



Maternal manipulation of offspring size can trigger the evolution of eusociality in promiscuous species

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Eusocial organisms typically live in colonies with one reproductive queen supported by thousands of sterile workers. It is widely believed that monogamous mating is a precondition for the evolution of eusociality. Here, we present a theoretical model that simulates a realistic scenario for the evolution of eusociality. In the model, mothers can evolve control over resource allocation to offspring, affecting offspring's body size. The offspring can evolve body-size-dependent dispersal, by which they disperse to breed or stay at the nest as helpers. We demonstrate that eusociality can evolve even if mothers are not strictly monogamous, provided that they can constrain their offspring's reproduction through manipulation. We also observe the evolution of social polymorphism with small individuals that help and larger individuals that disperse to breed. Our model unifies the traditional kin selection and maternal manipulation explanations for the evolution of eusociality and demonstrates that—contrary to current consensus belief—eusociality can evolve despite highly promiscuous mating.

maternal manipulation | kin selection | eusociality | evolutionary models | social insects

Reproductive altruism, where individuals forfeit their own reproduction by committing to nonreproductive helper roles, has evolved independently multiple times across animal societies (1, 2). For instance, in naked mole rats, a sole female breeds while the remaining females perform nest building and foraging (3, 4). In termites, ants, some bees, and some wasps, the queen is supported by numerous smaller workers that may not reproduce, instead partaking in foraging, nest defense, and care for young (5–7). Explaining the evolution of such eusocial breeding is a core issue of evolutionary biology, since sterile helpers do not reproduce—a behavior that should be selected against (8–10).

Natural selection favors individuals to be reproductively altruistic if the direct fitness costs of forgoing their own reproduction are outweighed by the indirect fitness benefits of reproductive altruism (11, 12). Such benefits can be gained if the reproductively altruistic individual (the worker) can enhance the success of genes shared with the beneficiary of the altruistic behavior (the queen) through behaving altruistically. Thus, high genetic relatedness between the beneficiary and the helping individual should make the evolution of reproductive altruism and eusociality more likely (9, 10). It has therefore been proposed that lifetime monogamy of the breeding female is an essential prerequisite for the evolution of eusociality, as it enables newly emerged offspring to help raise their full siblings, to whom they are highly related (13–16).

Another essential requirement for the evolution of eusociality is the presence of overlapping generations to allow offspring to care for their siblings from the subsequent generation (17, 18). The simplest form of such overlapping generations is an annual life cycle where a breeding female produces two broods per year, enabling offspring from the first brood to help raise their siblings from the second brood. This life cycle—a partially bivoltine life cycle—is found in many noneusocial species of bees and wasps that are closely related to eusocial species, and it is hypothesized to be ancestral to the evolution of eusociality (19–22).

Partial bivoltinism can facilitate the evolution of eusociality because breeding females can temporally split offspring sex ratios across broods. This favors the evolution of reproductive altruism in haplodiploid organisms (e.g. ants, bees, and wasps) if females from the first brood are primarily raising their sisters to whom they are more closely related than to their brothers (23, 24). The two distinct broods of a partially bivoltine life cycle also enable pre-existing morphological and behavioral differences between broods to be co-opted for the evolution of worker- and queen-phenotypes (20, 25, 26). Such pre-existing differences could be based on differential maternal resource allocation strategies between broods. For instance, in some bees, mothers differentially allocate food to their daughters, causing some smaller daughters to remain at the natal nest where they can be coerced into a helper role (27–30).

Significance

Eusocial insects have a fascinatingly complex social organization where typically one queen monopolizes reproduction and is supported by thousands of sterile workers. It is currently widely believed that this form of sociality evolved from an ancestor with a strictly monogamous mating system because lifetime monogamy maximizes the indirect fitness benefits that workers can gain from helping. We present evolutionary simulations to demonstrate that eusociality can evolve, even if mating is not strictly monogamous, if mothers can control the investment in their offspring, manipulating their body size and fitness prospects when they were to breed independently. This manipulation leads to body size differences between queens and workers, as commonly found across eusocial insects.

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Kin selection and maternal manipulation have often been regarded as alternative explanations for the evolution of eusociality (31–33), but they are not mutually exclusive (34–36). Here, we present an evolutionary individual-based model to unify kin selection and maternal manipulation explanations for the evolution of eusociality while also explicitly modeling phenotypic evolution of queens and workers. We model a partially bivoltine population of haplodiploid organisms (Fig. 1). Female offspring from the first brood evolve a body-size-dependent dispersal strategy to remain at the natal nest as a helper or to disperse and breed independently. The breeding female, in turn, evolves a resource allocation strategy through which she has control over offspring body size. The simulations start with solitary populations; thus, initially, offspring disperse and mothers produce offspring that all have identical body sizes. However, if mothers evolve to produce smaller offspring and if smaller offspring have low breeding success, e.g., due to insufficient energy reserves to develop their ovaries, then the coevolution of maternal resource allocation strategy and body-size-dependent offspring dispersal could lead to the

evolution of eusociality, the production of small workers, and thus to queen–worker dimorphism.

