

**This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.**

Author(s): Rautiala, Petri; Helanterä, Heikki; Puurtinen, Mikael

Title: Unmatedness promotes the evolution of helping more in diplodiploids than in haplodiploids

Year: 2014

Version:

Please cite the original version:

Rautiala, P., Helanterä, H., & Puurtinen, M. (2014). Unmatedness promotes the evolution of helping more in diplodiploids than in haplodiploids. *American naturalist*, 184(3), 318-325. <https://doi.org/10.1086/677309>

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

Unmatedness Promotes the Evolution of Helping More in Diplodiploids than in Haplodiploids

Petri Rautiala^{1,2} (petri.rautiala@jyu.fi)

Heikki Helanterä^{2,3} (heikki.helantera@helsinki.fi)

Mikael Puurtinen^{1,2} (mikael.puurtinen@jyu.fi)

1 University of Jyväskylä, Department of Biological and Environmental Science, PO Box 35, FI-40014

University of Jyväskylä, Finland

2 Centre of Excellence in Biological Interactions

3 University of Helsinki, Department of Biosciences, PO Box 65, FI-00014 University of Helsinki,

Finland

Article

Keywords: Eusociality, haplodiploidy hypothesis, split sex ratios, virginity

Abstract

The predominance of haplodiploidy (where males develop from unfertilized haploid eggs and females from fertilized diploid eggs) among eusocial species has inspired a body of research that focuses on the possible role of relatedness asymmetries in the evolution of helping and eusociality. Previous theory has shown that in order for relatedness asymmetries to favor the evolution of helping, there needs to be variation in sex ratios among nests in the population (i.e., split sex ratios). In haplodiploid species, unmated females can produce a brood of all males, and this is considered the most likely mechanism for split sex ratios at the origin of helping. In contrast, in diplodiploids unmatedness means total reproductive failure. We compare the effect of unmatedness on selection for male and female helping in haplodiploids and diplodiploids. We show that in haplodiploids, unmatedness promotes helping in females but not in males within the empirical range. In diplodiploids, unmatedness promotes helping by both sexes, and the effect is stronger than in haplodiploids, all else being equal. Our study highlights the need to consider interactions between ecological and genetic factors in the evolution of helping and eusociality.

Introduction

The evolution of non-reproductive castes in eusocial organisms is among the most intriguing questions in evolutionary biology (Bourke 2011). An influential hypothesis suggested that haplodiploid sex-determination, where males develop from unfertilized haploid eggs and females from fertilized diploid eggs, could have facilitated the evolution of eusociality due to the relatedness asymmetries arising from this kind of sex determination. The original argument of this 'haplodiploidy hypothesis' (Hamilton 1964; Hamilton 1972) was that because a female is more related to her full sisters ($r = 3/4$, r is life-for-life relatedness in a population with 1:1 sex ratio (Hamilton 1972)) than to her own sons and daughters ($r = 1/2$), a female could gain higher inclusive fitness by helping her mother to produce more sisters than by producing her own offspring. The haplodiploidy hypothesis was refined by Trivers & Hare (1976), who argued that for the promoting effect to arise from haplodiploidy, the helping behavior needs to be directed to sisters more than their mother would prefer. Their argument was that if helping was directed evenly to sisters and brothers, the benefit of high sister-sister relatedness is cancelled out by low sister-brother relatedness ($r = 1/4$), resulting in the same average relatedness to siblings as to own offspring.

Further work however showed that relatedness asymmetries arising from haplodiploidy can indeed promote the evolution of helping, provided that there is variation in sex ratio among nests (i.e., there are 'split sex ratios') (Trivers and Hare 1976; Craig 1979; Craig 1980; Grafen 1986). When the potential (female) helper is in a nest with more female biased sex ratio than the population average, she values an average sibling more than an average offspring. However, the average sibling is valued more than the average offspring only when the individual reproductive value of males does not counter the benefits of high sister-sister relatedness, i.e., when the proportion of males in the population is more than 25 percent. Although several mechanisms for split sex ratios have been suggested in the literature, it seems that reproduction by unmated females is the only likely mechanism that could have been important at the origin of helping (reviewed in Gardner et al. 2012). In haplodiploid species, unmated females have

the option of laying unfertilized eggs, which develop to males. If a fraction of females in the population remain unmated and produce only males, sex ratio in nests of mated females is necessarily more female biased than the population average sex ratio (Godfray and Grafen 1988).

