



Queen–worker conflict can drive the evolution of social polymorphism and split sex ratios in facultatively eusocial life cycles

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Hamilton's idea that haplodiploidy favors the evolution of altruism—the haplodiploidy hypothesis—relies on the relatedness asymmetry between the sexes caused by the sex-specific ploidies. Theoretical work on the consequences of relatedness asymmetries has significantly improved our understanding of sex allocation and intracolony conflicts, but the importance of haplodiploidy for the evolution of altruism came to be seen as minor. However, recently it was shown that haplodiploidy can strongly favor the evolution of eusociality, provided additional “preadaptations” are also present, such as the production of multiple broods per season and maternal ability to bias offspring sex ratios. These results were obtained assuming no influence of workers on the sex ratio, even though worker control of the sex ratio is known to occur. Here, we model the evolution of sex-specific fratricide as a mechanism of worker control over the sex ratio. We show that fratricide can facilitate the initial evolution of helping. However, fratricide can also hamper the evolution of unconditional help. Instead, social polymorphism evolves a mixture of helping and dispersing offspring. Finally, we show that the co-evolution of sex-allocation strategies of workers (fratricide) and queens leads to a split production of the sexes, with some colonies specializing in males and others in females. Thus, the model predicts that fratricide spawns a diversity of co-existing life cycles that strongly vary in degree of sociality and sex ratios.

KEY WORDS: Altruism, co-evolution, queen–worker conflict, sex allocation, social insects.

Due to the notable abundance of eusocial species in the order Hymenoptera, where eusociality has arisen more often than in any other order, it has been suggested that some traits which are especially common in hymenopterans might facilitate the evolution of eusociality (Hamilton 1964; West-Eberhard 1987; Boomsma 2009; Hunt 2012; Quiñones and Pen 2017). The first proposal of a preadaptation to eusociality in hymenopterans was Hamilton's haplodiploidy hypothesis (Hamilton 1964). Hamilton argued that the evolution of reproductive division of labor, the hallmark of eusociality, was facilitated by the haplodiploid genetics of Hymenoptera. Under haplodiploidy, females develop from fertilized

diploid eggs, whereas males develop from unfertilized haploid eggs; thus, by sharing identical paternal halves of their genomes, full sisters have a higher coefficient of relatedness ($3/4$) than they would have under diploidy ($1/2$). Hamilton's (1964) argument was that females from a haplodiploid species, hatched in a nest founded by a singly mated queen, would be more inclined to forgo their own reproduction and stay in the nest to help their mother raise siblings.

However, a more comprehensive picture of the varying genetic relatedness in the nest also shows that females have a lower coefficient of relatedness to their brothers ($1/2$) than to their

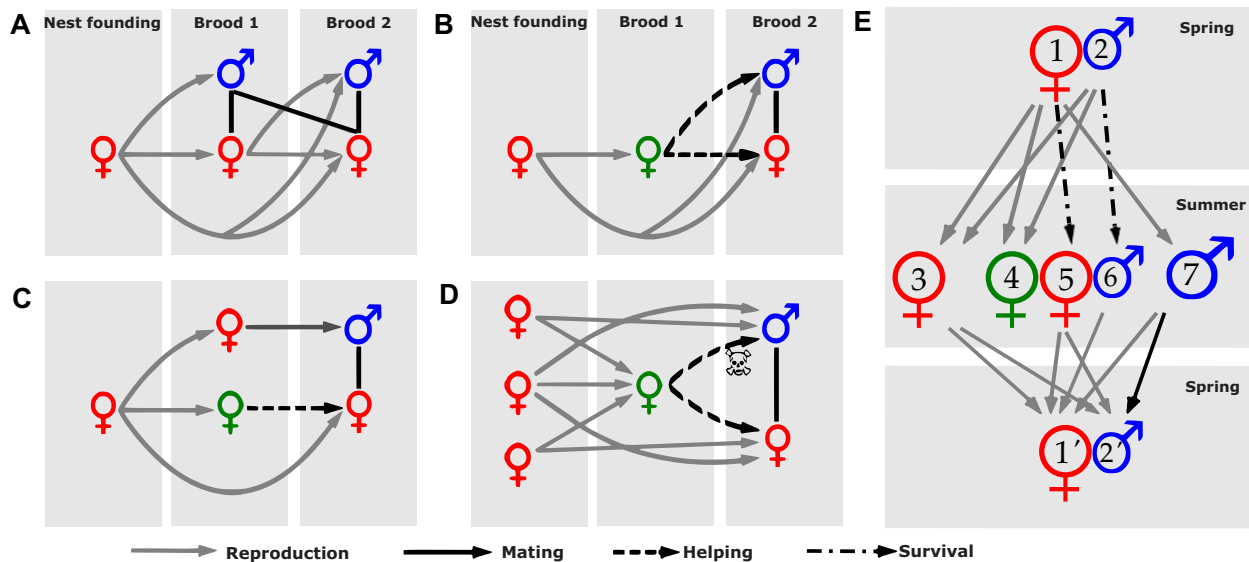


Figure 1. Life-history structures before and after the coevolution of helping behavior, sex ratios, and fratricide (A–D), and representation of the classes to which individuals are assigned in the model (E). (A) Female hibernation (FH) partially bivoltine life cycle is shown originally described by Seger (1983) and used in Quiñones and Pen (2017). Singly mated females (class 1) carrying sperm (class 2) from the previous year start the life cycle producing a spring brood and sometimes produce a second brood in the summer. Males (class 7) and females (class 3) hatched in the spring mate and produce offspring in a summer brood. If males (class 7) from spring broods survive, they can mate with the females from summer broods. Summer females after mating go into hibernation. (B) The eusocial univoltine life history is depicted that emerges from FH after the evolution of helping and sex ratios. Females come out of hibernation (class 1) and produce first a spring worker brood (class 4), and then a summer reproductive brood (classes 1 and 2). (C) A eusocial bivoltine life history is depicted that arises from FH after the coevolution of helping, sex ratios, and fratricide under low worker efficiency. Females (class 1) come out of hibernation and produce a daughter-only spring brood, of which some daughters become workers (class 4) and the rest become solitary breeders (class 3). In the summer brood, solitary females produce only males (class 2), and social females produce only females (class 1). (D) A eusocial bivoltine life history is depicted that arises from FH after the coevolution of helping, sex ratios, and fratricide under high worker efficiency. Three types of females come out of hibernation and produce first a spring worker brood. In the summer brood, one type of females produce only males, a second type produces only females, and a third type produces both males and females. (E) Seven classes are shown to which individuals from all life cycles presented are assigned in the mathematical model. Arrows in (E) show the genetic contribution of each class to every other class, discriminated according to whether the contribution is through reproduction, survival or sperm transfer (mating). Classes 2 and 6, which correspond to sperm carried by females, are shown by slightly smaller male symbols and are right next to the female class carrying the sperm. Similarly, the worker class (4) is right next to the female class it is helping.

sons (1), and this exactly cancels the benefit of raising siblings rather than offspring, assuming that broods have an even sex ratio. Therefore, haplodiploidy favors reproductive altruism only when the sex ratio is female biased in at least some nests of the population (Trivers and Hare 1976). This is the case when different nests specialize in either female or male production—a condition which has been referred to as split sex ratios (Grafen 1986; Boomsma and Grafen 1990). Split sex ratios can be achieved, for example, by females having different sex ratio strategies or by females having conditional sex ratio adjustment and experiencing different situations.

Conditions for natural selection to favor split sex ratios, such as described by Trivers and Hare (1976), are promoted by the partially bivoltine life histories often found in the Hymenoptera (Schwarz et al. 2007). Partially bivoltine life histories occur when

reproductive females can have up to two broods in a reproductive season. Under certain conditions, selection can drive the second brood to be female biased and the first one to be male biased (Charnov 1978; Seger 1983; Quiñones and Pen 2017). The logic is that if both broods are unbiased to begin with, and if males from the first brood survive to mate with females from the second brood, then there will be an excess of males in the second mating pool, which reduces the reproductive value of second brood males and favors female-biased sex ratios (Fig. 1A). This bias, however, requires that females are strictly monogamous and that the reproductive season starts with mated females (Quiñones and Pen 2017).

