_m = 0$, $h_f = 1$), and the right-hand side to female dispersal and male philopatry ($h_m = 1$, $h_f = 0$). In all cases, the sex ratio is assumed to have evolved to the equilibrium value (under maternal control) given the levels of female and male dispersal. Results are shown for different numbers of breeding queens per colony (n).

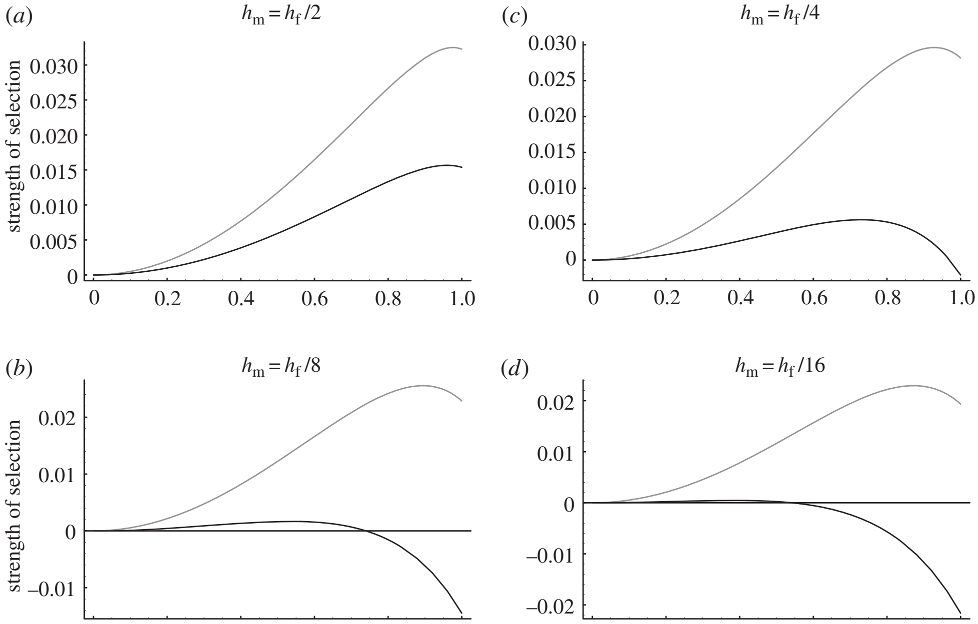

Figure 3. Strength of selection for helping or harming by adult queens under haplodiploidy (light line) compared with diploidy (dark line). Strength of selection is measured as the critical magnitude of the ratio of *c*/*b* below which an allele is favoured, with positive values representing selection for helping and negative selection for harming. Results are shown as a function of the level of female philopatry (h_f). Successive panels correspond to increasingly male-biased dispersal (i.e. to lower ratios of male philopatry compared with female philopatry). In all cases, $n = 5$ breeding queens per colony (other values of n yield qualitatively similar results).

helping behaviour. At the same time, it leads to local competition among the offspring of females on a patch, potentially favouring harming. The net effect of philopatry thus depends on the balance between these two effects. Under haplodiploidy, however, the unusually high relatedness between sisters leads to higher local relatedness within a patch than would be the case under diploidy, for the same level of female philopatry. When dispersal is male-biased, this high local relatedness is not diluted to the same extent by the low relatedness of haplodiploid females to their brothers, because males are more likely to leave their natal patch. The result is that helping yields greater kin-selected benefits in haplodiploids, while the intensity of local competition remains the same as in diploids, leading to stronger selection for helping.

But how common are female philopatry and male dispersal to mate among hymenopterans? Female philopatry is thought to be widespread in eusocial hymenopterans and their non-social sister lineages [12–14], but male dispersal has been less well studied. In primitively eusocial paper-wasps (*Polistes*), new queens each mate with a single male, then overwinter before initiating new nests in spring, often in groups where one queen dominates reproduction while the others act as helpers. Overwintered queens are philopatric, so that associations usually consist of close relatives (r life-for-life > 0.6 [15–17]). However, in three species where it has been measured, relatedness between the mates of joint-nesting queens is zero, so that mating is effectively non-local [15–17]. Similarly, in two species of *Myrmica* ants, the queens sharing a nest were relatives whereas their mates were probably unrelated [18,19], while in three additional studies there was no evidence of sex-biased dispersal [20–22]. A second way of testing whether dispersal is sex-biased is from studies in which gene flow has been estimated separately using mitochondrial and nuclear genes. In seven of nine such tests, including four *Formica* ant species, and in three other ant lineages in which tests have been conducted, gene flow was inferred to be male-biased [23–26]. Similarly, Clarke *et al.* [27] showed that Africanization of honeybees of the Yucatan initially involved mainly paternal gene flow, with negligible maternal gene flow.

In ants, there has been repeated evolution of a complex social organization known as ‘polygyny’, in which many queens share a nest. New queens are philopatric, commonly being readopted by their natal colonies after mating, or ‘budding off’ to start new nests adjacent to their natal colonies. Interestingly, there is some evidence that dispersal is more male-biased in polygynous populations than in conspecific monogynous populations, in which queens do not live in cooperative groups (so that there is only one queen per nest) [28,29]. Thus, while further tests for sex-biased dispersal are required, the data available imply that male-biased dispersal is widespread in the Hymenoptera.

