Sibling quality and the haplodiploid hypothesis

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The ‘haplodiploidy hypothesis’ argues that haplodiploid inheritance in bees, wasps, and ants generates relatedness asymmetries that promote the evolution of altruism by females, who are less related to their offspring than to their sisters (‘supersisters’ relatedness). However, a consensus holds that relatedness asymmetry can only drive the evolution of eusociality if workers can direct their help preferentially to sisters over brothers, either through sex-ratio biases or a pre-existing ability to discriminate sexes among the brood. We show via a kin selection model that a simple feature of insect biology can promote the origin of workers in haplodiploids without requiring either condition. In insects in which females must found and provision new nests, body quality may have a stronger influence on female fitness than on male fitness. If altruism boosts the quality of all larval siblings, sisters may, therefore, benefit more than brothers from receiving the same amount of help. Accordingly, the benefits of altruism would fall disproportionately on supersisters in haplodiploids. Haplodiploid females should be more prone to altruism than diplodiploid females or males of either ploidy when altruism elevates female fitness especially, and even when altruists are blind to sibling sex.

1. Introduction

In 1964, Hamilton proposed that haplodiploidy has been a major driving force behind the multiple origins of eusociality in the Hymenoptera (bees, wasps and ants) [1,2]. Males are haploid, inheriting genes only from the mother, while females are diploid, inheriting genes from both parents [3]. In monogamous haplodiploids, sisters share their entire haploid father’s genome, while maternal alleles have a 50 : 50 chance of being shared by sisters. Accordingly, a female is related to her sisters by $r = 0.75$ (i.e. 0.5 from the father and 0.5 × 0.5 from the mother). This ‘supersisters’ relatedness is 50% greater than a female’s relatedness to her own offspring ($r = 0.5$), suggesting that a female should prefer to raise sisters than attempt personal reproduction [1,2,4].

The haplodiploidy hypothesis has been repeatedly questioned [5–13], and other reasons for a possible link between haplodiploidy and female altruism have been suggested in its place (e.g. [14–16]). Theoretical objections have largely centred on the problem that the haplodiploidy hypothesis requires helper females to bias altruism towards sisters (sister-biased helping). If altruism is received equally by sisters and brothers, haplodiploids should be no more prone to eusociality than diplodiploid females or males of either ploidy (in which both sexes are diploid and produced sexually). This is because, under haplodiploidy, a female’s relatedness to brothers is only $r = 0.25$; indiscriminate sibling altruism will produce an average recipient relatedness of $r = 0.5$. Under both haplodiploidy and diplodiploidy, then, there would be no asymmetry in relatedness to offspring and siblings. Trivers and Hare [8] argued that sister-biased helping could arise if helpers tend to inhabit nests with a female-biased brood sex ratio, but noted that an increasingly female bias in the population diminishes the value of rearing sisters
and amplifies the value of rearing brothers. Accordingly, female sex-ratio biases in nests with helpers must be more extreme than elsewhere in the population (split sex ratios) for altruism to be promoted more by haplodiploidy than by diplodiploidy [8,17]. Because split sex ratios arise only under rare and often complex conditions [5], this requirement led to a consensus that the haplodiploidy hypothesis is an unlikely driver of eusociality. Recently, Rautiälä et al. [18] have argued that split sex ratios are unnecessary, and haplodiploidy can drive eusociality at all sex ratios—on the crucial assumption that the first-evolving workers discriminate among brood by directing their help preferentially towards females (‘the ability for helpers to treat sisters and brothers differently’ [18]). Although sex discrimination occurs in simple eusocial species (e.g. [19]) and is familiar in more advanced eusocial taxa [20,21], it remains unknown whether this ability evolved subsequent to the evolution of workers or characterized workers at the dawn of sociality.

Here, we highlight a scenario in which the classic haplodiploidy effect [1] can drive eusociality without split sex ratios and without females needing to treat developing sisters and brothers differently. Models of eusocial evolution have focused on the quantity of siblings raised by helpers [8,18,22], but recent empirical studies of facultatively and primitively social insects have found that effects on sibling quantity alone can be too small to drive voluntary altruism [23,24]. We suggest a need to incorporate additional effects that helpers may have on the quality of siblings.