Altogether, the relatedness asymmetry originally discussed by Hamilton (1964) can have an important role, but it seems that a set of other traits also need to be in place for eusociality to be

avored. Quiñones and Pen (2017) showed how haplodiploidy, together with lifetime monogamy, partial bivoltinism, and conditional sex ratios, can be regarded as preadaptations that facilitate not only the evolution of reproductive altruism but also a transition in life history from bivoltinism to univoltinism. This set of preadaptations occurs together in several taxa in the Hymenoptera, which may well explain why the transition to eusociality has occurred so often in this order (Hunt 1999; Schwarz et al. 2007; Crozier 2008).

The partially bivoltine life history considered by Seger (1983) and Quiñones and Pen (2017) highlights life-history differences between males and females, which partially align the interests of queens and workers regarding the sex ratio of the brood that workers help to raise. In the so-called female hibernation (FH) life cycle described earlier (Fig. 1A), the occurrence of mating before overwintering and the survival of spring males align the interests of queens and workers regarding the direction of the sex ratio bias in the summer brood. However, once helping behavior evolves, workers will help rear the second brood (composed only of reproductives), contributing to higher productivity. Thus, selection favors a larger worker force, which is achieved by a female-biased sex ratio in the spring brood. In response to a spring brood composed of only female workers, the sex ratio of the summer brood evolves to be even again (Fig. 1B). The lack of males in the first brood brings back the conflict between workers and the queen; the queen prefers an even sex ratio in the summer brood, and the workers prefer a female-biased brood. Consequently, worker control over the sex ratio of the colony could evolve after the evolutionary transition from solitary to eusocial life has occurred.

Trivers and Hare's (1976) original hypothesis did not consider the sex ratio biases described by Seger (1983); rather, it envisioned a population with split sex ratios driven by some nests having the sex ratio controlled by queens (unbiased sex allocation) and some by workers (female-biased sex allocation). Worker control over the sex ratio came to be seen both as a condition favoring eusociality (Charnov 1978), and a source of conflict between colony members (Mehdiabadi et al. 2003). Empirical studies show that workers often achieve at least partial control over the colony investment policy (but not always: see, e.g., Helms (1999); Jemielity and Keller (2003); Duchateau et al. (2004); for a meta-analysis, see Meunier et al. 2008) either by manipulating female development (Hammond et al. 2002) or by selective destruction of male brood (Sundström et al. 1996; Foster and Ratnieks 2000). In general, experimental studies support the idea that the queen and workers indeed have different sex allocation strategies and that both have at least some leverage in the conflict (Mehdiabadi et al. 2003).

Evolutionary models of split sex ratios have been very successful at explaining the patterns of sex allocation in advanced social insects (Kümmerli and Keller 2009; West 2009), but the

role of sex allocation in the initial evolution of eusociality has been questioned on theoretical grounds (Gardner et al. 2012). The evolution of split sex ratios is often driven by relatedness variation, caused by different degrees of polyandry, between nests that specialize in producing males or females (Boomsma and Grafen 1990; Kümmerli and Keller 2009). Such variation is now believed to have been very rare during the initial stages of eusociality (Boomsma 2009; Gardner et al. 2012) when lifetime monogamy appears to have been the rule (Hughes et al. 2008). Moreover, theoretical analysis of alternative conditions under which split sex ratios could have favored eusociality suggests their relevance to be either very minor or nonexistent (Gardner et al. 2012; Alpedrinha et al. 2014). Nevertheless, the models of Gardner, Alpedrinha, and collaborators did not consider the bivoltine life histories proposed by Seger (1983), nor did they let the traits involved in the determination of sex ratios coevolve with helping behavior (Quiñones and Pen 2017). Therefore, we assess the effect of worker control over the sex ratios in the coevolutionary scenario proposed by Quiñones and Pen (2017). We are interested both in the potential favoring effect that worker control could have on the evolution of reproductive altruism and the consequences of its presence in the later stages of social evolution. We model worker control as the tendency of workers to commit fratricide, that is, eliminate male brood and to partially "recycle" them to increase the survival of female offspring. Such "recycling" can come about in different ways, such as feeding the males to the females (Chapuisat et al. 1997) or diverting toward females resources that would otherwise be used on the developing males. Furthermore, we allow all the relevant traits to coevolve together. For this purpose, we use a combination of inclusive fitness models and individual-based simulations.

The Model

LIFE CYCLE

We will consider the life history originally described by Seger (1983) and further investigated by Quiñones and Pen (2017), modified to include the possibility of sex ratio manipulation by workers. The population is haplodiploid, meaning that haploid males develop from unfertilized eggs, whereas diploid females develop from fertilized eggs. For each evolving trait, individuals have one locus, at which they will have one (males) or two (females) alleles. For each gene, there are infinitely many possible allelic values, ranging from zero to one. Traits are expressed in codominance, meaning that the trait value is an average of the two allelic values. Recombination is free (i.e., there is no linkage between loci) and there is no epistasis.

The cycle starts with a population of singly mated reproductive females emerging from winter hibernation (throughout the life cycle, we assume that females are lifetime monogamous).

Their life history is partially bivoltine, meaning that reproductive females can have up to two broods in a reproductive season (Fig. 1A). They produce a first brood in the spring, and possibly a second brood in the summer. We divide individuals into seven classes based on their sex and the brood they belong to in order to quantify their reproductive contribution to future generations (Fig. 1E). We use the numbers of these classes as subscripts to identify class-specific reproductive values and stable class frequencies, as well as class-specific fecundities. Fecundity parameters, however, do not apply for every class, only to those classes that correspond to reproductive females (F_1 , F_3 , F_5 ; Fig. 1E).

Class 1 denotes the foundresses, females that emerge from hibernation in the early spring. Class 2 denotes the sperm cells that those foundresses carry from mating in the previous season. Foundresses' spring brood is composed of a proportion of z_1 males and $\bar{z}_1 = 1 - z_1$ females. So, we refer to z_1 as the sex ratio of females from class 1. As mentioned earlier, the expressed sex ratio is the average of the allelic value of the two loci of the individual.

Females born in the spring may forego their own reproduction to remain in their natal nest as helpers (or workers, class 4). Nests with workers are called social nests. Females hatched in the spring become workers with probability h (given by the average value of the newly hatched female's alleles at the corresponding locus). Thus, the mixed strategy h is the helping tendency of a spring-hatched female. With probability $\bar{h} = 1 - h$, they instead depart from their mother's nest and become solitary females (class 3). These spring-hatched, solitary females mate with spring-hatched males (class 7) and found their own nests. The offspring from this mating become part of the summer brood (classes 1 and 2).

In the summer, solitary females produce a summer brood. Meanwhile, the original females (foundresses) have a certain probability (S_f) of surviving until the summer. If those females survive (class 5), they also produce a summer brood. Given that females are lifetime monogamous, the summer brood of the foundresses is fathered by the surviving sperm (class 6). Depending on whether their daughters stayed or left the natal nest, those foundresses from class 5 may or may not have workers in the nest. The probability of having workers in the nest will depend on the helping tendency of daughters from the spring brood. Specifically, we assume that the number of workers in the nest is a Poisson random variable with mean $H = h\bar{z}_1 F_1$, hence $\pi = 1 - e^{-H}$ is the probability that at least one female from the spring brood stays and becomes a worker in the foundress' nest, in which case the expected number of workers per social nest is H/π .