Hamilton (1972) suggested that relatedness asymmetries arising from haplodiploidy could also explain why helpers in eusocial Hymenoptera are always female. Grafen (1986) later showed that with split sex ratios, potential female helpers do not need to discriminate among brothers and sisters as receivers of the help, which was previously considered necessary for haplodiploidy to promote the evolution of female helping (Trivers and Hare 1976). However, more recent analyses have shown that male workers should evolve as readily as female workers (Craig 1982; Pamilo 1991). Furthermore, eusocial haplodiploid thrips with both male and female helpers have been found (Crespi 1992; Kranz et al. 1999). These findings and new analyses suggest that ecological circumstances and pre-adaptations like maternal care are more important in determining the sex of helpers than the genetics of sex determination (Queller and Strassmann 1998; Ross et al. 2013).

In contrast to haplodiploids, in non-clonal diplodiploids the lack of a mate leads to a total reproductive failure for both males and females. This effect of unmatedness must be taken into account when comparing the conditions for the evolution of helping in haplodiploids and diplodiploids. A recent study by Gardner et al. (2012) investigated how unmatedness influences the inclusive fitness valuations a female places on siblings and offspring, and how this affects the evolution of helping. Here we compare the effects of unmatedness on the evolution of helping by females and males in haplodiploids and diplodiploids, accounting for both the inclusive fitness valuations of relatives of different classes, and the number of offspring produced by mated and unmated females.

Model and results

Table 1: Definitions of the symbols used in this article

Symbol	Description
u	fraction of females that remain unmated
b_{lr}	the benefit threshold for helping to evolve
z_m	mated female sex ratio (proportion of males)
z_p	population sex ratio (proportion of males)
c_m	class reproductive value of males
c_{mf}	class reproductive value of mated females
c_{uf}	class reproductive value of unmated females
y_{sis}	consanguinity between the focal individual and its sister
y_{bro}	consanguinity between the focal individual and its brother
y_{son}	consanguinity between the focal individual and its son
y_{dau}	consanguinity between the focal individual and its daughter
n	number of offspring produced by a reproductive female
b	number of siblings the focal individual gains by helping

In our model we are comparing panmictic, monogamous (Hughes et al. 2008; Boomsma 2009) haplodiploid and diplodiploid populations where helping has not yet evolved. Generations are non-overlapping, so that at the change of season the parent generation dies and all the offspring disperse to establish their own nests. We are looking at the behavior of an individual born early in the season who can either disperse and establish an own nest in the following season, or sacrifice own reproduction and become a helper at the natal nest, contributing to production of more siblings to the next cohort. The extra siblings produced by helping are assumed to follow the sex-ratio determined by the mother.

We assume that, due to some external factor, a constant fraction u of all females remain unmated (all symbols used in the model are given in Table 1). A female can remain unmated if she is not able to find a mate e.g. due to low population density (Godfray 1990; Rhainds 2010; Morse 2013). If a female does mate but the mating does not result in fertilization (possible reasons reviewed by Godfray 1990), she may become effectively unmated as remating can be obstructed (reviewed by Godfray 1990; Ode et al. 1997).

In order to analyze selection for helping behavior, we need to define the inclusive fitness valuation an individual places on its siblings and on its own offspring. The inclusive fitness valuation a potential helper places on different types of relatives depends on the consanguinity of the potential helper to those relatives and their individual reproductive values. Consanguinity is the probability that homologous genes drawn randomly from the two actors are identical by descent (Bulmer 1994). In an outbred population the consanguinities between a haplodiploid female and her brother, sister, son and daughter are $y_{bro} = 1/4$, $y_{sis} = 3/8$, $y_{son} = 1/2$ and $y_{dau} = 1/4$ respectively. Between a haplodiploid male and his brother, sister and daughter, consanguinities are $y_{bro} = 1/2$, $y_{sis} = 1/4$ and $y_{dau} = 1/2$ respectively. Between a diploid female (male) and her (his) son, daughter, brother and sister, consanguinities are all $1/4$.

