

Maternal manipulation facilitates the evolution of eusociality despite promiscuity

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Eusocial organisms live in colonies with one reproductive queen that is supported by thousands of sterile workers. Yet, the evolution of this complex sociality is still poorly understood. 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 and thereby affect their offspring's body size. The offspring, in turn, can evolve a body size-dependent dispersal strategy in response to the manipulation. We demonstrate that eusociality can evolve readily in this scenario if small females have low success at independent breeding. Furthermore, we observe the evolution of social polymorphisms, where some individuals become helpers and some disperse to breed independently. Our model unifies kin selection and maternal manipulation explanations for the evolution of eusociality and presents a realistic scenario in which – contrary to current consensus belief – eusociality can evolve despite promiscuous mating.

Introduction

Reproductive altruism, where individuals forfeit their own reproduction by committing to non-reproductive helper roles, has evolved independently multiple times across animal societies^{1,2}. For instance, in naked mole rats, a sole female breeds whilst the remaining females perform nest building and foraging^{3,4}. In termites, ants and some bees and wasps, the queen is supported by numerous smaller workers that may not reproduce, instead partaking in foraging, nest

defence, and care for young⁵⁻⁷. Explaining the evolution of such eusocial breeding is a core issue of evolutionary biology, since sterile helpers do not reproduce – a behaviour that should be selected against⁸⁻¹⁰.

Natural selection favours individuals to be reproductively altruistic if the fitness costs of forgoing their own reproduction are outweighed by the 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 behaviour (the queen) through behaving altruistically. Thus, high genetic relatedness between the beneficiary of the altruistic behaviour 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 related¹³⁻¹⁶. 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 non-eusocial species of bees and wasps that are closely related to eusocial species, and it is hypothesised to be ancestral to the evolution of eusociality¹⁹⁻²². Indeed, partial bivoltinism can facilitate the evolution of eusociality because breeding females can temporally split offspring sex ratios across broods. This favours 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 behavioural 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 daughters to remain at the natal nest being coerced into helping²⁷⁻³⁰.

Kin selection and maternal manipulation have often been regarded as alternative explanations for the evolution of eusociality³¹⁻³³, but they are not mutually exclusive³⁴⁻³⁶. We developed an evolutionary individual-based model to unify kin selection and maternal manipulation explanations for the evolution of eusociality whilst also explicitly modelling phenotypic evolution of queens and workers. We model a partially bivoltine population of haplodiploid

organisms (Fig. 1). 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 to offspring through which she has control over offspring body size. The simulations start with solitary populations; thus, initially all 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 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 and to the production of small workers, and thus to queen-worker dimorphism.