Summer fecundity is higher when the mother has workers in her nest. The expected fecundity of surviving foundresses' (class 5) is given by:

$$F_5 = F_3(1 + bH) = F_3(1 + bh\bar{z}_1 F_1), \quad (1)$$

where F_3 is the fecundity parameter of solitary females (class 3), b is the benefit per worker, and H is the expected number of workers defined earlier. Thus, surviving foundresses (class 5) without workers enjoy the same fecundity as solitary summer females (class 3). The benefit of workers b quantifies the number of extra offspring breeding females get per worker, relative to their fecundity as solitary breeders. This quantity has a clear demographic interpretation: it represents the efficiency with which workers raise siblings relative to their own offspring; thus, if b is equal to 1, workers are equally good at raising siblings as at raising offspring. If b is larger than 1, workers are better at raising siblings; conversely, if b is smaller than one, potential workers are better at raising offspring. The assumption of fecundity scaling linearly with the number of workers might seem unrealistic for a very large number of workers. But given our aim of capturing the initial stages of eusociality, we use baseline fecundity values that are not high enough to lead to large numbers of workers ($F_1 = 5$ in examples), and can be considered small compared to brood sizes in social insects.

The summer sex allocation strategy of reproductive females depends on whether their nests are social or not. Females whose nests lack workers (including all of the spring-hatched solitary females—class 3) produce summer broods with a proportion z_3 of males. This individual trait is determined by the average value of their alleles at the respective locus. In contrast, the proportion of males produced by a female in a social nest is given by z_5 . Thus, females make their summer sex allocation strategy dependent on the presence of workers. Note that for convenience we have used the class subscripts to denote the sex ratios of solitary (z_3) and social (z_5) females. However, surviving foundresses (class 5) will produce brood with a sex ratio given by z_3 if they lack helpers at the nest. Also, like in the notation of fecundities, not all classes have an associated sex ratio strategy, only reproductive females corresponding to classes 1, 3, and 5.

In the social nests, we allow workers to influence the sex ratio by selectively removing male brood (we do not specify the stage at which they are removed). Each male offspring is killed by the workers with probability $\bar{\phi}$, which is the average tendency among workers to kill male offspring or to commit fratricide (as determined by the average value of the worker's alleles at the respective locus). A fraction ρ of the resources represented by killed offspring is recycled toward the production of new individuals, whose sex is determined by z_5 ; hence, we call ρ the recycling efficiency ($\bar{\rho} = 1 - \rho$). After fratricide, the per capita probability that an egg from a social nest ends up being a male is $M = z_5(1 - \bar{\phi} + z_5\bar{\phi}\rho)$, where the factor inside the brackets is the effect of the fratricide stage. Out of the offspring before the fratricide stage, a proportion $1 - \bar{\phi}$ survives fratricide and a proportion $\bar{\phi}$ is killed, of which a proportion $z_5\rho$ is recycled and used to produce more males. In principle, there could be further rounds

of fratricide and recycling, but, for simplicity, we ignore this possibility, because each subsequent round would have a smaller and smaller effect. The per capita probability that an egg ends up being a male multiplied by the corresponding class-specific fecundity (F_5) gives the total number of males in the summer brood. Similarly, the per capita probability that an egg turns into a female is $N = \bar{z}_5(1 + \bar{z}_5\bar{\phi}\rho)$. Thus, the total number of females added by the worker's sex-ratio manipulation is $F_5\bar{z}_5\bar{\phi}\rho\bar{z}_5$ and $F_5\bar{z}_5\bar{\phi}\bar{\rho}$ is the total loss of males due to siblicide. The idea here is that killed male offspring can be fed back to the queen to produce more eggs, or they free resources to increase the survival of the rest of the progeny.

The males from the first brood survive after mating with probability S_m . If they do so, they become part of the mating pool in the autumn. Because males from the first brood may survive to mate a second time, the two broods are partially overlapping. At this stage, all surviving males (both the surviving first brood males and the second brood males, hatched in the summer from both social and solitary nests) compete to mate with the second brood females.

The mated second brood females, hatched in the summer, then go into hibernation. Density regulation occurs after females enter hibernation: a randomly chosen fraction of the hibernating mated females fail to start a nest in the spring, maintaining constant population size. In the spring, a new season begins with the emergence of the overwintering mated females. For more details, see Supporting Information.

EVOLVABLE TRAITS

Individuals are characterized by five phenotypic traits ($x = \{h, z_1, z_3, z_5, \phi\}$) that together determine their social behavior and sex allocation strategy, as described in the previous section.

We assume a monomorphic population for all traits, with resident trait values x_i^* , where i is an element of the trait vector described before, and $*$ denotes resident value. We are interested in the fate of mutants with a trait value $x_i \neq x_i^*$ in the context of a resident population with trait x_i^* . Therefore, we derive expressions for the inclusive fitness effect, or selection gradient, of those five types of mutant. We use those expressions to compute evolutionary equilibria and we use an adaptive dynamics approach, assuming uncorrelated mutations, to compute co-evolutionary dynamics (for details, see Supporting Information).

INCLUSIVE FITNESS AND SELECTION GRADIENTS

In order to assess the strength and direction of selection on each one of the evolving traits, we derive for each one the inclusive fitness effect of small phenotypic deviations (Taylor et al. 2007; Lehmann et al. 2016). Following equation 19 in Taylor et al. (2007), the inclusive fitness effect of a mutation in a given trait is given by the derivative of fitness with respect to the mutant

trait, weighted by the relatedness coefficients between the actor and the interacting partners whose fitnesses are affected by the trait. Under the assumption of weak selection, those relatedness coefficients can be approximated by the ratio of the coefficients of consanguinity between the focal and the partner, and the focal to itself. Coefficients of consanguinity are the probability that a randomly drawn allele from the one individual is identical by descent (IBD) to a randomly drawn allele from another individual (Bulmer 1994). Moreover, selection gradients include the reproductive values from the demographic model evaluated at the resident trait (Taylor et al. 2007; Lehmann et al. 2016). The expressions of the inclusive fitness effects correspond to the selection gradients of the different traits (Lehmann et al. 2016), which are the first-order derivative of the invasion fitness (W_i) of each trait. These selection gradients are evaluated at the value of resident trait while holding the other traits constant. The selection gradients capture the strength and direction of selection on each of the traits. A positive value for the selection gradient means directional selection toward higher trait values; conversely, negative values indicate selection toward lower values. Trait values for which the selection gradient is zero are evolutionary equilibria. In the Supporting Information, we show how to compute the selection gradients from the matrix population model. Here, we present the expressions for the selection gradients.

Sex ratios

The selection gradient or inclusive fitness effect of the spring brood sex ratio is given by

$$\left. \frac{\partial W_1}{\partial z_1} \right|_{z_1=z_1^*} = F_1 \left[-r_{\text{dau}} v_{f1}^* + r_{\text{son}} v_{m1}^* - h S_f F_3 F_1 \right. \\ \left. \times \left((b - \bar{\pi} h \bar{z}_1 F_1) \left(\frac{r_{\text{dau}} v_{f2}^* N}{r_{\text{son}} v_{m2}^* M} \right) + \bar{\pi} h \bar{z}_1 F_1 (r_{\text{dau}} v_{f2}^* \bar{z}_3 + r_{\text{son}} v_{m2}^* \bar{z}_3) \right) \right], \quad (2)$$

where r_{dau} and r_{son} are the coefficients of relatedness to the foundress of her daughters and sons, respectively; v_{f1}^* and v_{m1}^* are the reproductive values of the females and males from the first brood; v_{f2}^* and v_{m2}^* are the reproductive values of females and males of the second brood. The first term inside the square brackets of equation 2 represents the inclusive fitness effect of producing one fewer daughter in the spring; the second term represents the inclusive fitness effect of producing one extra son; and finally, the third term is the inclusive fitness effect, through her second brood, of producing one less female in the first brood. Inside the brackets of the third term in equation 2, the first term quantifies the fitness contribution of social nests (which is affected by fratricide and the recycling efficiency inside terms M

and N explained before), whereas the second term corresponds to the fitness contribution of solitary nests.