Across vertebrates and insects, the reproductive successes of males and females can depend differently on body condition [25,26], which can be influenced by the receipt of resources from helpers before reproductive maturity [27]. There has been no systematic and direct comparison of the extent to which male versus female fitness depends on body condition in nest-founding insects, and so the strength and sex asymmetry of condition-dependence remains largely unknown. However, greater condition-dependent variability in female fitness may plausibly arise when female nest-founding (including larval provisioning and any necessary female-only overwinter survival) is energetically challenging [27–30], and especially in contexts involving relatively limited scope for male–male competition or mate choice [29]. In nest-founding insects without biparental care, a female must face the extreme challenge of founding a new nest and raising larvae to adulthood [31] in addition to mating; a male must only mate. Empirical results suggest that higher condition females (larger, with more fat reserves acquired during development) have a stronger chance than those in the poorer condition of being successful nest-builders [32,33], and reveal heavy reliance on energy reserves by foundress females [31,34].

Using a kin selection model, we explore whether female-biased condition-dependence alters thresholds for eusociality under different ploidies. We focus on a situation requiring biased condition-dependence alters thresholds for eusociality reliance on energy reserves by foundress females [31,34]. Being successful nest-builders [32,33], and reveal heavy

2. Model

We assume a monogamous, outbreeding population. We build on the framework of Davies et al. [22], who analyse the evolution of eusociality under different ploidies, to incorporate sex-asymmetrical condition-dependence. Females develop to be sterile helpers with probability \( x \) (with a population average \( \bar{x} \)), males develop to be sterile helpers with probability \( y \) (with a population average \( \bar{y} \)) and the brood sex ratio (the proportion male) is \( z \) (with a population average \( \bar{z} \)). Help \( h \) is the sum of help from male and female helpers. We allow altruists to influence two different (not mutually exclusive) components of the fitness of brood in the nest. First, helpers may raise the probability \( B = B(h) \) that brood survive to reproductive maturity (i.e. helpers may raise the quantity of adult reproductive siblings). We follow Davies et al. [22] in denoting the fitness effect of female help on relative brood survival to reproductive maturity as \( b_f = c_f (d B/d h|_{h=0}) / B(h) \), where \( c_f \) denotes helping efficiency of females and \( B(h) \) is the population-average survival to reproductive maturity. Likewise, \( h_M = c_M (d B/d h|_{h=0}) / B(h) \) denotes the fitness effect of male help on relative brood survival to reproductive maturity, where \( c_M \) denotes helping efficiency of males. Second, helpers may raise the probability \( Q = Q(h) \) that, given a female brood member has reached reproductive maturity, she will successfully found a new nest (helpers, therefore, may influence the quality of adult reproductive sisters). We let the fitness effect of female help on female relative nest-founding success be \( q_f = c_f (d Q/d h|_{h=0}) / Q(h) \), where \( Q(h) \) is the population-average nest-founding success. Likewise, \( q_M = c_M (d Q/d h|_{h=0}) / Q(h) \) denotes the fitness effect of male help on female relative nest-founding success. Nest-founding success is a female-specific trait, affected by the amount of help a nest-founding female receives before her own reproductive maturity.

In the electronic supplementary material, we show that selection favours a small increase in female helping when:

\[
(b_f + q_f)(1 - z)(1 - \bar{z}) c_f p_{\text{self,f}} + b_f(1 - \bar{y}) c_M p_{\text{bro,f}} > v_y p_{\text{self,f}}
\]