The individual reproductive value represents the relative expected reproductive success of an individual. In our analysis, the population consists of three relevant classes, males (m), unmated females (uf) and mated females (mf). Class reproductive value is the probability that a random allele from an infinitely distant future generation originates from that class in the current generation. In haplodiploids, the probability for an allele to originate from a male (c_m) equals $1/3$ and from either unmated (c_{uf}) or mated female (c_{mf}) totals $(c_{uf} + c_{mf}) = 2/3$. In diploids, the allele originates from a mated female and from a male with the same probability of $1/2$, and from an unmated female with a probability of 0 . (Bulmer 1994; Taylor 1996) Individual reproductive values are then obtained by dividing the class reproductive value by the proportion of the respective class in the population (Taylor 1996; Taylor and Frank 1996).

We assume that both mated and unmated haplodiploid females produce equal numbers (n) of offspring, but unmated haplodiploid females produce only males (see Ode et al. 1997 and Metzger et al. 2008). For ease of notation and comparison, we assume that mated diploid females also produce the same (n) number of offspring. The assumption of identical numbers of offspring produced by reproductive females in both genetic systems is done only for convenience of comparison, and does not affect the

results or interpretation of the analysis. We further assume that mated females adjust their offspring sex ratio to maximize fitness. In haplodiploids, the mated female sex ratio strategy z_m (proportion of males a mated female produces) is then linked with the population sex ratio z_p (proportion of males in population) by the equation $z_p = u + (1 - u)z_m$. With a constant fraction u of females remaining unmated and producing all-male broods, mated females are selected to produce brood with a female-biased sex ratio. In Appendix A we give the derivation of the convergence stable mated female sex ratio

$$z_m = \begin{cases} \frac{1 - 2u}{2 - 2u}, & u < \frac{1}{2} \\ 0, & u \geq \frac{1}{2} \end{cases}, \quad (1)$$

which leads to a population sex ratio (see Figure 1)

$$z_p = \begin{cases} \frac{1}{2}, & u < \frac{1}{2} \\ u, & u \geq \frac{1}{2} \end{cases}. \quad (2)$$

These ratios are the same as derived by Gardner et al. (2012). For diploids, the convergence stable sex ratios (z_m and z_p) are $1/2$, regardless of u (Fisher 1930).

We study selection for helping by solving how many additional siblings a helper must rear instead of dispersing and producing own offspring in order for helping to be favored by natural selection. We call this quantity 'the benefit threshold' (b_{lr}), and it can be understood as the threshold efficiency of helping, below which helping is selected against and above which helping is selected for. The number of siblings actually gained by helping is denoted with b .

Next we derive the inclusive fitness valuations a newly born haplodiploid female and a diploid individual (male or female) place on siblings and on own offspring. Derivation of valuations a haplodiploid male places on siblings and own offspring is given in Appendix B.

The inclusive fitness valuation functions are comprised of three terms, one for each class. Each of these terms is formed by the probability that the relative (sibling or offspring) in question belongs to the respective class, multiplied by consanguinity and then multiplied by individual reproductive value. For a haplodiploid female and a diploid male or female, the inclusive fitness valuation an individual places on a sibling is

$$\begin{aligned}
 w_{sib} &:= z_m y_{bro} \frac{c_m}{z_p} + u(1 - z_m) y_{sis} \frac{c_{uf}}{u(1 - z_p)} + (1 - u)(1 - z_m) y_{sis} \frac{c_{mf}}{(1 - u)(1 - z_p)} \\
 &= \frac{z_m y_{bro} c_m}{z_p} + \frac{(1 - z_m) y_{sis} (c_{uf} + c_{mf})}{1 - z_p}, \quad (3)
 \end{aligned}$$

where the first term is the inclusive fitness valuation for brothers, the second for sisters that are expected to remain unmated as adults, and the third for sisters that are expected to mate.