The selection gradient of the sex ratio of solitary nests in the summer brood is given by

$$\left. \frac{\partial W_3}{\partial z_3} \right|_{z_3=z_3^*} = \frac{u_3 F_3 + u_5 F_5 \tilde{\pi}}{u_3 + u_5} (-r_{\text{dau}} v_{f2}^* + r_{\text{son}} v_{m2}^*), \quad (3)$$

where u_3 and u_5 are the class frequencies (in the resident population in demographic equilibrium) of the females from the spring brood and the surviving foundresses, respectively. The first term, inside the brackets in equation 3, is the inclusive fitness effect of producing one female less in the summer, whereas the second term is the inclusive fitness effect of producing one more son in the summer.

The selection gradient for the sex ratio in social nests is given by

$$\left. \frac{\partial W_5}{\partial z_5} \right|_{z_5=z_5^*} = S_f F_5 \pi [r_{\text{dau}} v_{f2}^* (-1 + \phi \rho - 2z_5 \phi \rho) + r_{\text{son}} v_{m2}^* (\tilde{\phi} + 2z_5 \phi \rho)], \quad (4)$$

where the first term inside the brackets quantifies the inclusive fitness effect of producing one daughter less in the summer, whereas the second term is the inclusive fitness effect of producing one more son in the summer.

Helping behavior

The selection gradient of helping behavior is given by

$$\left. \frac{\partial W_h}{\partial h} \right|_{h=h^*} = F_3 [- (\tilde{z}_3 r_{\text{dau}} v_{f2}^* + z_3 r_{\text{son}} v_{m2}^*) + B (r_{\text{sis}} v_{f2}^* N + r_{\text{bro}} v_{m2}^* M)], \quad (5)$$

where r_{sis} and r_{bro} are the relatedness coefficients between a worker and her sister and brother, respectively, and B is the expected contribution of a worker to her mother's fecundity, which is conditional on their mother's survival.

$$B = S_f b. \quad (6)$$

The first term inside the square brackets in equation 5 is the inclusive fitness effect of increasing the tendency to forgo own reproduction in the summer; in other words, it is the cost of helping. The second term inside the brackets of equation 5 is the marginal inclusive fitness increase accrue to helping raise siblings, or, the benefit of helping. Both of these terms are split up in male and female contributions. The cost is split up into daughters and sons, whereas the benefit is split up into sisters and brothers. All of these contributions are, as explained before, weighted by the relatedness coefficients and the reproductive values.

Fratricidal behavior

The selection gradient of fratricidal behavior is given by

$$\left. \frac{\partial W_\phi}{\partial \phi} \right|_{\phi=\phi^*} = F_5 h B [r_{\text{sis}} v_{f2}^* \tilde{z}_5 z_5 \rho + r_{\text{bro}} v_{m2}^* z_5 (-1 + z_5 \rho)]. \quad (7)$$

The first term inside the square brackets in equation 7 is the worker's inclusive fitness gain due to the extra sisters obtained from fratricide, whereas the second term is the worker's inclusive fitness loss due to killing their brothers.

We use these selection gradients to derive conditions for natural selection to favor helping and fratricidal behavior. Furthermore, we use an adaptive dynamics approach (Dieckmann and Law 1996; Pen and Taylor 2005) to compute the coevolutionary dynamics of the five traits. The rate of trait value change over time is proportional to the selection gradient of that trait (equation (5) in the Supporting Information).

Finally, we complement the analysis of the dynamics with individual-based simulations, where we keep track of a population of individuals that have the life cycle described above. In the simulations, each individual is characterized by one (males) or two (females) vectors of allelic values (each of which was restricted to lie between 0 and 1), which can experience small-effect mutations with a given probability per reproduction event. The population initially consists of 2500 mated females, but the number of individuals changes throughout the year as they die and/or reproduce. At the end of the year, 2500 randomly selected mated females survive the winter and restart the cycle. For more details on the simulations, see Supporting Information.

Results

COEVOLUTIONARY DYNAMICS

The analysis of the evolutionary dynamics shows that the coevolution of helping behavior with sex ratios and fratricide more strongly favors the emergence of social behavior relative to a model without fratricide. The conditions derived in Quiñones and Pen (2017) for the evolution of helping (equation (1)) provide a boundary of minimal worker benefits required for the evolution of helping in a bivoltine life history. The dynamics shown in Figure 2A,B are obtained assuming worker benefits below the Quiñones and Pen (2017) boundary; nevertheless, helping behavior emerges as an evolutionary outcome. However, the dynamics that lead to this are somewhat subtle. In the individual-based simulations (Fig. 2A), sex ratios of the spring and summer broods are first biased in opposite directions (continuous green and orange lines), in accordance with previous models (Seger 1983; Quiñones and Pen 2017). Second, we see fratricidal behavior (ϕ ; purple line Fig. 2A) and the sex ratio of social nests (z_5 ; dashed orange line) change subject to mutation and genetic drift. At this stage, fratricide and the sex ratio in social nests are not under