where consanguinities (\( p \)) denote the probabilities with which a random allele in the social partner is identical by descent to a random allele at the same locus in the actor [35]. Assuming monogamy, haplodiploid consanguinities from a focal female are \( p_{\text{self,f}} = 1/2 \) to self, \( p_{\text{bro,f}} = 3/8 \) to a sister and \( p_{\text{bro,f}} = 1/4 \) to a brother [5]. Diplodiploid consanguinities are \( p_{\text{self,f}} = 1/2 \) to self and \( p_{\text{bro,f}} = p_{\text{bro,f}} = 1/4 \) to siblings. Reproductive females and reproductive males have individual reproductive values \( v_y \) and \( v_M \), respectively (a measure of the probability with which males and females contribute to the distant future gene pool; see electronic supplementary material). The indirect fitness benefits of developing as a sterile altruist are on the left-hand side of inequality 2.1. The direct fitness cost (the loss of improvements to sister quality required to drive a small
rise in helping by females are for haplodiploids and diplodiploids, respectively:

$$ q_{\text{Hap}} = \frac{2}{3} \left( \frac{2}{(1-x)(1-z)} - 2b_p \right) $$

(2.2)

and

$$ q_{\text{Dip}} = \frac{2}{(1-x)(1-z)} - 2b_p. $$

(2.3)

In a non-social population ($x = y = 0$) with an equal sex ratio ($\bar{z} = 1/2$), $q_{\text{Hap}}$ and $q_{\text{Dip}}$ can be interpreted as the number of additional nephews and nieces (resulting from the sibling quality-boosting effect of becoming a sterile altruist) required to promote the initial invasion of altruists.

Next, we evaluate the costs and benefits of altruism ($y$) by males. Solving for the fitness effects (see electronic supplementary material), selection favours a small increase in male altruism when, for both diplodiploid and haplodiploid males:

$$ (b_M + q_M)(1-x)(1-z)r_M p_{\text{self}} + b_M(1-y)z_M p_{\text{self}} > r_M p_{\text{self}}. $$

(2.4)
haplodiploid consanguinities are ficing her reproduction, a haplodiploid female but 0.25 for a diplodiploid female. Life-for-life relatedness to oneself is 1. To break even when sacri-

a diplodiploid female through the improved quality of her reproductive sisters, but then result in 1

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<

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Assuming monogamy, diplodiploid consanguinities from a focal male are \( p_{\text{self}} = 1/2 \) and \( p_{\text{bro}} = p_{\text{sis}} = 1/4 \), while haplodiploid consanguinities are \( p_{\text{self}} = 1, p_{\text{bro}} = 1/4 \) and \( p_{\text{sis}} = 1/2 \). Holding \( b_{\text{M}} \) fixed, the threshold benefit level in terms of sister quality required to drive a small rise in helping by males of either ploidy is:

\[
q_{\text{HapM}} = q_{\text{DipM}} = \frac{2}{z(1 - y)} - 2 b_{\text{M}}. \tag{2.5}
\]

Thus, for instance, consider a non-social population

\((x = y = 0)\) with unbiased sex ratios \((z = 1/2)\), in the case where helpers will have no effect on the quantity of siblings produced \((b_{\text{F}} = b_{\text{M}} = 0)\). The thresholds for the invasion of altruism (due to the effects of sex-indiscriminate helping increasing female quality) are:

\[
\begin{align*}
q_{\text{HapF}} &= 2.6 & \text{for haplodiploid females} \\
q_{\text{DipF}} &= 4 & \text{for diplodiploid females} \\
q_{\text{HapM}} &= q_{\text{DipM}} = 4 & \text{for males of either ploidy.}
\end{align*}
\]

These thresholds can be understood in terms of life-for-

life relatednesses [5]: when \( z = 1/2 \), life-for-life relatedness to a sister’s offspring (nephews and nieces) is 0.375 for a haplodiploid female but 0.25 for a diplodiploid female. Life-for-life relatedness to oneself is 1. To break even when sacrific-

fying her reproduction, a haplodiploid female’s altruism must then result in \( 1/0.375 = 2.6 \) additional nieces and nephews through the improved quality of her reproductive sisters, but a diplodiploid female’s help must result in \( 1/0.25 = 4 \) additional nieces and nephews. A smaller boost to the quality of sisters \( q_{\text{F}} \) is required to justify altruism for haplodiploid females than for other actor types, unless altruists are able to provide a sufficient boost to sibling quantity \( (b_{\text{F}}) \) to make boosts to sibling quality unnecessary \( q_{\text{F}} = 0 \), which occurs at \( b_{\text{F}} = 2 \) for the initial invasion of altruists; figure 1a). The benefit thresholds for haplodiploid females (dashed lines in figure 1b; \( q_{\text{HapF}} \)) are lower than those required for diplodiploid females (solid lines in figure 1b; \( q_{\text{DipF}} \)) throughout the invasion of altruists \((x\) ranging from 0 to 1).