The inclusive fitness valuation a newly born individual places on an own offspring is

$$\begin{aligned}
 w_{off} &:= \frac{z_p y_{son} c_m}{z_p} + \frac{u(1 - z_p) y_{dau} c_{uf}}{u(1 - z_p)} + \frac{(1 - u)(1 - z_p) y_{dau} c_{mf}}{(1 - u)(1 - z_p)} \\
 &= y_{son} c_m + y_{dau} (c_{uf} + c_{mf}), \quad (4)
 \end{aligned}$$

where the first term is the inclusive fitness valuation for sons, the second for daughters that are expected to remain unmated as adults, and the third for daughters that are expected to mate.

To take into account the effect of unmatedness on the benefit threshold b_{tr} , we need to weigh the inclusive fitness valuations of the average sibling and the average offspring of a potential helper by their expected numbers. Because both unmated and mated haplodiploid females produce the same amount of offspring, the expected number of offspring for a haplodiploid female is simply n . Fraction u of diploid females do not mate, and thus produce zero offspring. Hence, the number of offspring a newly born diploid female expects to have is $(1 - u)n$. Assuming 1:1 sex ratio, the expected

number of matings for a diploid male is $1 - u$, and the expected number of offspring is $(1 - u)n$, the same as for a diploid female.

Now we can write the inequalities that give conditions for the helping allele to spread in the population and define the benefit thresholds. For a haplodiploid female this inequality is that $bw_{sib} > nw_{off}$ which is equivalent with $b > nw_{off}/w_{sib} =: b_{tr}$. After substituting in the sex ratios, consanguinities and reproductive values we obtain the benefit threshold for helping

$$b_{tr} = \begin{cases} \frac{2 - 2u}{2 - u} n, & u < \frac{1}{2} \\ \frac{4}{3(1 - u)} n, & u \geq \frac{1}{2} \end{cases} \quad (5)$$

The benefit threshold for a haplodiploid male (see Appendix B for derivation) is

$$b_{tr} = \begin{cases} n, & u < \frac{1}{2} \\ 2(1 - u)n, & u \geq \frac{1}{2} \end{cases} \quad (6)$$

For a diploid male or female, the inclusive fitness inequality condition is that $bw_{sib} > (1 - u)nw_{off}$ which is equivalent with $b > (1 - u)nw_{off}/w_{sib} =: b_{tr}$, from which after substituting in the sex ratios, consanguinities and reproductive values we obtain that

$$b_{tr} = (1 - u)n. \quad (7)$$

To see the full effect of unmatedness on the evolution of helping behavior in haplodiploids and diploids, we compare the benefit thresholds b_{tr} (Figure 2). In both genetic systems unmatedness promotes helping behavior by females. The evolution of female helping becomes easier as the frequency of unmated females in the population increases in both haplodiploids and diploids. However, for any frequency of unmated females in the population, the benefit threshold b_{tr} is lower for diploids than for haplodiploids. Unmatedness thus makes the evolution of female helping easier in diploids than in haplodiploids.

Looking at the effect of unmatedness on selection for male helping behavior, we see that unmatedness does not promote male helping in haplodiploid species, as long as at least half of the females mate ($u < 1/2$) (Appendix B, see Figure 2). The reason is that the decrease in the expected number of matings with increasing unmatedness is exactly counterbalanced by the more female-biased sex-ratio of mated females. A more female-biased sex-ratio means that per mating, a male sires more offspring (remembering that in haplodiploids males only have daughters). In diplodiploids on the other hand, unmatedness affects males and females similarly (both unmated males and females have zero reproductive output), and selection on helping behavior is the same for both sexes. When $u = 0$, we also see that without any outside factors, helping should evolve as readily in males as in females in both haplodiploids and in diplodiploids.