Results

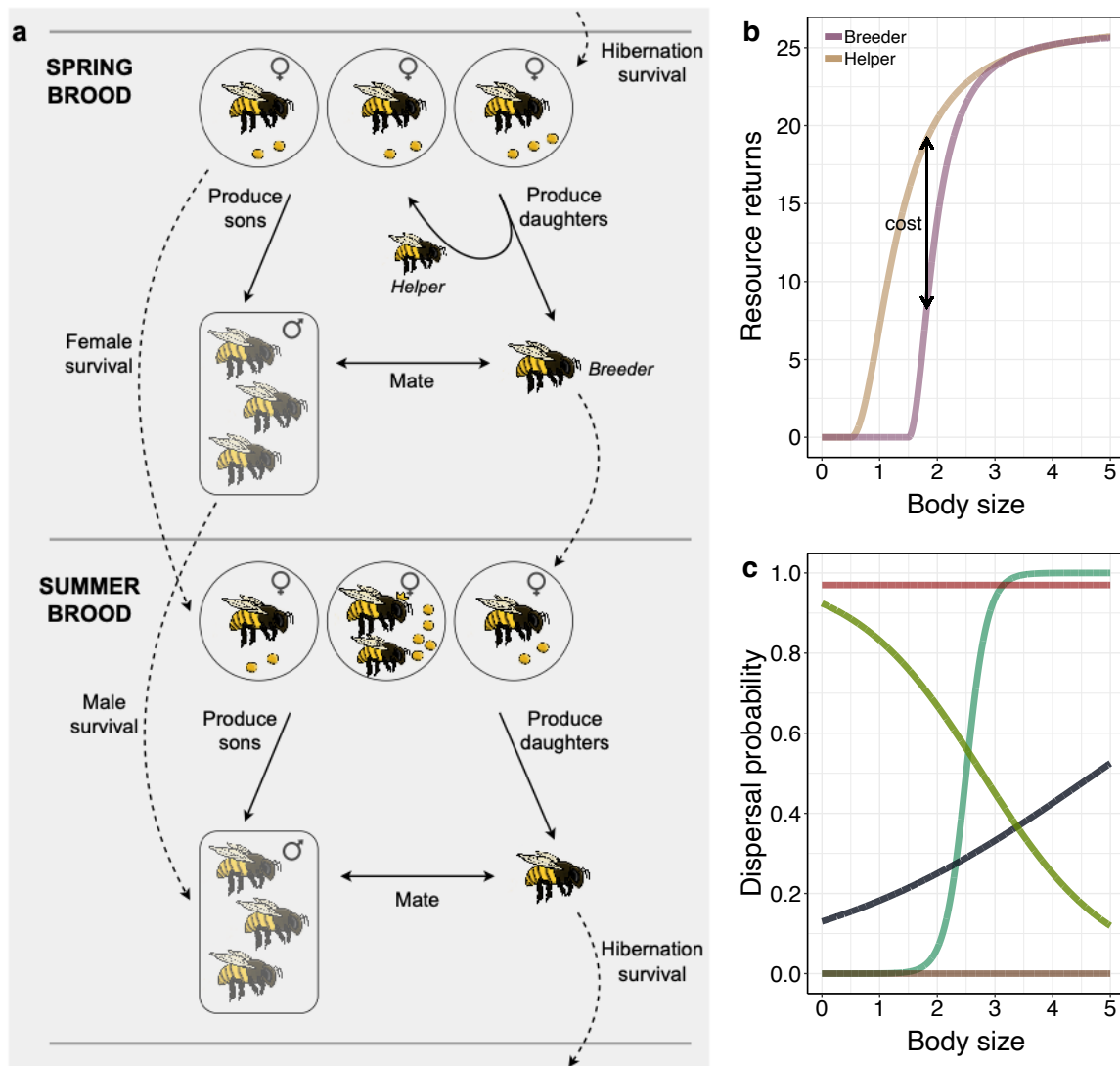


Fig. 1 | Life cycle, resource return functions and dispersal reaction norms in the model. a A partially bivoltine life cycle consists of two reproductive periods per year – the spring (top)

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 or a spring-brood female that dispersed, or they are eusocial if the foundress has at least one helper. Females again acquire resources, with eusocial nests gaining resources by both the breeder and helper(s), and produce offspring. The female summer-brood offspring mates 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 cost of independent breeding, rendering small individuals more successful as helpers than they were as breeders. **c** Examples of dispersal reaction norms, showing possible relationships between dispersal probability and body size of an individual. All females are initiated with the red reaction norm; thus, the populations are initially preliminarily solitarily breeding (unless stated otherwise).

Partial bivoltinism favours the evolution of eusociality, even under low levels of polyandry. As a baseline, we simulated the model by assuming that both breeders and helpers have the same resource return functions (the ‘helper’ function in Fig. 1b now applies to both breeders and helpers). Under these conditions, eusociality evolves below a mating frequency of 1.2. At 1.2 mating frequency, only some nests become eusocial. At mating frequencies higher than 1.2, the populations remain solitary. Consequently, even in this most basic scenario, strict lifetime monandry is not a necessary requirement for the evolution of eusociality. 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 capitalise on the relatedness asymmetries from haplodiploidy between their sisters and brothers from the summer brood²⁴. 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, benefit-cost ratios 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 are subfertile.

Empirical studies on social insects hypothesised that small females might have low breeding success, leading them to forfeit reproduction and become a helper²⁷⁻³⁰. Limited energy reserves in small females might, for instance, hinder their ovarian development, making them subfertile or even incapable of breeding³⁷⁻⁴¹, or make them less likely to obtain breeding sites^{42,43}. We therefore introduced a body size-specific cost of independent breeding, causing smaller females to gain more resources as helper than they would as breeders (Fig. 1b). In the absence of maternal control over offspring body size, eusociality still only evolves under low levels of polyandry. However, if mothers are capable of controlling offspring body size, then eusociality occurs even under high levels of polyandry (mating frequency of 1.5). At even higher levels of polyandry (mating frequency of 2.0), social polymorphisms emerge with some spring-brood females evolving a disperser- and some a helper-strategy. This demonstrates that eusociality and social polymorphisms can evolve under high levels of polyandry.