As helpers evolve, mothers are expected to bias offspring sex ratios in favour of the more helpful sex [15,22]. We therefore plot the coevolution of sex ratios and female altruism in figure 1c–f. When help boosts sister quality especially, haplodiploids can evolve female altruism when diplodiploids cannot (figure 1c,d). When the boost to sister quality is enough to drive altruism in diplodiploids, haplo-
diploids evolve a higher level of female altruism than diplodiploids (figure 1e,f).

3. Discussion

We find that haplodiploid females enjoy lower thresholds for altruism, in comparison to either diplodiploid females or males of either ploidy, on the condition that staying to pro-

vision the brood increases the quality of sisters more than that of brothers (figure 2). This effect arises even in the absence of split sex ratios [8] or helpers preferentially biasing help towards one sex in the brood [18]. A major bottleneck in the success or failure of a primitive social insect colony may be the hopeful queen’s nest-founding quality, affected by the level of help she received in her own development. This is similar to the effects of sunk-cost hysteresis in economics [36]: initiating a new nest (a firm entering the market) demands a huge expenditure of effort, but maintaining an established nest (a firm trading in the market) is relatively easier. At the dawn of sociality, a large effect of workers’ help may in principle not be visible until the following
generation, as higher levels of worker help may result in
more successful future nest-founding by sibling queens.

A role for sex-asymmetrical condition-dependence has pre-
viously been proposed for the haplodiploidy hypothesis. In this
verbal ‘synergism model’, Frank and Crespi [27] suggest that
Trivers–Willard effects [26] drive split sex ratios. First, helpers
increase sibling condition. Then, mothers with helpers evolve
to adjust sex ratios towards daughters, who benefit most from
the high condition. Resulting split sex ratios increase selection
for helping (by increasing recipient relatedness). The synergism
model assumes that helpers have already evolved (and so can
explain their maintenance and spread but not origin), and
the necessity of split sex ratios has been challenged [18].
Our model shows that condition-dependence can also play a
more fundamental role, not only amplifying the spread of altru-
ism by haplodiploid females [27] but driving its origins in
populations without sex-ratio biases.

Empirical work is needed to assess the general plausibility
of the premise that nest-founding females experience higher
condition-dependent variability in reproductive success than
males. In scenarios where males face intense male–male com-
petition [37] or where post-insemination sperm survival is highly
altered in females, we may observe higher condition-dependence
in offspring [21–23], which predicts split sex ratios [8].

Second, does variable maternal condition at reproduction lead
to Trivers–Willard effects [25,26], altering indirect fitness pay-
offs for female helpers? Third, do mothers face quantity–quality
trade-offs in the brood, favouring smaller broods before helpers
would receive sufficient per capita resources fall on
daughters to sustain competitiveness? Fourth, does the limited
help received by first-emerging daughters lead to a relatively
’subfertile’ class [42] for whom altruism is the best available
option? Fifth, when benefits of altruism arise through boosting
sibling quality, to what extent does any redundant resource con-
sumption by males (having less need than females) act as a
constraint on the evolution of altruism in general, regardless
of ploidy? Lastly, does load lightening by first helper brood
compensate for poor condition in foundress females, reducing
the importance of female condition as sociality evolves?

In summary, we highlight a simple effect capable of
promoting higher levels of altruism in haplodiploids than in
diploidos without requiring split sex ratios [8], sex differences in
helping efficiency [22], or strategic targeting of help to one sex in the brood [18]. Our aim is not to
challenge the plausibility of sister-biased helping at the
origin of eusociality, but rather to highlight that—contrary
to a prevailing consensus—such a bias is not vital for the
haplodiploidy hypothesis.

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