Discussion

We have shown that when the effects of unmatedness on relatedness asymmetries and reproductive output are fully taken into account for both haplodiploids and diplodiploids, diplodiploidy may be more favorable to evolution of helping than haplodiploidy. While the existence of unmated females favors the evolution of helping in both systems, the effect is stronger in diplodiploids. Interestingly, the reasons why the benefit threshold decreases with the frequency of unmated females are different in the two genetic systems. In diplodiploids, the benefit threshold decreases when frequency of unmated females increases simply because the decision to disperse carries risk u of complete reproductive failure for females (and for males). In haplodiploids, unmated females produce brood consisting of males only, which results in split sex ratios in the population. The split sex ratios reduce the benefit threshold for females because they are in nests with a more female-biased sex ratio than the population average sex ratio, and can thus capitalize on the high sister-sister relatedness.

While population density and structure are important parts of the suite of ecological constraints that underlie the evolution of helping (Emlen 1982; Hatchwell 2009), their impact on resource levels and chances of obtaining a territory or a nest site have been studied more than their effects on possible mating failures. Studies of unmatedness in haplodiploids have mainly concentrated on demonstrating whether mated females shift their offspring sex ratio as a response to the presence of unmated females, as suggested by Godfray (1990). In species where unmatedness is common, mated females do indeed produce female biased broods. The female-biased sex ratio of mated females seems to be an evolved response to the mean frequency of unmated females in the population over evolutionary time, rather than a plastic response to the current mating situation in the population (Ode et al. 1997; Kranz et al. 2000; Metzger et al. 2008).

We have shown that, all else being equal, unmatedness promotes helping more in diplodiploids than in haplodiploids. However, if unmatedness is more common in haplodiploids, then its importance as a driver of helping in haplodiploids would be elevated. As has been pointed out by Godfray (1990), at the incipient stages of social evolution, remaining unmated is not strongly selected against in haplodiploid females (apart from sex ratio selection against all male broods when population is not at sex ratio equilibrium). Thus, any costs related to mate search or mating itself, such as predation, male harming, and sexually transmitted pathogens, could even select for voluntary virginity in females (Godfray 1990; Guertin et al. 1996). The ability of males (who need to mate in order to gain offspring) to find mates will then be an important factor determining the proportion of virgins. In contrast, remaining unmated is strongly selected against in both sexes in diplodiploids, and is thus expected to stay extremely rare. Estimates of frequencies of virgins in haplodiploids range from 0% to 29% (Godfray and Hardy 1992), but many of the estimates come from species where local mating competition and inbreeding prevail. Although unmated females in species with characteristics similar to the ancestors of social

Hymenopterans, and our model life-history assumptions, seem to be fairly rare (Gardner et al. 2012), at least one system exists that fits our model assumptions, and exhibits high virgin frequencies. In *Kladothrips rugosus*, an outbreeding haplodiploid gall-inducing thrip, 24% of females remain unmated and produce only sons, and the mated females compensate by producing female-biased sex ratio (Kranz et al. 2000). Empirical data on unmatedness is however relatively scarce, and the evolution of voluntary virginity and its connection to the evolutionary origins of helping under various life history and breeding system assumptions clearly merit further study.

A recent analysis by Ross et al. (2013) suggested that instead of ploidy levels, the ecological benefits favoring eusociality (nest defence vs. brood care (Queller and Strassmann 1998)) and possible pre-adaptations (maternal vs. biparental care as an ancestral state (Wade 2001; Linksvayer and Wade 2005; Gardner 2012)) could explain the observed patterns in helper sex-ratios across taxa. Our analysis however suggests that haplodiploidy, together with unmatedness, could have contributed to the evolution of exclusive female help in outbreeding species like eusocial Hymenoptera by lowering the benefit threshold female helping. In contrast to Hymenoptera, in eusocial haplodiploid thrips both male and female offspring participate in nest defense (Crespi 1992; Kranz et al. 1999). The evolution of both male and female helpers in eusocial thrips may be linked to lack of pre-adaptations in either sex to soldiering, as suggested by Ross et al. (2013), but also to the high degree of ancestral inbreeding in these species (McLeish et al. 2006), which reduces the importance of relatedness asymmetries (Chapman et al. 2000). For diploid species, our model predicts equal benefit thresholds for males and females. In nature, diploid species show variable patterns of helper sex, and the patterns may be linked to preadaptations to certain helper tasks (Ross et al. 2013).