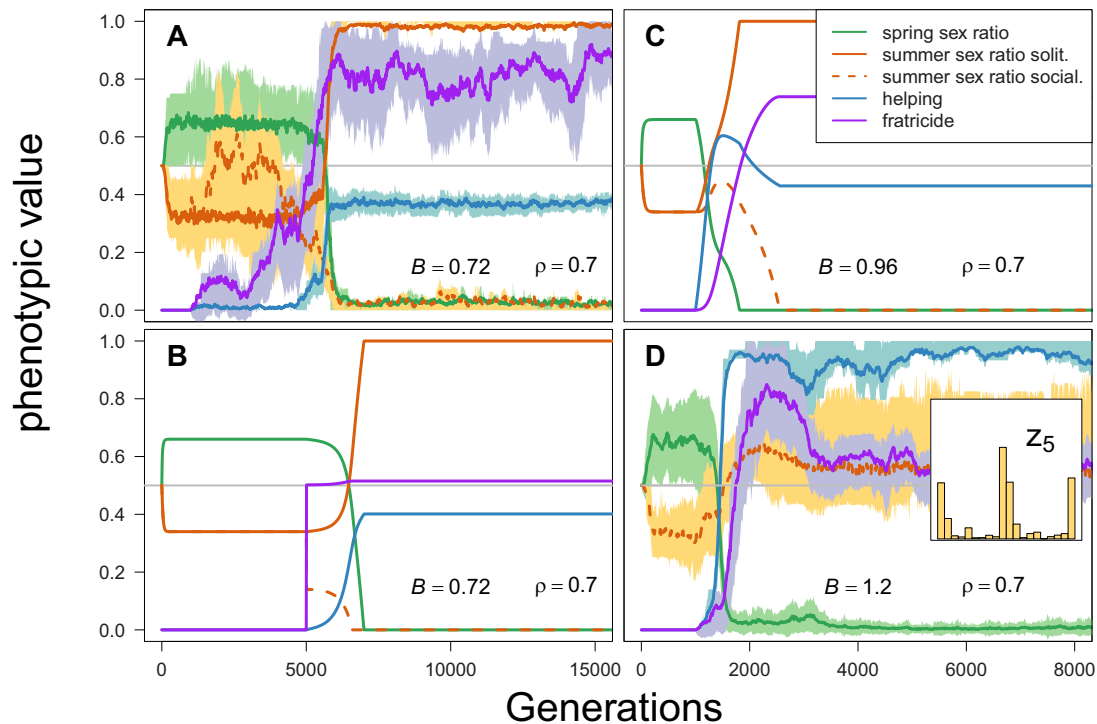


Figure 2. Coevolutionary dynamics of helping, fratricide, and sex ratios. (A) Individual-based simulations (IBS) show the coevolution of the five traits (thick lines represent the mean of the trait in one representative run, and color ribbons represent the area of the interquartile range) for a parameter combination where helping is not expected to evolve without fratricide. During the first 5000 generations, spring and summer sex ratios evolve opposite biases, and helping does not evolve; hence, the sex ratio in the social nests and fratricide evolve subject to mutation and genetic drift. Once the sex ratio of social nests turns female biased and fratricide increases, helping behavior takes off. The evolution of helping drives the spring sex ratio toward daughters only, and fratricide causes a split in the production of the sexes between solitary and social nests. (B) Predictions from the deterministic model with the same parameter combination. During the first 5000 generations, helping and fratricide do not evolve. At generation 5000, we perturb the equilibrium level of fratricide and sex ratio of social nests. We do that following the stochastic changes seen in the IBS. This perturbation leads to coevolutionary dynamics that match the IBS, where helping and fratricide evolve and the sex ratios are split. (C) Predictions of the deterministic model for a combination of parameters where helping is expected to evolve without fratricide. The evolution of fratricide splits the production of the sexes as in (A), and reduces the final level of helping with respect to a situation without fratricide. (D) An IBS run with relatively high expected worker benefits (B) and recycling efficiency (ρ). The higher level of helping and fratricide causes a lack of males, which triggers evolutionary branching of the sex ratio in social nests. The inset shows the distribution of the sex ratio in social nests at the end of the simulation. Parameters values are as follows: $S_f = 0.8$, $S_m = 0.8$, $F_1 = F_3 = 5.0$.

selection because helping behavior has not evolved, and hence there are no workers or social nests ($\pi = 0$). At around 5000 generations, the phenotypic value associated with alleles determining the sex ratio of social nests would correspond to a female bias if it were expressed, whereas the phenotypic value associated with alleles determining with fratricide increases. These two changes imply that, at this point, nests with mutant workers produce a female biased sex ratio (second brood) and kill some of the male offspring. These two changes pave the way for helping behavior to evolve (blue line). The emergence of helping, in turn, influences the direction of selection on sex ratios. The spring sex ratio (green line) turns female only, the summer sex ratio of social nests evolves a stronger female bias (dashed orange line), and the summer sex ratio of solitary nests (continuous orange line)

becomes male only. Fratricide is selected for while the sex ratios still evolve. But once social nests produce females only, there are no more male offspring to be killed, and therefore the tendency to commit fratricide is again subject to random forces only. Note that the mating pool at the end of the spring is completely composed of females; however, those reproductive females only produce males, and thus, do not need to mate to lay eggs. The dynamics shown in Figure 2A are representative of the system's behavior. Figure A1 in the Supporting Information shows 10 more replicate simulations with the same parameter combination. All simulations in Figure A1 in the Supporting Information eventually lead to similar levels of helping behavior and to the split production of the sexes. Simulations do differ in the timing in which populations go through the described transition. That is because the transition

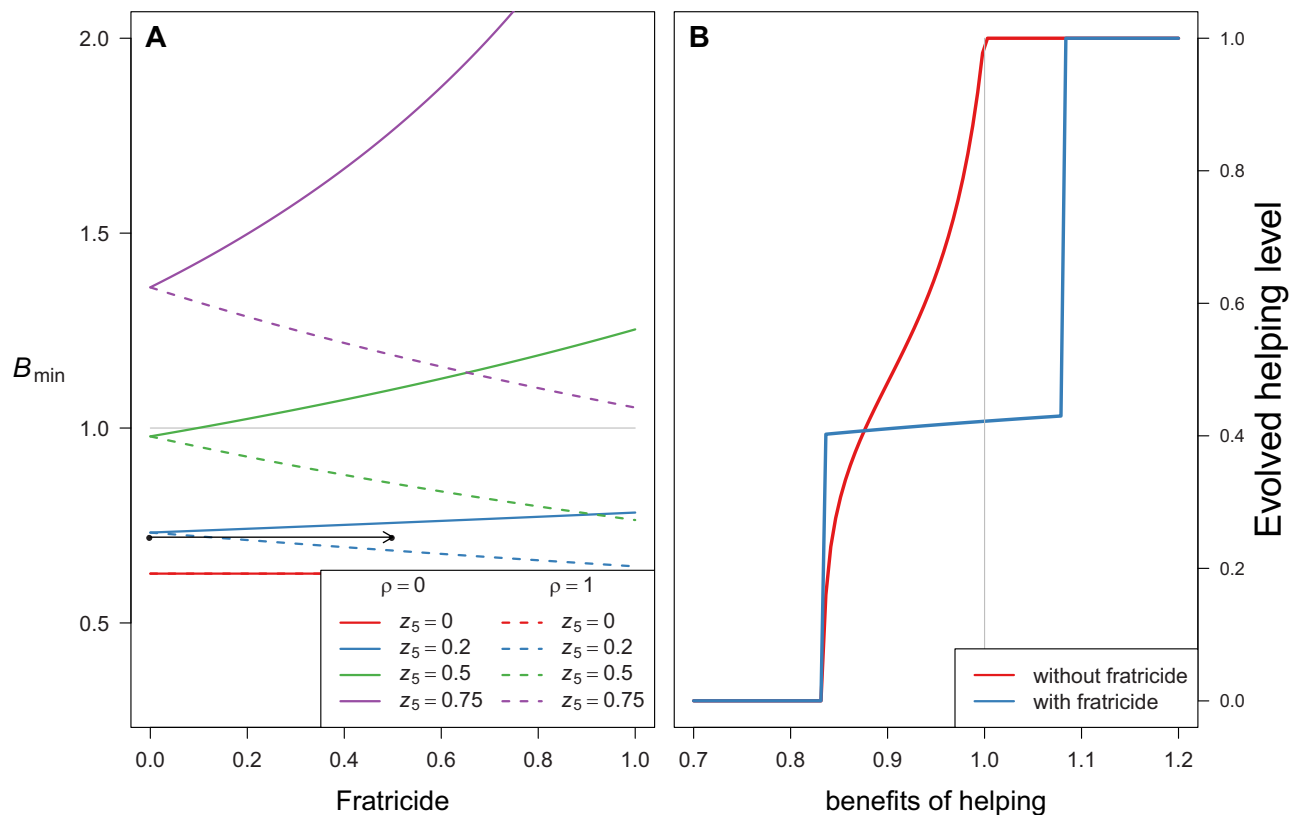


Figure 3. Effect of fratricide in the evolution of helping behavior. In (A), minimal worker benefits required for the emergence of helping behavior as a function of fratricidal strategy and the sex ratio (proportion sons) of social nests. The effect of fratricide depends strongly on the recycling efficiency ρ of the killed male offspring: the higher the efficiency, the more strongly fratricide facilitates the evolution of helping. More female-biased sex ratios in social nests strongly favor the evolution of helping. The black arrow shows the perturbation performed in the numerical simulations shown in Fig. 2B. With the new combination of state variables, helping is expected to evolve, and that leads to further changes in fratricide and sex ratio. In (B), helping level resulting from the coevolutionary scenario without the evolution of fratricide (red line), and with the evolution of fratricide (blue line). With low benefits, higher values of helping evolve with fratricide than without; while the opposite is true for higher benefits. Gray lines on both panels show the benefits for which workers are as efficient at raising siblings as at raising offspring. Other parameters values are as follows: $S_f = 1$, $F_1 = F_3 = 5.0$, $\rho = 0.7$ (unless stated differently).

requires the sex ratio of social nests to be sufficiently biased toward females, and at the very beginning of the simulation the trait is only driven by stochastic factors.