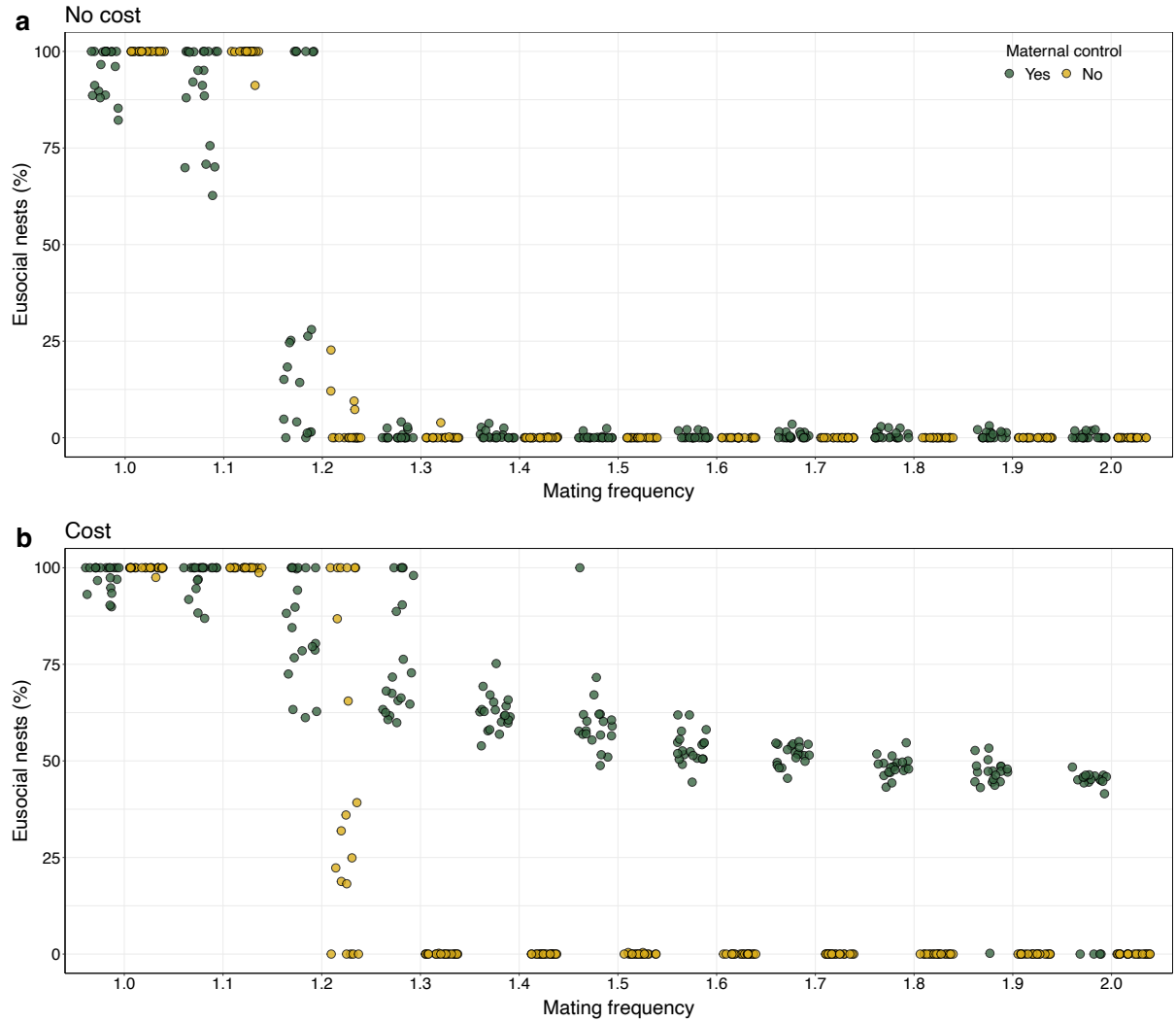


Fig. 2 | The effect of maternal control over offspring body size and cost of independent breeding for small females on the evolution of eusociality. a Percentage of eusocial nests across different mating frequencies with and without maternal control over offspring body size, assuming no body size-specific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

Mothers evolve to produce subfertile daughters in order to manipulate them into helping.

In order to investigate whether mothers really manipulate their daughters into helping, we ran three different scenarios of the model. First, we prevented the dispersal reaction norms from evolving, causing daughters to become helpers by default (“Monandry with fixed helping”). We then obtained an offspring body size distribution that results from the evolved maternal allocation strategy if daughters become helpers (Fig. 3a). Second, we allowed the dispersal

probability to evolve under a mating frequency of 1.0 (“Monandry”; Fig. 3b). The body size distributions obtained under these two scenarios do not differ from one another (*stats*). Third, we simulated a case of polyandry where eusocial nests only evolved if mothers were able to control offspring body size and small daughters were subfertile (“Polyandry”). Helpers from these simulations were smaller than helpers from the two other scenarios (*stats*) showing that mothers produce smaller offspring in order to manipulate them into helping. Under polyandry, slightly larger females evolved to disperse and breed independently (Fig. 3c), resulting in a S-shaped dispersal reaction norm that underlies the social polymorphisms evolved in Fig. 2.