Results

Partial Bivoltinism Favors the Evolution of Eusociality, Even Under Low Levels of Polyandry. First, we simulated the model by assuming that both breeders and helpers have the same resource return functions (the “helper” function in Fig. 1*B* now applies to both breeders and helpers). We refer to this as “no reproductive constraint”, where the ability to reproduce vs. to help is not limited in small females. Mothers are capable of controlling their offspring’s size through resource allocation to offspring; for instance, mothers could evolve to produce many small offspring, few large offspring, or a mixture of small and large offspring. We vary the mating frequency from 1.0 to 2.0 to investigate the effect of polyandrous mating on the evolution of eusociality. As an example, a mating frequency of 1.3 could result from 30% of the females in the population mating with two males and 70%

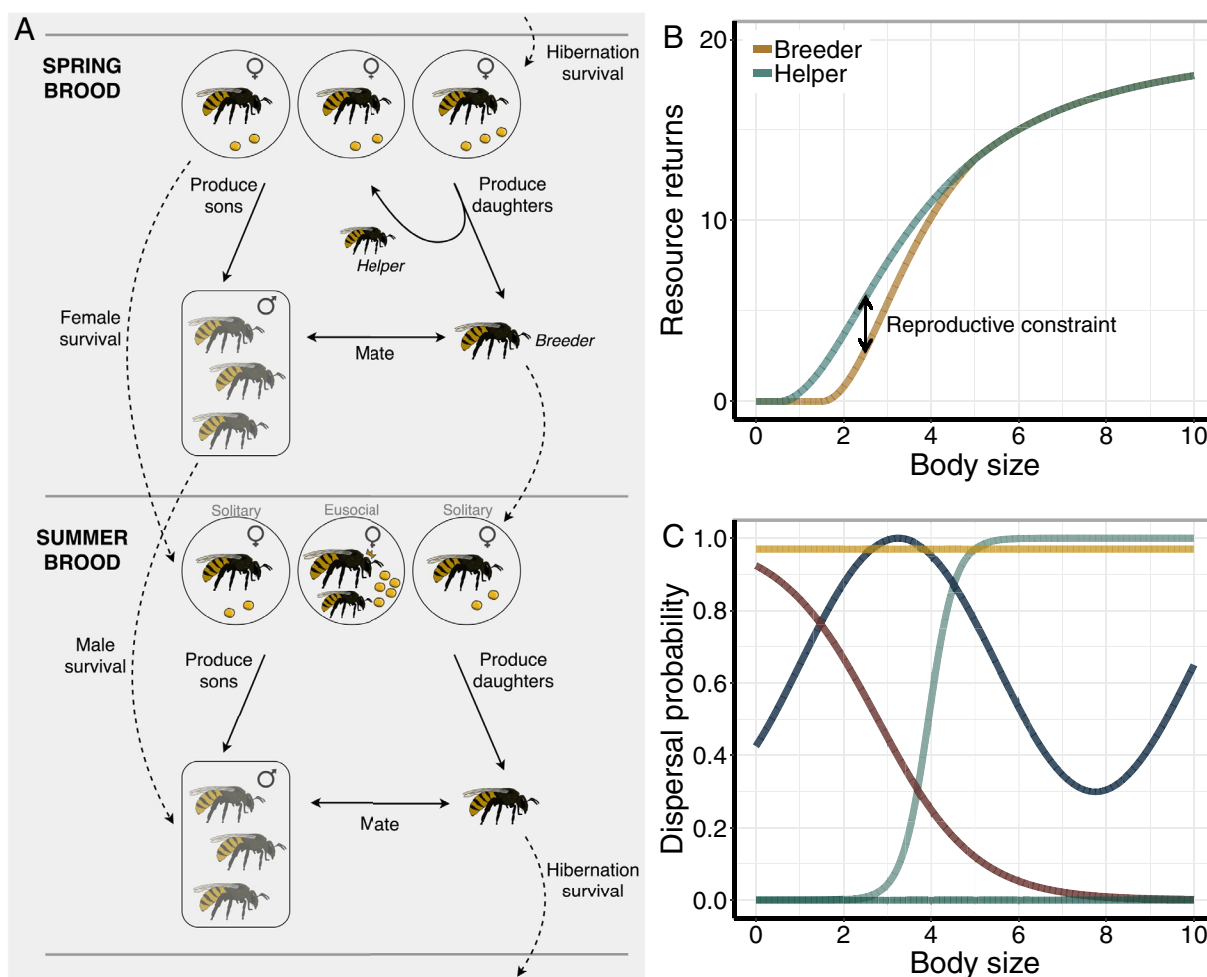


Fig. 1. Life cycle, resource return functions, and possible dispersal reaction norms in the model. (A) A partially bivoltine life cycle consists of two reproductive periods per year—the spring (Top) and summer brood (Bottom). In spring, solitary foundresses acquire resources (yellow circles) which they use to produce offspring. Female spring-brood offspring evolve a body-size-dependent dispersal probability, which determines whether they mate, disperse, and breed or remain at the natal nest as a helper. During the summer brood, nests can either be solitary, including a surviving foundress (Left summer nest) or a spring-brood female that dispersed (Right nest), or they are eusocial if the foundress has at least one helper (Middle nest). Females again acquire resources, with eusocial nests gaining resources by both the breeder and helper(s) and produce offspring. The female summer-brood offspring mate with males from the summer brood or surviving spring-brood males. All males and breeding and helping females die at the end of summer. The female summer-brood offspring hibernate to become solitary foundresses during the following spring. (B) The amount of resources gained by a female is dependent on her body size. Small individuals do not acquire any resources. At large body sizes, resource returns diminish. In some model scenarios, we assume a body-size-specific reproductive constraint, rendering small individuals more successful as helpers than they would be as breeders (see main text for explanation). (C) Examples of dispersal reaction norms, showing possible evolutionary outcomes for the relationship between dispersal probability and body size of an individual. All females are initiated with the yellow reaction norm; thus, the populations are initially preliminarily solitarily breeding (unless stated otherwise).

with one male. Assuming identical resource return functions for breeders and helpers, eusociality evolves below a mating frequency of approx. 