The evolutionary transition in social behavior and life history, triggered by stochastic changes, can be understood with our deterministic inclusive fitness model (Dieckmann and Law 1996; Lehmann and Rousset 2014). In Figure 2B, we show the trajectories of the five traits derived from the inclusive fitness model. During the first 2000 generations, only the spring and summer sex ratios of solitary nests were allowed to evolve, and they change in opposite directions (Seger 1983; Quiñones and Pen 2017). Between generation 2000 and 5000, fratricide and helping were allowed to evolve; however, the population remained at equilibrium with solitary nests. At generation 5000, we perturbed the equilibrium mimicking the stochastic changes seen in the individual-based simulation (Fig. 2A,B), changes in traits that

were not expressed and therefore not under selection. The sex ratio of social nests (z_5) was changed from the equilibrium value in solitary nests to more daughters (0.2 added to the evolved proportion of sons), whereas fratricide is increased from 0 to 0.5. Instead of returning to the previous equilibrium values, the traits follow an evolutionary trajectory very similar to the one found in the individual-based simulation. In the next section, we use the inclusive fitness model to show the precise combination of sex ratios and fratricide that are required to allow the evolution of helping behavior, and thus, to start the dynamic changes seen in the individual-based simulations (see Fig. 3A).

Despite having a positive effect on the emergence of helping, fratricide has a negative effect on the long-term equilibrium of helping. The dynamics presented in Figure 2C correspond to a parameter combination where helping is expected to emerge without fratricide; the worker benefits ($B = 0.96$) are above the

boundary derived by Quiñones and Pen (2017). As expected, helping behavior initially evolves (blue line), but the increasing level of fratricide (purple line) at some point causes a reversal in the direction of selection on helping. Helping behavior then decreases until social nests (dashed orange lines) produce only females. At that point, fratricide obviously no longer has fitness consequences because there is no male offspring to be killed in the social nests. How general the negative effect of fratricide is on the long-term magnitude of the helping tendency can be seen in Figure 3B, where we show the evolved helping tendency as a function of the benefits of helping both in scenarios with and without fratricide. The scenario without fratricide (red line in Fig. 3B) corresponds to the model of Quiñones and Pen (2017). The evolved helping tendency shown by the blue line (coevolved with fratricide) is above the red line when the benefits of helping are low. However, when the benefits of helping are higher, the red line is above the blue line. Moreover, the maximum helping tendency requires higher benefits when helping coevolves with fratricide.

The evolution of fratricide also promotes the evolution of split sex ratios among summer broods. The dynamics are shown in Figure 2A–C, indicating that as fratricide increases in frequency, the sex ratio of social nests (dashed orange lines) becomes female biased. In contrast, the sex ratio of solitary nests evolves a strong male bias (Fig. 1C). Once split sex ratios have emerged, the proportions of males and females in the mating pool depend on the prevalence of helping, which in turn depends on the helping tendency h of spring females. Given that higher worker benefits (B) promote selection for greater helping tendencies, leading to fewer solitary nests, high worker benefits ultimately cause a shortage of males in the population, as these are only produced by solitary nests. This shortage of males generates a trade-off for social nests: if they produce male eggs, some will be killed by the workers, but the surviving males will enjoy a high reproductive success. This trade-off apparently triggers evolutionary branching (Geritz et al. 1997) toward allelic values encoding extreme sex ratios. One of the two peaks of the bimodal distribution corresponds with extremely male-biased sex ratios when homozygous, and causes lower colony fecundity due to the costs of fratricide, and the other peak corresponds with extremely female-biased sex ratios when homozygous. In the end, social nests are of three types: one that produces almost exclusively males, one that produces almost exclusively females, and one with a heterozygote queen that produces nearly even sex ratios (inset in Fig. 2D). We have not been able to derive mathematically conditions for the existence of the branching point in the sex ratio of social nests. Our inclusive fitness approach captures only the first-order effects of selection (Taylor et al. 2007; Wakano and Lehmann 2014), while to obtain the conditions for branching we would need to compute second-order effects of selection (Wakano and Lehmann 2012, 2014). Despite not having such derivations, we can say, from our

individual-based simulations, that branching occurs in parameter combinations that allow both the evolution of fratricide and the evolution of high levels of helping behavior, that is to say that high recycling efficiencies and high benefits of helping favor the existence of the branching point (see next section, Figs. 3 and 4).

These evolutionary changes cause the population to undergo a substantial life-history transition: depending on the magnitude of worker benefits (B) and the recycling efficiency (ρ), the population goes from the initial bivoltine life history (Fig. 1A) to either (1) a life-cycle characteristic of univoltine eusocial species (if recycling efficiency is low, and fratricide does not evolve, Fig. 1B), (2) a life cycle with polymorphism in helping behavior (if fratricide evolves, Figs. 1C and 2A–C), and the production of the sexes is split between social and solitary nests, or (3) a eusocial life cycle, with split sex ratios (Figs. 1D and 2D).

EUSOCIALITY THRESHOLD

To better understand the effects of fratricide and sex ratio manipulation on the evolution of helping behavior, we derived the conditions for natural selection to favor helping in terms of the per-capita benefits that workers provide to the colony (B in equation 1). Similar conditions are derived for bivoltine life histories in Quiñones and Pen (2017), where it is shown that $B > 1$ is sufficient for diploids. For haplodiploids with the FH life history, the minimally required benefits are less stringent and decrease with increasing survival probability of males (S_m). In the Supporting Information, we derive an analogous condition, taking into account fratricide and conditional sex ratio adjustment. For the sake of clarity, we present an expression assuming that the spring and summer sex ratios of nests (z_1, z_3) are at an evolutionary equilibrium before the emergence of helping, just as in the evolutionary dynamics presented in Fig. 2A,B (for details, see Supporting Information, section A4.2). In such a case, natural selection favors the evolution of helping whenever

$$B > \frac{2}{3 - 2z_5 + z_5\phi(\rho(3 - 2z_5) - 1)}. \quad (8)$$

This inequality shows that fratricide can both increase and decrease the minimally required benefits for helping to evolve, depending on how efficient male offspring are recycled into new offspring (Fig. 3A). The sign of the third term in the denominator depends on ρ : for sufficiently high recycling efficiency, it is positive, and fratricide facilitates the evolution of helping. Fratricide biases the sex ratios toward females, increasing the inclusive fitness that workers gain by staying to work at their mother's nest. A higher efficiency makes the process less costly. Inequality (8) also implies that more female-biased sex ratios (smaller z_5) in social nests facilitate the evolution of helping (Fig. 3A). In fact, Figure 3 shows that the most extreme level of female-biased sex ratios in social nests (red line) yields the lowest benefits required for the evolution of

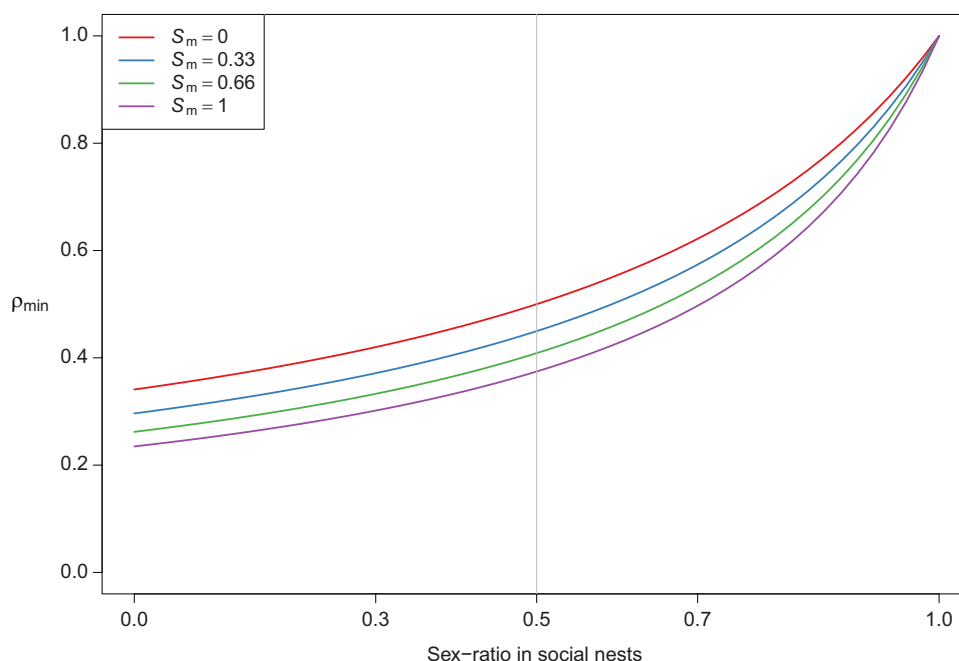


Figure 4. Minimal level of recycling efficiency required for the evolution of fratricide as a function of the sex ratio in social nests. Female-biased sex ratios in social nests provide more lenient conditions for the evolution of fratricide. Higher male survival also favors the evolution of fratricide. Parameters values are as follows: $S_f = 1$, S_m , $F_1 = F_3 = 5$.