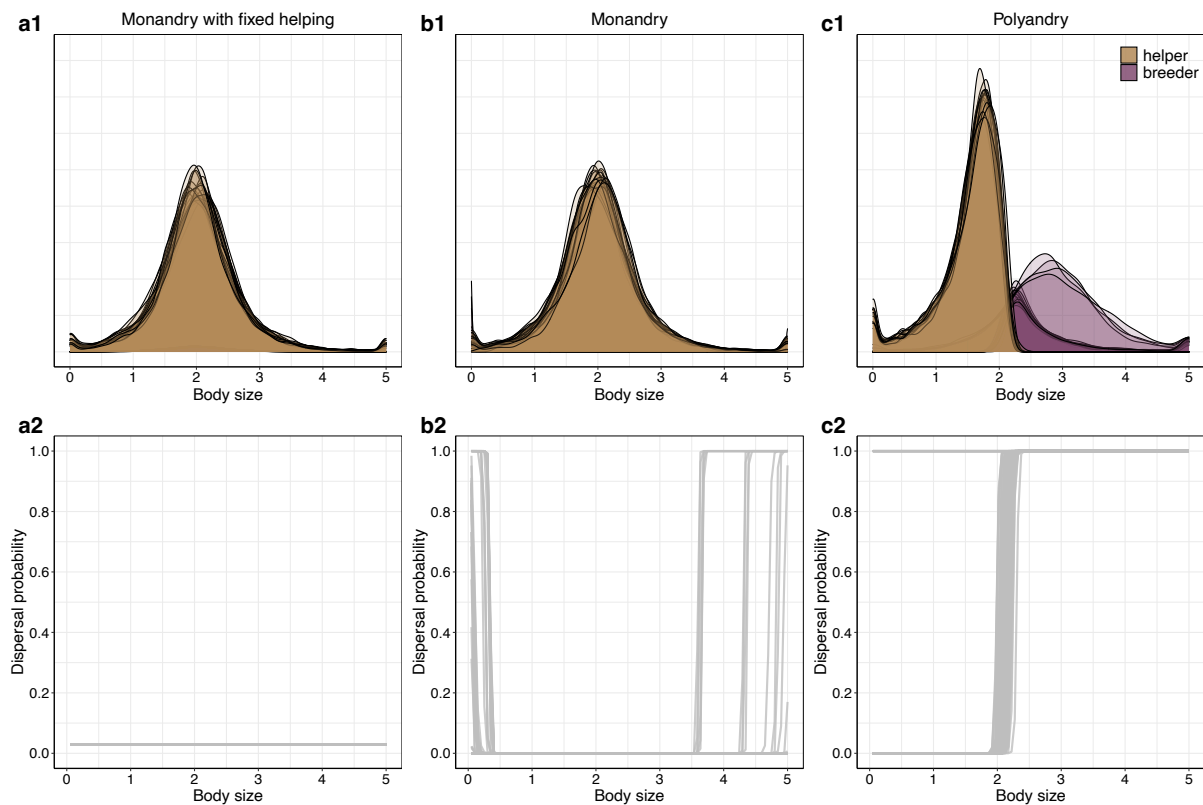


Fig. 3 | Evolved body size distributions and dispersal reaction norms for three model scenarios. a1, b1, c1 Body size distribution of helpers (brown) and breeders (purple). Each distribution represents the body size distribution from one replicate simulation ($n = 20$ per scenario). **a2, b2, c2** Evolved dispersal reaction norms of 100 random females across replicate simulations. **a1, 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, b2** Simulations with a mating frequency of 1.0 and with evolving dispersal reaction norms. Note that the high dispersal probabilities for small and large body sizes originate from cryptic genetic variation that accumulated because this section of the reaction norm is only rarely expressed. **c1, c2** Simulations with a mating frequency of 2.0 and evolving dispersal reaction norms.

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 favour the evolution of eusociality. However, in the realistic scenario^{27–30,37–43}, where small females have reduced success at independent breeding, mothers evolve to produce smaller offspring that is manipulated into helping. The offspring, in turn, evolves to help since its fitness gains from independent breeding are outweighed by those of helping. Equivalently, other models also demonstrated that maternal manipulation of offspring behaviour and its fitness prospects widens the conditions under which helping and eusociality can evolve^{44–47}.