In general, our work highlights the need to consider interactions between ecological and genetic factors in the evolution of helping and eusociality. We show that features of mating systems, that on the one

hand define the degree of relatedness within families, may also shape the direct costs and benefits relevant to the evolution of helping. Specifically, we suggest that studying the coevolutionary relationship between voluntary virginity and helping behavior may shed light on early stages of eusociality in outbreeding haplodiploid species.

Acknowledgments

We would like to thank Andy Gardner for comments on an early version of the manuscript, and associate editor Peter D. Taylor, João Alpedrinha and an anonymous reviewer for comments and suggestions that greatly improved the clarity of this manuscript.

Appendix A: Derivation of convergence stable sex ratio.

Here we calculate the convergence stable mated female sex ratio strategy for an infinite haplodiploid population with fixed fraction (u) of unmated females. The model has a class structured population with three classes: males (m), unmated females (uf) and mated females (mf), where only the last can control their offspring sex ratios. The mated females are the balancing class, optimizing their sex ratio z_m to yield maximal fitness (Taylor 1996; Taylor and Frank 1996). The mated female sex ratio determines the population sex ratio z_p . From the perspective of a mutant mated female that follows a sex ratio strategy z in a population of females following z_m , we define the inclusive fitness valuation she places on an average offspring as

$$\begin{aligned} w(z, z_m) &:= \frac{zy_{son}c_m}{u + (1-u)z_m} + \frac{u(1-z)y_{dau}c_{uf}}{u(1-u)(1-z_m)} + \frac{(1-u)(1-z)y_{dau}c_{mf}}{(1-u)(1-u)(1-z_m)} \\ &= \frac{zy_{son}c_m}{u + (1-u)z_m} + \frac{(1-z)y_{dau}(c_{uf} + c_{mf})}{(1-u)(1-z_m)}. \quad (A8) \end{aligned}$$

We can find a candidate for the convergence stable mated female sex ratio strategy by solving

$$\left. \frac{\partial w(z, z_m)}{\partial z} \right|_{z=z_m} = \frac{1}{6[u + (1-u)z_m]} - \frac{1}{6(1-u)(1-z_m)} = 0, \quad (A9)$$

which gives

$$z_m = \begin{cases} \frac{1-2u}{2-2u}, & u < \frac{1}{2} \\ 0, & u \geq \frac{1}{2} \end{cases} \quad (A10)$$

To see if this candidate is in fact convergence stable, we need to check if natural selection favors higher than average sex ratio strategies when the population average is lower than the candidate and vice versa. First we look at the case of $u < 1/2$. When the population follows on average a strategy of $z_m < (1 - 2u)/(2 - 2u)$, the partial derivative of w is positive for any z , meaning that natural selection favors any strategy that is greater than z_m . Also when the population follows on average a strategy of $z_m > (1 - 2u)/(2 - 2u)$, the partial derivative of w is negative for any z , meaning that natural selection favors any strategy that is less than z_m . Next we look at the case of $u \geq 1/2$. When the population follows on average a strategy of $z_m > 0$, the partial derivative of w is negative for any z , meaning that natural selection favors any strategy that is less than z_m . This analysis shows that our candidate is the convergence stable mated female sex ratio strategy (Geritz et al. 1997). This is the same sex ratio as derived by Gardner et al. (2012) and reported by Godfray (1990).

Appendix B: The benefit threshold for haplodiploid males.

Here we calculate the threshold benefit for the evolution helping for a haplodiploid male in a population where mated females follow their evolutionarily stable sex ratio strategy. Unlike in diplodiploids where the inclusive fitness model for females corresponds with the model for males, in haplodiploids the model for males differs from the model for females for two reasons. First, the male can be either a son of an unmated or mated female, meaning that the inclusive fitness valuation of siblings needs to take the probabilities of either into account. Second, since males can only have daughters, the number of

offspring a dispersing male expects to have depends on the expected number of matings, and on how many daughters a mated female produces.