helping behavior. Overall, female-biased sex ratios in social nests have a stronger effect favoring the evolution of helping than fratricide does. As shown earlier (Fig. 2A), the evolution of helping behavior leads to a set of changes that end up in a population with social polymorphism and split-sex ratios. Therefore, conditions for the evolution of helping (Fig. 3A) are also the conditions for the beginning of the coevolutionary changes portrait in Figure 2A. The arrow in Figure 3A shows the perturbation performed in fratricide level to obtain the dynamics in Figure 2B that correspond to the IBD in Figure 2A. The resulting combination of variables and parameters, after the perturbation, is above the minimum level of benefits required for the evolution of helping. Consequently, the dynamics lead to a transition in social behavior and life history.

As seen in the coevolutionary dynamics and shown by the conditions derived for the evolution of helping, fratricide and female-biased sex ratios in social nests considerably favor the evolution of helping. Compared to the situation without fratricide and the same sex ratio for solitary and social nests (Quiñones and Pen 2017), the benefits required for the evolution of helping can be twice as low when fratricide and female-biased sex ratios are present in social nests (see Supporting Information).

CONDITIONS FOR FRATRICIDE TO EVOLVE

Using the selection gradient for fratricide, we derive conditions for natural selection to favor fratricide, assuming a current level

of zero (equation (55) in the Supporting Information). Figure 4 shows the minimal recycling efficiency necessary for the evolution of fratricide (ρ_{\min}) as a function of the sex ratio in social nests for different levels of male survival (S_m). Fratricide is favored when social nests have female-biased sex ratios, and the pattern is strengthened by higher male survival.

SEX RATIO EVOLUTION

We use the selection gradients of the sex ratio traits to assess the effect that fratricide has on the proportions of males and females. Figure 5A shows that fratricide imposes selection for more female-biased sex ratio in social nests; this effect is stronger with lower levels of recycling efficiency. This is a response to the cost of fratricide, which increases with lower recycling efficiency. Foundresses are selected to produce fewer males because workers kill a fraction of those males. At the same time, the solitary nests, which do not have fratricide, are selected to produce more males whenever sex ratios in the social nests are female biased (Fig. 5B, blue and green dashed lines). Therefore, the presence of fratricide, as a form of worker control, triggers opposite selective pressures on the sex ratio of social and solitary nests, which effectively splits the production of females and males. Figure 5B, however, also shows that the sex ratio in solitary nests can be selected toward female bias whenever sex ratios are even (red and blue full lines). Under even sex ratios, and given the level of male overlap ($S_m = 1$ in Fig. 5B), selection for female-biased sex ratios is expected in

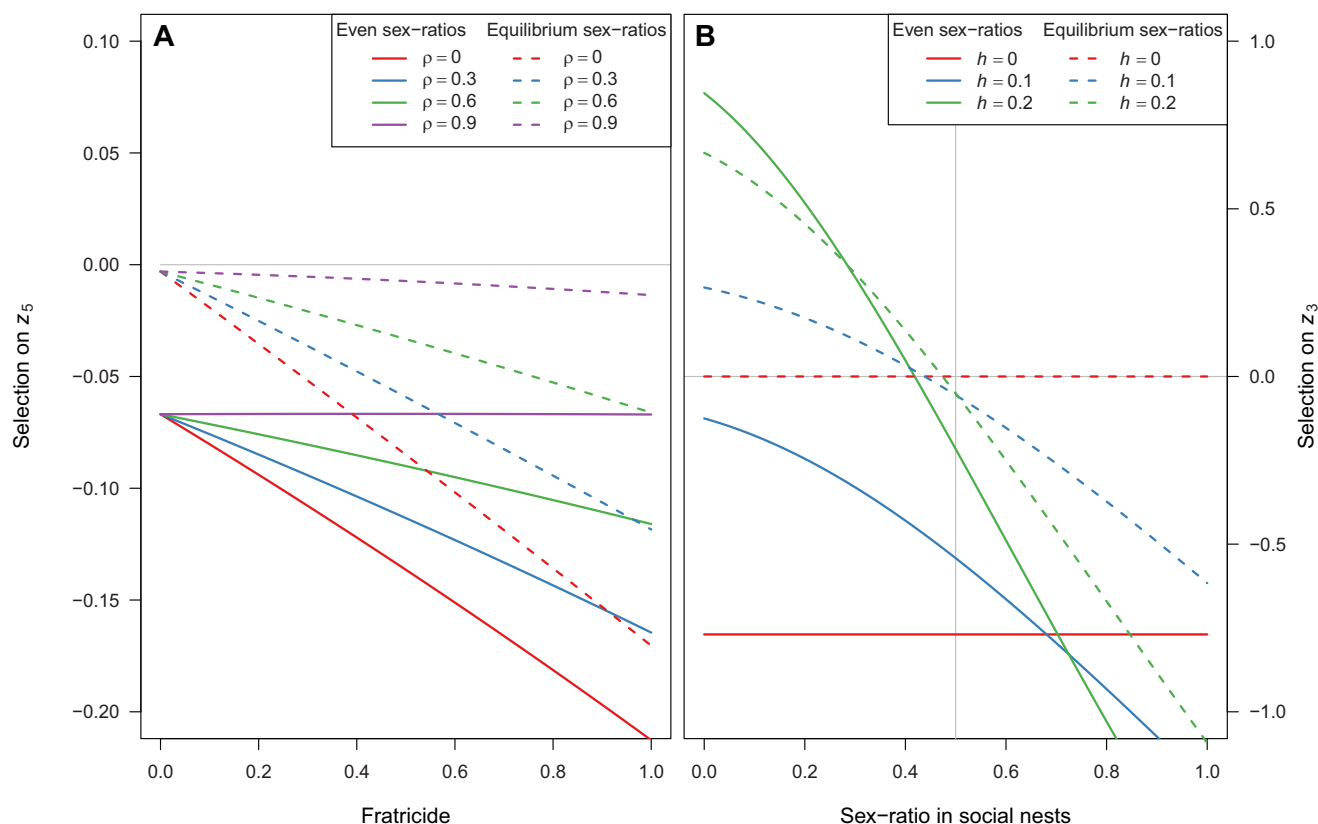


Figure 5. Strength and direction of selection in the summer sex ratios of social (A) and solitary nests (B). In (A), higher levels of fratricide promote higher proportions of daughters in social nests (selection for lower z_5), more strongly so for lower levels of recycling efficiency. In (B), more females in social nests favor more males in solitary nests when helping is present in the population (blue and green lines). When spring and summer (for solitary females; z_1 , z_3) sex ratios are even (continuous lines), male overlap inherently biases the summer brood toward females. After evolution has acted and sex ratios are at equilibrium (dashed lines), the sex ratios are only biased by the presence of fratricide by workers ($h > 0$, blue and green lines). Horizontal thin gray lines represent the boundary between selection for more or fewer males. The vertical thin gray line represents even sex ratio in social nests. Parameters values are as follows: $S_f = 1$, $S_m = 1$, $F_1 = F_3 = 5$, $b = 1$ for both panels; $\phi = 0.8$ and $\rho = 0.8$ in panel B.

the solitary bivoltine life cycle due to the excess of males in the second brood (Seger 1983; Quiñones and Pen 2017). But, as the level of helping increases (blue and green dashed lines Fig. 5B), selection favors more male-biased solitary nests. Thus, as seen in the individual-based simulation, we expect fratricide to split the production of the sexes between social and solitary nests once there are social nests.