To conclude, while our results do not call into question the importance of ecological factors for the evolution of eusociality [30], they indicate that haplodiploidy can also play a significant role. Hamilton [1] did not explicitly consider the significance of sex-specific dispersal for the evolution of altruism, but our results show that when dispersal is male-biased, he was indeed right to claim that ‘family relationships in Hymenoptera are potentially very favourable to the evolution of reproductive altruism’ (p. 28 of [1]).

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APPENDIX A. PROBABILITIES OF GENETIC IDENTITY

For diploids, at equilibrium, we have (following Taylor [31] and many subsequent analyses of the infinite island model, including Lehmann *et al.* [9] and Johnstone & Cant [8])

$$Q_{\mathrm{f}} = Q_{\mathrm{m}} = \frac{(1+Q_{\mathrm{fm}})}{2},$$

$$\begin{aligned} Q^{\mathrm{J}}_{\mathrm{ff}} = Q^{\mathrm{J}}_{\mathrm{fm}} = Q^{\mathrm{J}}_{\mathrm{mf}} = Q^{\mathrm{J}}_{\mathrm{mm}} &= \frac{1}{4}\left[\frac{1}{n}Q_{\mathrm{f}} + \frac{(n-1)}{n}Q_{\mathrm{ff}}\right] + \frac{1}{2}Q_{\mathrm{fm}} \\ &\quad + \frac{1}{4}\left[\frac{1}{n}Q_{\mathrm{m}} + \frac{(n-1)}{n}Q_{\mathrm{mm}}\right], \end{aligned}$$

$$Q_{\mathrm{ff}} = h_{\mathrm{f}}^2 Q^{\mathrm{J}}_{\mathrm{ff}}, \quad Q_{\mathrm{fm}} = h_{\mathrm{f}} h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{fm}}, \quad Q_{\mathrm{mf}} = h_{\mathrm{m}} h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{mf}} \quad \text{and} \quad Q_{\mathrm{mm}} = h_{\mathrm{m}}^2 Q^{\mathrm{J}}_{\mathrm{mm}},$$

$$Q^{\mathrm{W}}_{\mathrm{ff}} = h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{ff}}, \quad Q^{\mathrm{W}}_{\mathrm{fm}} = h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{fm}}, \quad Q^{\mathrm{W}}_{\mathrm{mf}} = h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{mf}} \quad \text{and} \quad Q^{\mathrm{W}}_{\mathrm{mm}} = h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{mm}},$$

$$t_{\mathrm{ff}} = \frac{1}{2}, \quad t_{\mathrm{fm}} = \frac{1}{2}, \quad t_{\mathrm{mf}} = \frac{1}{2} \quad \text{and} \quad t_{\mathrm{mm}} = \frac{1}{2},$$

and

$$v_{\mathrm{f}} = v_{\mathrm{m}} = \frac{1}{2}.$$

For haplodiploids, the corresponding equations are

$$Q_{\mathrm{f}} = \frac{(1+Q_{\mathrm{fm}})}{2} \quad \text{and} \quad Q_{\mathrm{m}} = 1,$$

$$\begin{aligned} Q^{\mathrm{J}}_{\mathrm{ff}} &= \frac{1}{4}\left[\frac{1}{n}Q_{\mathrm{f}} + \frac{(n-1)}{n}Q_{\mathrm{ff}}\right] + \frac{1}{2}Q_{\mathrm{fm}} \\ &\quad + \frac{1}{4}\left[\frac{1}{n}Q_{\mathrm{m}} + \frac{(n-1)}{n}Q_{\mathrm{mm}}\right], \end{aligned}$$

$$Q^{\mathrm{J}}_{\mathrm{fm}} = Q^{\mathrm{J}}_{\mathrm{mf}} = \frac{1}{2}\left[\frac{1}{n}Q_{\mathrm{f}} + \frac{(n-1)}{n}Q_{\mathrm{ff}}\right] + \frac{1}{2}Q_{\mathrm{fm}},$$

$$Q^{\mathrm{J}}_{\mathrm{mm}} = \frac{1}{n}Q_{\mathrm{f}} + \frac{(n-1)}{n}Q_{\mathrm{ff}},$$

$$Q_{\mathrm{ff}} = h_{\mathrm{f}}^2 Q^{\mathrm{J}}_{\mathrm{ff}}, \quad Q_{\mathrm{fm}} = h_{\mathrm{f}} h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{fm}}, \quad Q_{\mathrm{mf}} = h_{\mathrm{m}} h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{mf}} \quad \text{and} \quad Q_{\mathrm{mm}} = h_{\mathrm{m}}^2 Q^{\mathrm{J}}_{\mathrm{mm}},$$

$$Q^{\mathrm{W}}_{\mathrm{ff}} = h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{ff}}, \quad Q^{\mathrm{W}}_{\mathrm{fm}} = h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{fm}}, \quad Q^{\mathrm{W}}_{\mathrm{mf}} = h_{\mathrm{f}} Q^{\mathrm{J}}_{\mathrm{mf}} \quad \text{and} \quad Q^{\mathrm{W}}_{\mathrm{mm}} = h_{\mathrm{m}} Q^{\mathrm{J}}_{\mathrm{mm}},$$

$$t_{\mathrm{ff}} = \frac{1}{2}, \quad t_{\mathrm{fm}} = \frac{1}{2}, \quad t_{\mathrm{mf}} = 1 \quad \text{and} \quad t_{\mathrm{mm}} = 0,$$

and

$$v_{\mathrm{f}} = \frac{2}{3} \quad \text{and} \quad v_{\mathrm{m}} = \frac{1}{3}.$$

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