1.3. At 1.3 mating frequency, only some nests become eusocial. At mating frequencies higher than 1.3, the populations remain solitary. Consequently, strict lifetime monandry is not a necessary requirement for the evolution of eusociality from a partially bivoltine life cycle. This is because male generational overlap in a partially bivoltine life cycle decreases the reproductive value of summer-brood males, thus enabling spring-brood females to capitalize on the relatedness asymmetries from haplodiploidy between their sisters and brothers from the summer brood (24). Maternal control of body size has no impact on the evolution of eusociality, if the resource returns for breeders and helpers are identical (Fig. 2A). Although resource returns depend on body size, fitness benefits or costs of helping are independent of body size, providing no incentive for spring-females to evolve a body-size-specific dispersal strategy. This demonstrates that maternal control of offspring body size alone is not sufficient for the evolution of eusociality through maternal manipulation.

Eusociality Evolves despite High Levels of Polyandry, If Small Females Face a Reproductive Constraint. Empirical studies on social insects hypothesized that small females might have low breeding success, leading them to forfeit reproduction and become a helper (27–30). Small females that become helpers do not need to invest in developing ovaries, which could free energetic resources to invest into foraging behaviors. This could make small females more efficient at foraging when they are a helper than as a breeder. It has also been suggested that limited energy reserves in small females might hinder ovarian development, making them less fertile or even incapable of breeding (37–41). This implies that resources foraged by small females are more

effectively used for offspring production if the small female is a helper (mother's reproduction) than if it is a breeder (own reproduction) since it is reproductively impaired. Small females could also be less likely to obtain breeding sites (42, 43), which would make a small female more likely to contribute resources to offspring production as a helper (mother's reproduction) than as a breeder (own reproduction). In line with these three scenarios, we therefore introduced a body-size-specific reproductive constraint, where small females can obtain more resources if they are a helper than if they were a breeder (Fig. 1B). In the absence of maternal control over offspring body size, eusociality only evolves under low levels of polyandry. However, if mothers are capable of controlling offspring body size, then eusociality occurs even under intermediate levels of polyandry (mating frequency of 1.4). At even higher levels of polyandry (mating frequencies of 1.5 and above), social polymorphism emerges with some spring-brood females from the same nest evolving a disperser- and some a helper-strategy. If the reproductive constraint in small females is stronger, eusociality can evolve at those higher mating frequencies, replacing social polymorphism (SI Appendix, Figs. S1–S3). This demonstrates that, with maternal control, eusociality and social polymorphism can evolve under high levels of polyandry.

Mothers Manipulate Daughters into Helping by Imposing a Reproductive Constraint on Them. In order to investigate whether mothers really manipulate their daughters into helping in our model, we ran three different scenarios of the model (all assuming a reproductive constraint for smaller females as in Fig. 2B). First, we prevented the dispersal reaction norm from evolving, causing daughters to become helpers by default ("Monandry + helping by default"). We then obtained an offspring body size distribution that results from the evolved maternal allocation