With a probability of $u/[u + (1 - u)z_m]$ the focal male is a son of an unmated female and has only brothers as siblings, and with the probability of $(1 - u)z_m/[u + (1 - u)z_m]$ the focal male is a son of a mated female and has both sisters and brothers as siblings. Thus the inclusive fitness valuation the focal male places on his average sibling can be written as

$$\begin{aligned}
 w_{sib} &:= \frac{(1 - u)z_m}{u + (1 - u)z_m} \left[\frac{z_m y_{bro} c_m}{z_p} + \frac{u(1 - z_m) y_{sis} c_{uf}}{u(1 - z_p)} + \frac{(1 - u)(1 - z_m) y_{sis} c_{mf}}{(1 - u)(1 - z_p)} \right] \\
 &\quad + \frac{u}{u + (1 - u)z_m} \frac{y_{bro} c_m}{z_p} \\
 &= \frac{[(1 - u)z_m^2 + u] y_{bro} c_m}{z_p^2} + \frac{z_m y_{sis} (c_{uf} + c_{mf})}{z_p}. \quad (B11)
 \end{aligned}$$

Since males can only have daughters, the inclusive fitness valuation a male places on an offspring of his is

$$w_{off} := \frac{u y_{dau} c_{uf}}{u(1 - z_p)} + \frac{(1 - u) y_{dau} c_{mf}}{(1 - u)(1 - z_p)} = \frac{y_{dau} (c_{uf} + c_{mf})}{1 - z_p}. \quad (B12)$$

The expected number of matings for a male is $(1 - u)(1 - z_p)/z_p$, so the number of offspring (daughters) a male expects to get when dispersing is $n(1 - z_m)(1 - u)(1 - z_p)/z_p$. With that we can write the inequality that gives the condition for the helping gene expressed in a male to spread: $b w_{sib} > n(1 - z_m)(1 - u)(1 - z_p) w_{off}/z_p$ which is equivalent with $b > n(1 - z_m)(1 - u)(1 - z_p) w_{off}/(z_p w_{sib}) =: b_{tr}$. Substituting in the consanguinities of the male to his daughter ($y_{dau} = 1/2$), to his sister ($y_{sis} = 1/4$) and to his brother ($y_{bro} = 1/2$), the reproductive values given in the model section and sex ratios calculated in Appendix A and model section, we get that for a haplodiploid male the benefit threshold $b_{tr} = n$ when $u < 1/2$ and $b_{tr} = 2(1 - u)n$ when $u \geq 1/2$.

References

Boomsma, J. J. 2009. Lifetime monogamy and the evolution of eusociality. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* 364:3191–3207.

Bourke, A. 2011. *Principles of social evolution*. Oxford University Press, Oxford.

Bulmer, M. 1994. *Theoretical evolutionary ecology*. Sinauer Associates, Sunderland, MA.

Chapman, T. W., B. J. Crespi, B. D. Kranz, and M. P. Schwarz. 2000. High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips. *Proceedings of the National Academy of Sciences of the United States of America* 97:1648–1650.

Craig, R. 1979. Parental manipulation, kin selection, and the evolution of altruism. *Evolution* 33:319.

Craig, R. 1980. Sex investment ratios in social hymenoptera. *The American Naturalist* 116:311–323.

Craig, R. 1982. Evolution of male workers in the hymenoptera. *Journal of Theoretical Biology* 94:95–105.

Crespi, B. J. 1992. Eusociality in Australian gall thrips. *Nature* 359:724–726.

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. *The American Naturalist* 119:29–39.

Fisher, R. A. 1930. *The genetical theory of natural selection*. The genetical theory of natural selection. The Clarendon Press, Oxford.

Gardner, A. 2012. Evolution of maternal care in diploid and haplodiploid populations. *Journal of Evolutionary Biology* 25:1479–1486.

Gardner, A., J. Alpedrinha, and S. A. West. 2012. Haplodiploidy and the evolution of eusociality: split sex ratios. *The American Naturalist* 179:240–256.

Geritz, S. A. H., G. Mesze, and J. A. J. Metz. 1997. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35–57.

Godfray, H. C. J. 1990. The causes and consequences of constrained sex allocation in haplodiploid animals. *Journal of Evolutionary Biology* 3:3–17.