It is currently widely believed that eusociality can only evolve from an ancestor with strict lifetime monogamy. Boomsma¹⁵, 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 towards 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 solitary ancestors¹⁶, and in mammals⁴⁸ and birds⁴⁹, cooperatively 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 capitalise on relatedness asymmetries to their sisters vs. brothers from the summer brood due to haplodiploidy. Quiñones & Pen²⁴ 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. 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.

Partial bivoltinism also plays a key role in more mechanistic explanations for the evolution of eusociality. The diapause ground plan hypothesis suggests that pre-existing morphological or behavioural 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 eusociality⁸ by showing that phenotypic differences between broods can originate from maternal manipulation of offspring body size. These size differences are most extreme under high mating frequencies when populations evolve social polymorphisms. Large well-nourished females evolve to disperse and breed whereas small 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^{20,25,26,50,51}. Furthermore, many eusocial insects with irreversible castes have a nutrition-dependent caste determination system where caste is determined by food obtained during larval development^{52,53}. 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^{26,54}. Our model demonstrates that large phenotypic differences between breeders and helpers can originate from maternal manipulation and thus coincide with the origin of helping behaviours, leading to the evolution of social polymorphisms. These social polymorphisms could easily be converted into 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^{30,55,56}, as predicted by our model. The evolution of queen-worker dimorphism might thus coincide with the evolution of helping behaviour and originate from ancestral polyandry and maternal manipulation.

Social polymorphisms, where some individuals breed solitarily and some breed socially, are widespread among bees and wasps^{21,25}. Our model shows a broad range of conditions under which such social polymorphisms evolve. Under polyandrous mating, mothers evolve to produce offspring of small body size, which is coerced into helping at the natal nest. In some socially polymorphic 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 behaviours, and both species have been reported to exhibit some degree of polyandry^{27,28,56–59}.

Overall, our model demonstrates that maternal manipulation can lead to the evolution of eusociality despite polyandrous mating. Queen-worker dimorphisms might originate at the emergence of helping behaviours from maternal manipulation instead of being an elaboration of eusocial breeding. Lastly, our model seems realistic in that it qualitatively explains body size differences between breeders and helpers across a range of bee species, as well as the occurrence of eusocial breeding and social polymorphisms.

Methods

Model overview

The evolutionary individual-based simulation model follows a population of haplodiploid organisms with a partially bivoltine life cycle over 2,000,000 years. Each simulation starts with N identical solitarily breeding females ($N = 1,000$). Individuals have a body size x , which can vary between 0.0 and 5.0 arbitrary units.

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 ($f = 1.0$). Spring males survive with probability m to mate with newly emerged female offspring from the summer brood ($m = 0.9$). 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 and surviving males from the spring brood, and subsequently enter hibernation to become the foundresses of the next year. All males die and thus do not hibernate. During hibernation, population size is re-established by randomly selecting N of the hibernating females. During the summer brood, population size can overshoot N .

Dispersal and mating

We assume a highly flexible natural cubic spline function whose shape is determined by 8 gene values to model the propensity 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; details in

supplementary materials). We logistically transform this dispersal propensity to a dispersal probability. 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 the sperm to create all future offspring, and thus do not remate. Across simulations, we varied the mating frequency s to manipulate relatedness between first- and second-brood offspring. A parameter value of 1.0 implies 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 inspected several different functions that satisfy these requirements (Fig. S1). In the main manuscript, we use the function

$$R = \frac{a(x-d)^2}{b+c(x-d)^2} \quad (1)$$

where a , b , and c are shaping parameters and d represents the minimum body size required to gain resource returns (we set $R = 0$ when $x < d$). In solitary nests, the total resources available are equal to that foraged by the sole female. In social nests, the total resource amount is the sum of the resources obtained by the breeder and those obtained by the helper(s). We focussed on two main parameterisation scenarios of eq. 1: (1) The function is identical for all females, independently of whether they are breeders or helpers ($a = 98.3$, $b = 2.5$, $c = 3.7$, $d = 0.5$; ‘helper’ function in Fig. 1b); (2) For body sizes of 3.0 and above, all females have approximately the same resource returns for the same body size, but below 3.0, helpers are more efficient in resource acquisition than breeders (function unchanged for helpers, but for breeders $a = 96.5$, $b = 0.8$, $c = 3.7$, $d = 1.5$; ‘breeder’ function in Fig. 1b). Further parameterisations of eq. 1 are explored in the supplementary materials (Fig. S1).