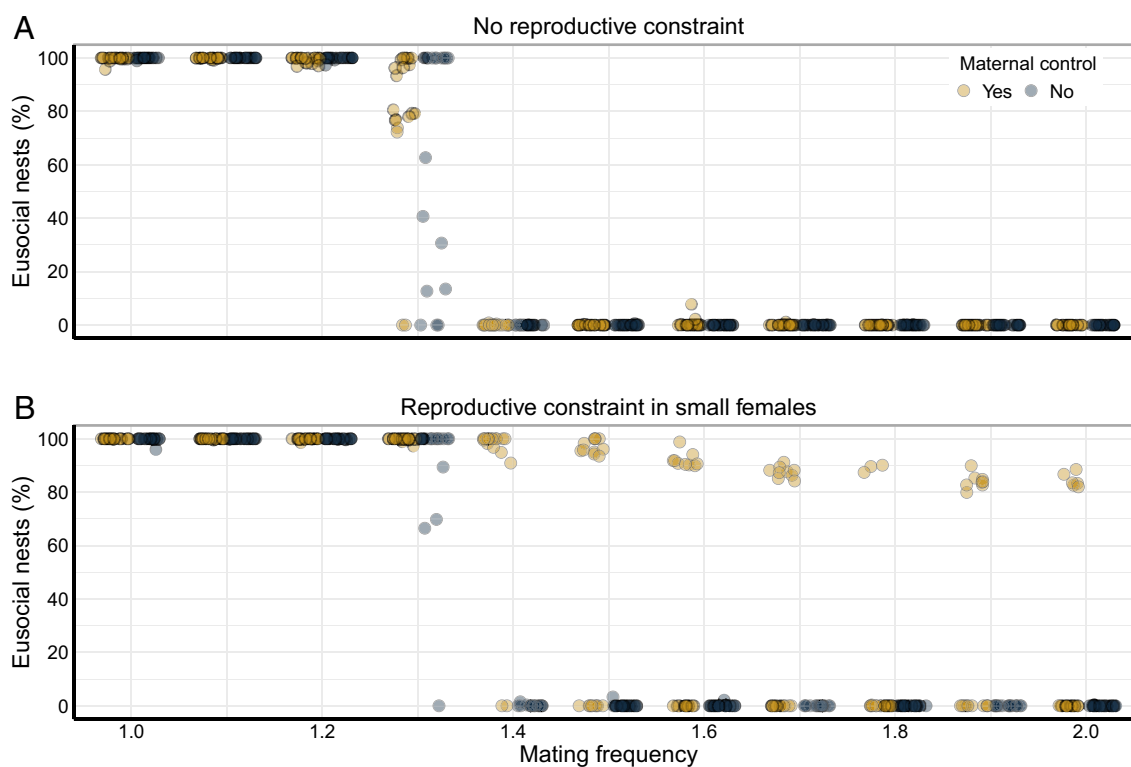


Fig. 2. The effect of maternal control over offspring body size and reproductive constraint for small females on the evolution of eusociality. (A) Percentage of eusocial nests across different mating frequencies with and without maternal control over offspring body size, assuming no body-size-specific reproductive constraint for small females. (B) The same as Fig. 2A, but now assuming a reproductive constraint for small females (Fig. 1B). Each dot represents the percentage of eusocial nests in the population at the end of a replicate simulation ($n = 20$ per parameter setting).

strategy if daughters become helpers (Fig. 3A). Second, we allowed the dispersal probability to evolve under a mating frequency of 1.0 (“Monandry + evolved helping”; Fig. 3B). The body size distributions of helpers obtained under these two scenarios do not differ from one another (mean (0.95 CI): 4.15 (4.10, 4.20) vs. 4.15 (4.10, 4.20); $p = 0.54$), demonstrating that maternal manipulation plays no role in the evolution of eusociality under monandry (though see *SI Appendix*, Figs. S4 and S5). Third, we simulated a case of polyandry (mating frequency 2.0) where eusocial nests only evolved if mothers were able to control offspring body size and small daughters were reproductively constrained (“Polyandry + evolved helping”). Helpers from these simulations were smaller than helpers from the two other scenarios (mean (0.95 CI): 2.83 (2.78, 2.89); $p = 1.00$ in comparison with both monandry scenarios), showing that mothers produce smaller offspring in order to manipulate them into helping. Under polyandry, slightly larger females evolve to disperse and breed independently (Fig. 3C), resulting in an S-shaped dispersal reaction norm that underlies the social polymorphism in Fig. 2.

Discussion

We here presented an evolutionary individual-based simulation model to unify kin selection and maternal manipulation explanations for the evolution of eusociality. Maternal control of offspring body size alone does not favor the evolution of eusociality. However,

if small females have reduced success at independent breeding, mothers evolve to produce smaller offspring. The offspring, in turn, evolve to help presumably because the inclusive fitness gains from helping outweigh the direct fitness gains from independent breeding. This is maternal manipulation, where the mothers alter the state of the daughters such that the daughters’ optimal state-dependent response is to switch from dispersing to helping. Several empirical studies on bees, ants, and wasps have demonstrated that individuals of small size and malnourished individuals adopt a worker role or a reproductively subordinate role (27–30, 37–41). Our model predicts that such behavior can evolve if small or malnourished individuals face a reproductive constraint, but this prediction still requires empirical confirmation.