Godfray, H. C. J., and A. Grafen. 1988. Unmatedness and the evolution of eusociality. *The American Naturalist* 131:303–305.

Godfray, H. C. J., and I. C. W. Hardy. 1992. Sex ratio and virginity in haplodiploid animals. In D. L. Wrensch & M. A. Ebbert, eds., *Evolution and Diversity of Sex Ratio in Insect and Mites* (pp. 402–441). Chapman and Hall, New York.

Grafen, A. 1986. Split sex ratios and the evolutionary origins of eusociality. *Journal of Theoretical Biology* 122:95–121.

Guertin, D. S., P. J. Ode, M. R. Strand, and M. F. Antolin. 1996. Host-searching and mating in an outbreeding parasitoid wasp. *Ecological Entomology* 21:27–33.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17–52.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3:193–232.

Hatchwell, B. J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* 364:3217–3227.

- Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* 320:1213–1216.
- Kranz, B. D., M. P. Schwarz, L. C. Giles, and B. J. Crespi. 2000. Split sex ratios and virginity in a gall-inducing thrips. *Journal of Evolutionary Biology* 13:700–706.
- Kranz, B. D., M. P. Schwarz, L. A. Mound, and B. J. Crespi. 1999. Social biology and sex ratios of the eusocial gall-inducing thrips *Kladothrips hamiltoni*. *Ecological Entomology* 24:432–442.
- Linksvayer, T. A., and M. J. Wade. 2005. The evolutionary origin and elaboration of sociality in the aculeate hymenoptera: maternal effects, sib-social effects, and heterochrony. *The Quarterly Review of Biology* 80:317–336.
- McLeish, M. J., T. W. Chapman, and B. J. Crespi. 2006. Inbreeding ancestors: the role of sibmating in the social evolution of gall thrips. *The Journal of Heredity* 97:31–38.
- Metzger, M., C. Bernstein, and E. Desouhant. 2008. Does constrained oviposition influence offspring sex ratio in the solitary parasitoid wasp *Venturia canescens*? *Ecological Entomology* 33:167–174.
- Morse, D. H. 2013. Reproductive output of a female crab spider: the impacts of mating failure, natural enemies, and resource availability. *Entomologia Experimentalis et Applicata* 146:141–148.
- Ode, P. J., M. F. Antolin, and M. R. Strand. 1997. Constrained oviposition and female-biased sex allocation in a parasitic wasp. *Oecologia* 109:547–555.
- Pamilo, P. 1991. Evolution of the sterile caste. *Journal of Theoretical Biology* 149:75–95.
- Queller, D. C., and J. E. Strassmann. 1998. Kin selection and social insects. *BioScience* 48:165–175.

Rhainds, M. 2010. Female mating failures in insects. *Entomologia Experimentalis et Applicata* 136:211–226.

Ross, L., A. Gardner, N. Hardy, and S. a West. 2013. Ecology, not the genetics of sex determination, determines who helps in eusocial populations. *Current Biology* 23:2383–2387.

Taylor, P. D. 1996. Inclusive fitness arguments in genetic models of behaviour. *Journal of Mathematical Biology* 34:654–674.

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *Journal of Theoretical Biology* 180:27–37.

Trivers, R., and H. Hare. 1976. Haplodiploidy and the evolution of the social insect. *Science* 191:249–263.

Wade, M. J. 2001. Maternal effect genes and the evolution of sociality in haplo-diploid organisms. *Evolution* 55:453–458.

Figure 1: The convergence stable sex ratios for a haplodiploid population when a constant fraction (u) of females remain unmated and produce all male broods. The dashed line represents the convergence stable sex ratio strategy of mated females (equation (1)), and the solid line represents the population sex ratio (equation (2)).

Figure 2: The benefit threshold of helping (b_{tr}) in panmictic populations for different frequencies of unmated females, assuming that mated females are monogamous and optimize their offspring sex ratios. For all frequencies of unmated females, evolution of helping is easier for diplodiploids (solid gray line for both males and females, equation (7)) than for haplodiploid females (solid black line, equation (5)) and males (dashed black line, equation (6)).