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 sex allocation to

evolve and instead fixed it at 50:50 resource allocation to males vs. females. Results with evolving sex ratios recover the results obtained by Quiñones & Pen²⁴ and are included in the supplementary materials (Fig. S2). 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 (mean = 3.0, SD = 0.1). If a female has insufficient resources to create a final offspring, we stochastically decide whether this offspring is still produced by flipping a coin with probability r/x , where r are the remaining resources and x is the body size of the offspring that is potentially produced. The default body size (mean = 3.0, SD = 0.1) applies to male offspring from both the spring and summer broods, and to female offspring produced in the summer brood.

Maternal control of daughter body size

To explore the effect of maternal control over resource allocation to offspring, we allow breeding females to have control over resource allocation to a female offspring in the spring brood. Consequently, females can evolve strategies where their spring broods consist of many small or few large daughters. We model this relationship with a highly flexible natural cubic spline function, whose shape is determined by 8 gene values (details in supplementary materials). 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 18 homologous genes in total (8 genes determining the shape of the dispersal reaction norm, 8 genes determining the shape of the maternal control function, and 1 gene each for the spring- and summer-brood sex allocation). When new females emerge, mutations occur by the per-locus mutation rate p ($p = 0.06$). If a mutation occurs, the gene value is altered by a value sampled from a normal distribution (mean = 0.0, SD = 0.12). Recombination can occur during gene transmission to offspring. Genes are only expressed in females, and males only function as gene carriers. Females randomly express either the maternal or paternal copy of each gene.

Model analysis

The model was constructed in C++ and compiled with g++ 11.3.0. We used the Augmented Dickey-Fuller test to determine if simulations had reached an evolutionary equilibrium by running the test on the time series of the proportion of eusocial nests in the population (details in supplementary material). We accepted the assumption of stationarity for p-values less than 0.05. Subsequently, we ran all simulations for 2,000,000 years since this was sufficient time for the simulations to reach an equilibrium. 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 was conducted in R v4.2.1⁶⁰ using the R-packages *ggplot2* v3.4.0⁶¹, *ggpubr* v0.5.0⁶², *stringr* v1.5.0⁶³, *dplyr* v1.1.0⁶⁴, and *tseries* v0.10-53⁶⁵.

Data availability

All data generated during this study is available under ??

Code availability

Simulation code and data analysis scripts are available under ??

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Author Contributions Statement

Conceptualisation: ERB, IP, JJK; Implementation: ERB, IP, JJK; Model analysis: ERB; Writing: ERB, IP, JJK.

Competing Interests Statement

The authors declare no competing interests.

Literature

1. Rubenstein, D. R. & Abbot, P. *Comparative Social Evolution*. (Cambridge University Press, 2017).

2. Taborsky, M., Cant, M. A. & Komdeur, J. *The evolution of social behaviour*. (Cambridge University Press, 2021).
3. Jarvis, J. U. M. Eusociality in a Mammal: Cooperative Breeding in Naked Mole-Rat Colonies. *Science* **212**, 571–573 (1981).
4. O’Riain, M. J. & Faulkes, C. G. African mole-rats: eusociality, relatedness and ecological constraints. in *Ecology of social evolution* 207–223 (Springer, 2008).
5. Hölldobler, B. & Wilson, E. O. *The Ants*. (Harvard University Press, 1990).
6. Oster, G. F. & Wilson, E. O. Caste and ecology in the social insects. *Monogr. Popul. Biol.* **12**, 1–352 (1978).
7. Thorne, B. L. Evolution of eusociality in termites. *Annu. Rev. Ecol. Syst.* **28**, 27–54 (1997).
8. Kreider, J. & Pen, I. The evolution of eusociality: Kin selection theory, division of labour models, and evo-devo explanations. Preprint at <https://doi.org/10.32942/osf.io/c9p2e> (2022).
9. West, S. A., Griffin, A. S. & Gardner, A. Evolutionary Explanations for Cooperation. *Curr. Biol.* **17**, R661–R672 (2007).
10. West, S. A. & Gardner, A. Altruism, Spite, and Greenbeards. *Science* **327**, 1341–1344 (2010).
11. Hamilton, W. D. The genetical evolution of social behaviour I. *J. Theor. Biol.* **7**, 1–16 (1964).
12. Hamilton, W. D. The genetical evolution of social behaviour II. *J. Theor. Biol.* **7**, 17–52 (1964).
13. Boomsma, J. J. Kin Selection versus Sexual Selection: Why the Ends Do Not Meet. *Curr. Biol.* **17**, R673–R683 (2007).
14. Boomsma, J. J. Lifetime monogamy and the evolution of eusociality. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 3191–3207 (2009).
15. Boomsma, J. J. Beyond promiscuity: mate-choice commitments in social breeding. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 20120050 (2013).
16. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral Monogamy Shows Kin Selection Is Key to the Evolution of Eusociality. *Science* **320**, 1213–1216 (2008).
17. Michener, C. D. Comparative Social Behavior of Bees. *Annu. Rev. Entomol.* **14**, 299–342 (1969).
18. Wilson, E. O. *The insect societies*. (Belknap Press of Harvard University Press, 1971).