It is currently widely believed that eusociality can only evolve from an ancestor with strict lifetime monogamy. Boomsma (15), for instance, states that “strict lifetime monogamy [...] appears to have been a universally necessary, although not sufficient, condition for allowing the evolution of differentiated eusocial worker castes”. The logic behind this argumentation is intuitive and compelling—strict lifetime monogamy causes relatedness between siblings to be identical to the relatedness between a mother and her offspring. Therefore, the smallest benefit of group living over solitary breeding can tip the balance toward the evolution of eusocial breeding (13–15). Furthermore, ancestral state reconstruction indicates that the eusocial hymenopterans (ants, bees, and wasps) most likely evolved from monogamous

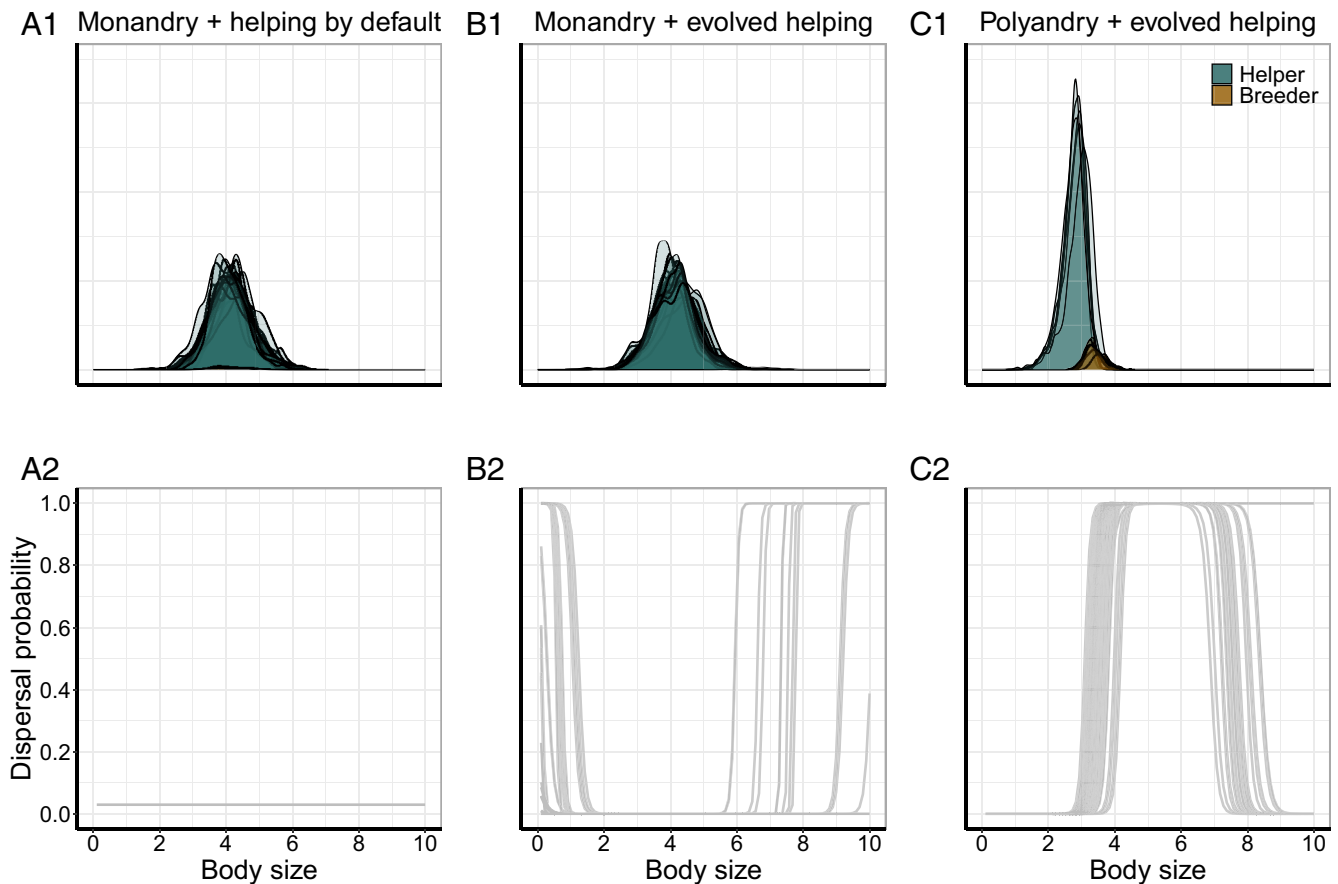


Fig. 3. Evolved body size distributions and dispersal reaction norms. (A1, B1, and C1) Body size distribution of helpers (blue) and breeders (brown). Each distribution represents the body size distribution from one replicate simulation ($n = 20$ per scenario, but see below). (A2, B2, and C2) Evolved dispersal reaction norms of 100 random females across replicate simulations, in which eusociality or social polymorphism evolved. (A1 and A2) Simulations with a mating frequency of 1.0, where dispersal probability was not allowed to evolve and thus females become helpers by default. (B1 and B2) Simulations with a mating frequency of 1.0 and with evolving dispersal reaction norms. High dispersal probabilities occur at body sizes that are rarely expressed and thus represent cryptic genetic variation. (C1 and C2) Simulations with a mating frequency of 2.0 and evolving dispersal reaction norms. Only replicates in which social polymorphism evolved are shown ($n = 6$; $n = 14$ replicates with solitary breeding; all replicates in *SI Appendix*, Fig. S14).