Discussion

The role of split sex ratios at the initial stages of the evolution of eusociality has been questioned in light of the comparative evidence and theoretical grounds (Hughes et al. 2008; Boomsma 2009; Gardner et al. 2012). In contrast, we have shown here how eusociality and split sex ratios can coevolve in monogamous populations, even mutually reinforcing each other. Rather than being imposed by the mating system (polyandry), relatedness differences among nests can emerge due to the flexible sex ratios

that depend on both the time of the season and the presence of workers. In our model, solitary and social nests produce different summer sex ratios; hence, the average relatedness between the workers and their siblings is also different. Social nests produce only females, which, given the higher relatedness between workers and their sisters, is a sex allocation strategy in line with workers evolutionary interests. Solitary nests produce only males, which, given the frequency-dependent nature of selection on sex ratios and the extreme sex ratios strategy of social nests, is in line with the foundresses evolutionary interests. The evolutionary conflict between queens and workers over sex ratio drives splits sex ratios and intermediate helping levels. Thus, we conclude that split sex ratios can have an important role in the initial evolution of eusociality in a bivoltine life history common among primitively social insects and related taxa.

In the stochastic individual-based simulations, fratricide can initially evolve to higher values by nondeterministic forces such as mutation and genetic drift (Fig. 1). Strictly speaking—given

that, at this initial stage, there are no workers—fratricide as a trait (in the sense of workers selectively removing male brood) is undefined. Thus, this initial neutral evolution of the trait is an artifact of our simplified model. However, we believe that fratricide could have been present before the evolution of helping behavior through a different mechanism. Egg cannibalism is part of insect societies in different contexts like policing (Wenseleers and Ratnieks 2006), offspring conflict (Schultner et al. 2014), parasitoid lifestyle (Hopper and Mills 2015), and brood parasitism (Litman et al. 2013; Quiñones and Wcislo 2015). The presence of egg cannibalism in some of these contexts is not restricted to social insects, but it is also present in subsocial or solitary species. Thus, the behavioral machinery necessary for ovide has been present in the hymenopteran lineage from the start. For fratricide to favor helping behavior in the scenario our model presents, it is only necessary to express egg cannibalism in the context of worker behavior with a bias toward killing males. Such bias would require either that queens lay male and female eggs on different locations or workers being able to discriminate between male and female eggs. In some ant species, there is evidence that workers cannot discriminate the sex of the eggs (Nonacs and Carlin 1990; Menten et al. 2005; Iwanishi et al. 2007; Moore and Liebig 2013). However, workers do eliminate their brothers at later developmental stages (Aron et al. 1994, 1995; Keller et al. 1996; Passera and Aron 1996; Sundström et al. 1996; Helms et al. 2000), just like honey-bees do (Wharton et al. 2008). This evidence suggests that sex discrimination, due to its mechanistic underpinnings, is inherently more difficult at early developmental stages, or that males have evolved to mimic females to avoid being killed (Nonacs 1992). How early male eggs are recognized and killed directly influences the recycling efficiency with which killed male offspring can be turned into new offspring, that is, because eggs killed earlier free-up more resources for future offspring. Overall, there is plenty of evidence that workers influence the sex ratio of the colony in many advanced social insects and that male elimination is one strategy available to them to realize their influence. Notably, empirical studies on the relevance of fratricide in primitively social insects are lacking. Our model, inspired by primitively social insects, points to the relevance of studying fratricide in those taxa.

Primitively social insects have a wide variety of social and life-history structures (Schwarz et al. 2007), but we understand very little of the causes underlying that diversity. Our model predicts the evolution of three different life histories, depending on the values of two parameters (b , ρ ; Fig. 1). These life-history structures are common in taxa with primitively social insects (Schwarz et al. 2007). Therefore, using comparative methods to match the predictions of the model with data from primitively social insects might shed light on the processes shaping the diversity of life history of social insects (Kocher and Paxton 2014; Kocher

et al. 2014). A preliminary overview indicates that some of the patterns predicted by the model are present in some species. For example, the bumblebee *Bombus terrestris* shows split sex ratios despite having a monogamous mating system (Duchateau et al. 2004); thus, it is not explained by traditional models based on differential mating frequencies (Boomsma and Grafen 1990). Also, *Megalopta genalis* is a facultatively eusocial bee with a polymorphism in social behavior; solitary nests are known to produce mostly males and social ones mostly females (Kapheim et al. 2013; Smith et al. 2019); however, there is yet no evidence of fratricide in social nests. More generally, our model provides an evolutionary explanation for the existence of social polymorphism, in contrast to the common belief that such species are an intermediate stage on the path to obligate eusociality (Schwarz et al. 2007; Séguret et al. 2016). Alternatively, Rautiala (2018) discuss a scenario where split sex ratios temporarily favor the original emergence of helping behavior; they argue that during such period the evolution of morphological and behavioral changes might increase the benefits of helping. That same reasoning could apply to our evolutionary equilibrium with intermediate levels of helping behavior. If that were the case, those changes would lead to the scenario presented in Figures 1D and 2D, where all females stay and help, and sex ratios are split by genetic polymorphism.

We have assumed here that the only exchange of information between the queen and her workers is the presence or absence of the workers, and this influences the queen's sex ratio strategy. However, more elaborate schemes for the exchange of information can have an important influence on the evolutionary dynamics (Pen and Taylor 2005). The worker fratricidal strategy could potentially be dependent on the sex ratio strategy of the queen, or the other way around. Such extra channels of information exchange will probably result in less extreme biases, and thus, constrain the divergence of the sex ratios. That is because responsiveness at the behavioral timescale would diminish the benefits of certain behavioral strategies. For instance, if a queen knew that workers kill her sons, she might not produce sons at all. Such response on the side of the queen would weaken selection for higher levels of ovide, which in turns weakens selection for extreme sex ratio strategies. Less split sex ratios will lift the benefits required for helping behavior to get off the ground. Formal models are, nevertheless, necessary to assess the effect of information flow in the coevolution of the traits. Another important assumption of the model is which class of individual determines the social behavior of females. We have assumed that females determine their own helping behavior. However, maternal manipulation, when mothers influence the behavior of their offspring, has been proposed as a mechanism favoring the evolution of eusociality (Alexander 1974; González-Forero and Gavrillets 2013; González-Forero 2014). Given that foundresses are equally related to both their male and female offspring, we expect sex ratios

to play a milder role than the one depicted in the scenario we modeled. However, formal models of such interaction would require including the coevolution of manipulation and resistance to that manipulation. Furthermore, during more advanced stages of eusociality, the helping trait could also be influenced by the behavior of other workers. Larval nourishment, provided by workers, is known to partly determine the fate of female larvae.

In conclusion, we have shown that, given a life history that is prevalent among primitively social insects, the evolutionary conflict between queens and workers over sex allocation can drive the coevolution of split sex ratios and eusociality.

AUTHOR CONTRIBUTIONS

AEQ, GLBH, and IP design the model. GLBH and IP run the individual-based simulations. AEQ and GLBH derived the analytical model. AEQ, GLBH, and IP wrote the paper.

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DATA ARCHIVING

All the code necessary to replicate results from the model can be found in this repository: <https://doi.org/10.5281/zenodo.3361665>. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sn02v6x0n>.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table A1. Main model parameters and variables.

Figure A1. Ten replicate simulations of the dynamics portrait in Fig 2A.