19. Field, J., Paxton, R. J., Soro, A. & Bridge, C. Cryptic Plasticity Underlies a Major Evolutionary Transition. *Curr. Biol.* **20**, 2028–2031 (2010).
20. Hunt, J. H. & Amdam, G. V. Bivoltinism as an Antecedent to Eusociality in the Paper Wasp Genus *Polistes*. *Science* **308**, 264–267 (2005).
21. Schwarz, M. P., Richards, M. H. & Danforth, B. N. Changing Paradigms in Insect Social Evolution: Insights from Halictine and Allodapine Bees. *Annu. Rev. Entomol.* **52**, 127–150 (2007).
22. Seger, J. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* **301**, (1983).
23. Quiñones, A. E., Henriques, G. J. B. & Pen, I. Queen–worker conflict can drive the evolution of social polymorphism and split sex ratios in facultatively eusocial life cycles. *Evolution* **74**, 15–28 (2019).
24. Quiñones, A. E. & Pen, I. A unified model of Hymenopteran preadaptations that trigger the evolutionary transition to eusociality. *Nat. Commun.* **8**, 15920 (2017).
25. Hunt, J. H. *The Evolution of Social Wasps*. (Oxford University Press, 2007).
26. Hunt, J. H. A conceptual model for the origin of worker behaviour and adaptation of eusociality. *J. Evol. Biol.* **25**, 1–19 (2012).
27. Lawson, S. P., Ciccio, K. N. & Rehan, S. M. Maternal manipulation of pollen provisions affects worker production in a small carpenter bee. *Behav. Ecol. Sociobiol.* **70**, 1891–1900 (2016).
28. Lawson, S. P., Helmreich, S. L. & Rehan, S. M. Effects of nutritional deprivation on development and behavior in the subsocial bee *Ceratina calcarata* (Hymenoptera: Xylocopinae). *J. Exp. Biol.* **220**, 4456–4462 (2017).
29. Kapheim, K. M., Bernal, S. P., Smith, A. R., Nonacs, P. & Weislo, W. T. Support for maternal manipulation of developmental nutrition in a facultatively eusocial bee, *Megalopta genalis* (Halictidae). *Behav. Ecol. Sociobiol.* **65**, 1179–1190 (2011).
30. Brand, N. & Chapuisat, M. Born to be bee, fed to be worker? The caste system of a primitively eusocial insect. *Front. Zool.* **9**, 35 (2012).
31. Alexander, R. D. The Evolution of Social Behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383 (1974).
32. West-Eberhard, M. J. The Evolution of Social Behavior by Kin Selection. *Q. Rev. Biol.* **50**, 1–33 (1975).
33. Michener, C. D. & Brothers, D. J. Were workers of eusocial Hymenoptera initially altruistic or oppressed? *Proc. Natl. Acad. Sci.* **71**, 671–674 (1974).