solitary ancestors (16), and in mammals (44) and birds (45), cooperative breeding is associated with lower levels of promiscuity than solitary breeding. However, our model demonstrates that while a monogamous mating system is beneficial for the evolution of eusociality, it is not at all a necessary condition, since eusociality evolved in our simulations even if the mating frequency was not strictly one. This happens for two reasons. First, male generation overlap in a partially bivoltine life cycle decreases the reproductive value of summer-brood males and thus enables spring-brood females to capitalize on relatedness asymmetries to their sisters vs. brothers from the summer brood due to haplodiploidy (*SI Appendix, Figs. S6 and S7*). Quiñones & Pen (24) showed that this effect is reinforced if mothers can bias sex ratios of the spring and summer brood. In a solitary partially bivoltine life cycle, male generation overlap leads to the evolution of a male-biased spring and a female-biased summer brood. Due to haplodiploidy, females from the spring brood are thus more closely related to their siblings from the summer brood than to their own offspring, leading to the evolution of helping spring-brood females (*SI Appendix, Fig. S8*). Second, in our model, breeding females evolve to impose a fitness cost for independent breeding on their offspring by producing offspring of small body sizes. The offspring consequently evolve to rather help than disperse and breed, even if mothers are multiply mated.

In our model, the mating frequency is fixed and cannot evolve. If the mating frequency was evolving, a plausible outcome would be that monandry evolves, and as a result, eusociality effectively always evolves in a monogamous population. However, the evolution of monogamy could also be counteracted by direct benefits of promiscuity (46). In any case, these considerations do not alter our main conclusion that there is no necessity for eusociality to evolve from a monogamous ancestral state.

Similar to our model, other models have also demonstrated that maternal manipulation of offspring behavior and the offspring's fitness prospects widens the conditions under which helping and eusociality can evolve (47–50). Furthermore, it has been suggested that high rates of adult mortality can render helping relatively more beneficial than independent breeding since helping contributions pay off after a shorter time than independently raising offspring to maturity (51). This results in high benefit–cost ratios of helping vs. independent breeding which could additionally alleviate the requirement of lifetime monogamy for the evolution of eusociality (52). Monogamous mating can also disfavor the evolution of helping behaviors if individuals can avoid competition with relatives by dispersing (53). Population genetic models have supported the relevance of a monogamous mating system for the evolution of eusociality (54, 55). However, it has also been proposed that polyandrous mating could favor the evolution of helping if helpers can inherit the breeder position after the breeder's death because multiple mating increases the probability that at least one daughter in a nest inherits a helping allele, even though it also lowers the probability that helpers help raise individuals that are also carriers of a helping allele (56, 57). If helpers have the opportunity to inherit the nest and become a breeder, this, however, does not satisfy the definition of eusociality that is typically adopted by the proponents of the lifetime monogamy hypothesis, who consider as a necessary condition for eusociality the irreversible commitment of sterile helpers to helping (15, 58, 59). Some of our model scenarios, contrarywise, do satisfy this more restrictive definition of eusociality because small daughters are manipulated into sterility. A sterile caste of workers—the hallmark of eusociality according to the restrictive definition (15, 58, 59)—can thus evolve due to maternal manipulation of offspring size despite promiscuous mating. Promiscuity could additionally reinforce selection for worker sterility during the transition

to eusociality by enhancing policing of worker reproduction (60–63).

Partial bivoltinism plays a key role in mechanistic explanations for the evolution of eusociality. The diapause ground plan hypothesis suggests that pre-existing morphological or behavioral differences between the two broods of a partially bivoltine life cycle could be co-opted for the evolution of worker- and queen-phenotypes (20, 25, 26). Our model combines such more mechanistic explanations with the more classic ultimate explanations for the evolution of eusociality (8) by demonstrating that phenotypic differences between broods can originate from maternal manipulation of offspring body size. Under high mating frequencies, larger well-nourished females evolve to disperse and breed whereas smaller malnourished females evolve to become helpers. This result matches the prediction of the diapause ground plan hypothesis that a nutrition-dependent developmental switch regulates the production of the worker- and queen-phenotype (20, 25, 26, 64, 65). Accordingly, many eusocial insects with irreversible castes have a nutrition-dependent caste determination system where caste is determined by food obtained during larval development (66–68).

It is usually assumed that queen-worker dimorphism is an elaboration of eusocial breeding that evolves from a dominance-based breeding system where individuals only temporarily commit to helping (26, 69). Our model demonstrates that phenotypic differences between breeders and helpers can originate from maternal manipulation and thus coincide with the origin of helping behaviors, leading to the evolution of social polymorphism. Such social polymorphism could easily be converted into fully eusocial breeding by a modulation of the partially bivoltine life cycle, which causes breeding females from the spring brood to enter diapause to breed in the next season instead of breeding in the summer. Such an early diapause strategy is indeed observed in some species of partially bivoltine halictine bees, who also exhibit body size differences between helping and breeding females (30, 70, 71). The evolution of queen–worker dimorphism might thus coincide with the evolution of helping behavior and originate from ancestral polyandry and maternal manipulation. Interestingly, in some species of bees (*Halictus rubicundus* and *Ceratina calcarata*), helping females tend to be smaller than breeding females, suggesting a role of maternal manipulation for the evolution of helping behaviors, and both species have been reported to exhibit some degree of polyandry (20% polyandrous nests in *H. rubicundus* and 9.4% in *C. calcarata*) (27, 28, 71–74).

Overall, our model presents a realistic scenario for the evolution of eusociality, where eusociality can evolve despite polyandrous mating due to maternal manipulation of offspring body size—a scenario that is realistic because evidence for manipulation, body size differences between breeders and helpers, and polyandrous mating have been found in some social bees. This challenges the current consensus beliefs that monogamous mating is a necessary prerequisite for the evolution of eusociality and that queen–worker dimorphism is a secondary elaboration of eusociality that does not originate at the evolutionary emergence of eusociality.

Methods

Model Overview. The evolutionary individual-based simulation model follows a population of haplodiploid organisms with a partially bivoltine life cycle over 1,000,000 y. Each simulation starts with N identical solitarily breeding females (parameter values in Table 1). We set N to 1,000 nests to sufficiently reduce random genetic drift, although this population size is larger than estimated effective population sizes in, for instance, halictine bees (75). Individuals have a body size X , which can vary between 0.0 and 10.0 arbitrary units.

Table 1. Parameter values used in the simulations, unless stated otherwise

| Parameter | Value | Meaning |
|-----------------------|------------|---|
| N | 1,000 | Population size |
| f | 1.0 | Foundress survival from spring to summer brood |
| m | 0.9 | Male survival from spring to summer brood |
| s | 1.0 to 2.0 | Mating frequency |
| a | 10, 6.05 | Shaping parameter for resource return function |
| b | 0.5, 1.5 | Minimum body size to gain resources |
| c | 20 | Shaping parameter for resource return function |
| μ_X | 5.0 | Average default body size |
| σ_X | 0.1 | SD default body size |
| h | 6.2 | Location of logistic baseline larval survival function |
| g | 7.7 | Steepness of logistic baseline larval survival function |
| ρ | 0.05 | Mutation rate |
| σ_{mut} | 0.06 | Mutational standard deviation |

Life Cycle. We implemented a partially bivoltine life cycle (Fig. 1A). Each season begins with N mated, solitary foundresses, who produce the spring brood. Female offspring from the spring brood disperse to mate with spring-brood males and breed during the summer or they stay at the natal nest to become a helper. Foundresses survive with probability f to breed again in the summer. We assume that death of a queen results in the death of her helpers too, but explore the effects of nest inheritance in *SI Appendix, Figs. S11 and S12*. Spring-brood males survive with probability m until the summer-brood females emerge. Other parameterizations of f and m are explored in *SI Appendix, Figs. S4–S7*. The summer brood is produced by surviving foundresses and dispersing female offspring from the spring brood. Female offspring from the summer brood mate with males from the summer brood or surviving males from the spring brood and subsequently enter hibernation to become the foundresses of the next year. All males die and do not hibernate. During hibernation, population size is re-established by randomly selecting N of the hibernating females without replacement. During the summer brood, population size can overshoot N .

Dispersal and Mating. We assume a flexible natural cubic spline function whose shape is determined by four gene values to model the probability of spring-brood females to disperse instead of becoming a helper at the natal nest as a function of their body size (examples in Fig. 1C). Natural cubic splines consist of connected cubic polynomials, which allows them to take highly flexible shapes (though both ends are linear; for details, *SI Appendix*) (68). The simulations start with high dispersal probabilities of 0.97; thus, initially, solitary breeding prevails in the population (unless stated otherwise). Females from the spring brood mate during dispersal, and females from the summer brood mate before hibernation. Females store sperm to create their offspring, and do not remate. Across simulations, we varied the mating frequency s to manipulate relatedness between siblings from the same nest. A parameter value of 1.0 implies that all females adhere to strict lifetime monandry, whereas values greater than this imply different extents of polyandry. For instance, $s = 1.5$ means that, on average, 50% of females mate once and 50% of females mate twice. The mate(s) is/are selected at random from a global pool of males.