34. Linksvayer, T. A. & Wade, M. J. The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: maternal effects, sib-social effects, and heterochrony. *Q. Rev. Biol.* **80**, 317–336 (2005).
35. Charnov, E. L. Evolution of eusocial behavior: Offspring choice or parental parasitism? *J. Theor. Biol.* **75**, 451–465 (1978).
36. Craig, R. Parental manipulation, kin selection, and the evolution of altruism. *Evolution* **33**, 319–334 (1979).
37. Molina, Y. & O'Donnell, S. A developmental test of the dominance-nutrition hypothesis: linking adult feeding, aggression, and reproductive potential in the paperwasp *Mischocyttarus mastigophorus*. *Ethol. Ecol. Evol.* **20**, 125–139 (2008).
38. Fiocca, K. *et al.* Reproductive physiology corresponds to adult nutrition and task performance in a Neotropical paper wasp: a test of dominance-nutrition hypothesis predictions. *Behav. Ecol. Sociobiol.* **74**, 114 (2020).
39. O'Donnell, S. *et al.* Adult nutrition and reproductive physiology: a stable isotope analysis in a eusocial paper wasp (*Mischocyttarus mastigophorus*, Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **72**, 86 (2018).
40. Krishnan, J. U., Brahma, A., Chavan, S. K. & Gadagkar, R. Nutrition induced direct fitness for workers in a primitively eusocial wasp. *Insectes Sociaux* **68**, 319–325 (2021).
41. Bernadou, A. *et al.* Stress and early experience underlie dominance status and division of labour in a clonal insect. *Proc. R. Soc. B Biol. Sci.* **285**, 20181468 (2018).
42. Ostwald, M. M., Fox, T. P., Harrison, J. F. & Fewell, J. H. Social consequences of energetically costly nest construction in a facultatively social bee. *Proc. R. Soc. B Biol. Sci.* **288**, 20210033 (2021).
43. Weissel, N., Mitesser, O., Poethke, H.-J. & Strohm, E. Availability and depletion of fat reserves in halictid foundress queens with a focus on solitary nest founding. *Insectes Sociaux* **59**, 67–74 (2012).
44. Crespi, B. J. & Ragsdale, J. E. A skew model for the evolution of sociality via manipulation: why it is better to be feared than loved. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 821–828 (2000).
45. Kapheim, K. M., Nonacs, P., Smith, A. R., Wayne, R. K. & Weislo, W. T. Kinship, parental manipulation and evolutionary origins of eusociality. *Proc. R. Soc. B Biol. Sci.* **282**, 20142886 (2015).
46. González-Forero, M. Stable eusociality via maternal manipulation when resistance is costless. *J. Evol. Biol.* **28**, 2208–2223 (2015).

47. González-Forero, M. & Peña, J. Eusociality through conflict dissolution. *Proc. R. Soc. B Biol. Sci.* **288**, 20210386 (2021).
48. Lukas, D. & Clutton-Brock, T. Cooperative breeding and monogamy in mammalian societies. *Proc. R. Soc. B Biol. Sci.* **279**, 2151–2156 (2012).
49. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972 (2010).
50. Hunt, J. H. *et al.* A diapause pathway underlies the gyne phenotype in *Polistes* wasps, revealing an evolutionary route to caste-containing insect societies. *Proc. Natl. Acad. Sci.* **104**, 14020–14025 (2007).
51. Hunt, J. H., Buck, N. A. & Wheeler, D. E. Storage proteins in vespid wasps: characterization, developmental pattern, and occurrence in adults. *J. Insect Physiol.* **49**, 785–794 (2003).
52. Schwander, T., Lo, N., Beekman, M., Oldroyd, B. P. & Keller, L. Nature versus nurture in social insect caste differentiation. *Trends Ecol. Evol.* **25**, 275–282 (2010).
53. Buttstedt, A., Ihling, C. H., Pietzsch, M. & Moritz, R. F. A. Royalactin is not a royal making of a queen. *Nature* **537**, E10–E12 (2016).
54. Rehan, S. M. & Toth, A. L. Climbing the social ladder: the molecular evolution of sociality. *Trends Ecol. Evol.* **30**, 426–433 (2015).
55. Yanega, D. Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl. Acad. Sci.* **85**, 4374–4377 (1988).
56. Yanega, D. Caste determination and differential diapause within the first brood of *Halictus rubicundus* in New York (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **24**, 97–107 (1989).
57. Shell, W. A. & Rehan, S. M. The price of insurance: costs and benefits of worker production in a facultatively social bee. *Behav. Ecol.* **29**, 204–211 (2018).
58. Field, J., Paxton, R., Soro, A., Craze, P. & Bridge, C. Body size, demography and foraging in a socially plastic sweat bee: a common garden experiment. *Behav. Ecol. Sociobiol.* **66**, 743–756 (2012).
59. Gruber, J. & Field, J. Male survivorship and the evolution of eusociality in partially bivoltine sweat bees. *PLOS ONE* **17**, e0276428 (2022).
60. R Core Team. R: A language and environment for statistical computing. (2021).
61. Wickham, H. ggplot2: Elegant Graphics for Data Analysis. (2016).
62. Kassambara, A. ggpvr: Publication Ready Plots. (2019).
63. Wickham, H. stringr: Simple, Consistent Wrappers for Common String Operations. (2022).

64. Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. dplyr: A Grammar of Data Manipulation. (2023).
65. Trapletti, A. & Hornik, K. tseries: Time Series Analysis and Computational Finance. (2023).