Resource Acquisition. The amount of resources R a female can obtain depends on her body size X . We selected a function to model this relationship, where very small individuals do not obtain resources and where resource returns level off at large body size. We use the function

$$R(X) = \frac{c(X-b)^2}{a + (X-b)^2}, \quad [1]$$

where a and c are shaping parameters and b represents the minimum body size required to gain resources (we set $R(X) = 0$ when $x < b$). In solitary nests, the total resources available are equal to that foraged by the sole female. In eusocial nests, the total resource amount is the sum of the resources obtained

by the breeder and those obtained by the helper(s) (but *SI Appendix, Figs. S9 and S10* for diminishing foraging success with increasing local foraging effort). We focused on two main parameterization scenarios of Eq. 1: 1) No reproductive constraint for small females—the function is identical for all females, independently of whether they are breeders or helpers ($a = 10$, $b = 0.5$; “helper” function in Fig. 1B); 2) A body-size-specific reproductive constraint for small females—for body sizes of 5.0 and above, all females have the same resource returns for the same body size, but below 5.0, helpers are more efficient in resource acquisition than breeders [function as in (1) for helpers, and breeders with a body size above 5.0, but for breeders smaller than 5.0, $a = 6.05$, $b = 1.5$; “breeder” function in Fig. 1B]. Other parameterizations of (2) are explored in *SI Appendix, Figs. S1–S3*.

Sex Allocation and Reproduction. Females carry one gene for spring-brood and one gene for summer-brood sex allocation. These genes are associated with numbers that are logistically transformed to determine the proportion of resources invested into males. In the main manuscript, we did not allow resource allocation to the different sexes to evolve and instead fixed it at 50:50 resource allocation to males vs. females. Results with evolving sex allocation are included in *SI Appendix, Fig. S8*. Females produce offspring of both sexes until they run out of resources. We assume that resources invested in offspring translate linearly to offspring body size. We assume some variation in offspring body size which is determined by sampling a normal distribution with mean μ_X and SD σ_X . If a female has insufficient resources to create a final offspring, we stochastically decide whether this offspring is still produced by performing a weighted coin flip with a probability given by dividing the remaining resources by the body size of the offspring that is potentially produced. The default body size applies to male offspring from the spring and summer broods, and to female offspring from the summer brood, and is independent of the body size of the mother and the helpers in the nest. All offspring have a body-size-dependent survival probability that determines whether they develop from a larva into an adult. The survival probability increases with the amount of resources that a larva obtained and is given by

$$l = \frac{1}{1 + e^{(h-gX)}}, \quad [2]$$

where h and g are parameters that affect the function's steepness and location.

Maternal Control of Daughter Body Size. We allow breeding females to have control over resource allocation to female offspring in the spring brood. Females can evolve strategies where their spring broods consist of many small or few large daughters, or where they produce daughters of different sizes. We model this relationship with a flexible natural cubic spline function, whose shape is determined by four gene values (details in *SI Appendix*). This function determines the body size on the y-axis of the x -th daughter produced by the breeding female. Again, females produce offspring until they run out of resources, and again, it is

stochastically decided whether the final daughter, for which insufficient resources exist, is created.

Genetics and Mutation. We assume haplodiploid sex determination; thus, females are diploid and males are haploid. Females carry two sets of 10 genes in total (four genes determine the shape of the dispersal reaction norm, four genes determine the shape of the maternal control reaction norm, and one gene each determines spring- and summer-brood sex allocation). Mutations occur by the per-locus mutation rate p at each meiotic event. If a mutation occurs, the gene value is altered by a value sampled from a normal distribution with mean 0 and SD σ_{mut} . Females inherit a haploid set of genes from one father (selected at random from the sperm stored in the mother in the case of multiple matings), whereas genes inherited from the diploid mother can recombine freely. Genes are expressed in females; males only function as gene carriers. Females randomly express either the maternal or paternal gene copy on a per-gene basis.

Model Analysis. The model was constructed in C++ and compiled with g++ 12.3.0. We used the Augmented Dickey–Fuller test from the R-package *tseries* v0.10-53 (76) to determine whether simulations had reached an evolutionary equilibrium by running the test on the time series of the proportion of eusocial nests in the population. We accepted the assumption of stationarity for p -values

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smaller than 0.05. We excluded and reran replicate simulations that were not stationary after 1,000,000 y. We report a nest as being “eusocial” when it had at least one helper in the summer brood, whereas we refer to nests without helpers in the summer brood as being “solitary”. All data analysis and plotting were conducted in R v4.2.1 (77) using the R-packages *tidyverse* v2.0.0 (78), *cowplot* v1.1.1 (79), *stringr* v1.5.0 (80), and *MetBrewer* v.0.2.0 (81). For Fig. 3, we derived probabilities of direction (pd), which represents the posterior probability that an effect occurs in a particular direction, from Bayesian models implemented with the *brms* v2.20.4 (82–84) package in combination with the MCMC sampler of *cmdstanr* (85) and posterior means with the *emmeans* v1.8.8 (86) package (details in *SI Appendix*).

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*. Simulation code and data analysis scripts are available under <https://doi.org/10.34894/OBFUVJ> (87).

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