The evolution of eusociality: Kin selection theory, division of labour models, and evo-devo explanations

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The evolution of eusociality has long been recognized as an evolutionary paradox. We identify three different but complementary approaches to the study of the evolution of eusociality. Kin selection models explain why individuals can evolve to have distinct reproductive or non-reproductive roles. Division of labour models elucidate how specialisation can emerge and evolve. Conceptual models from evolutionary developmental biology propose hypotheses for the origin and evolutionary fixation of a helper-phenotype. However, we argue that none of these three approaches is a sufficient explanation for the evolution of eusociality on its own. Consequently, we plead for novel unifying explanations and formal models to better understand the interrelation of reproductive altruism, task specialisation and phenotypic plasticity.

The evolution of eusociality has puzzled evolutionary biologists for a long time. Already Darwin wondered how trait modifications of sterile workers could be transmitted through generations[1,2], and the question how natural selection can favour reproductive altruism has led to general insights on social evolution[3–9]. By now, research on eusocial organisms has diversified into many research themes, ranging from research on ageing[10], social genomics[11,12], phylogenetics[13–15], and social immunity[16,17], to cognition[18] and collective behaviour[19]. All of these research themes are affected by our conception of eusociality. This conception – often implicitly – includes a prioritisation of the aspects of eusociality that require an evolutionary explanation.

Three particularly interesting and inseparable features of eusocial organisms are: (1) The commitment of individuals to either reproductive or non-reproductive tasks; (2) Behavioural and morphological specialisation; (3) The occurrence of a helper-phenotype that (in some cases) forms a caste distinct from reproductives, which has lost reproductive totipotency.[*] Here, we argue that these three features of eusocial organisms are mirrored by three different approaches to the study of the evolution of eusociality: (1) Kin selection models; (2) Division of labour models; (3) Models from evolutionary developmental biology ("evo-devo"). We highlight the conceptual insights that each of these approaches has yielded; yet we argue that none of them is a sufficient explanation for the evolution of eusociality on its own. Consequently, we plead for novel explanations and formal models that combine the three approaches to the study of the evolution of eusociality. We give a short prospect of the potential benefits of synthesizing them.

Box 1 | Glossary

Reproductive altruism: The sacrifice of own reproduction in order to enhance reproduction of another individual.

Caste: A developmentally irreversible phenotype; for instance, workers, soldiers, queens and kings are castes.

Reproductive totipotency: The ability to independently produce reproductive offspring of both sexes (in sexual species) that is also capable of independent reproduction.

Behavioural totipotency: The ability to express the full behavioural repertoire of a population.

Subsociality: A social system where mothers interact with their offspring.

Semisociality: A social system where individuals interact with other individuals from the same generation.

Haplodiploidy: A sex determination system in which females develop from fertilised diploid eggs and males develop from unfertilised haploid eggs.

Diplodiploidy: Both males and females develop from fertilised diploid eggs.

Reproductive skew: The uneven distribution of reproduction among members of a group.

Indirect fitness: The spread of genes through helping relatives.

Direct fitness: The spread of genes through reproduction.

Partially bivoltine: A life cycle with two broods per season and within-season generation overlap.

Phenotypic accommodation: A non-genetic adjustment of the phenotype caused by an adaptive regulatory mechanism in response to a novel stimulus during development.

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[*] The defining characteristics of eusociality have been heavily debated (Box 2). We here purposefully leave this issue open. We do not claim that these three features are defining characteristics of eusociality but we here operationally refer to organisms as eusocial if they exhibit those three features.

Genetic accommodation: The evolution of regulatory changes for expressing stimulus-induced phenotypes.

Genetic assimilation: The evolution of regulatory changes that lead to a loss of phenotypic plasticity. The formerly plastic phenotype becomes genetically encoded.

Box 2 | The many meanings of eusociality.

In 1966, Batra[20] invented the term eusociality to describe the subsocial biology of some halictine bees where some offspring become helpers and cooperate with their mother to raise her offspring. Subsequently, the concept of eusociality has been more broadly applied to bees in general by Michener[21] and beyond bees by Wilson[22,23]. According to this Michener-Wilson conception of eusociality, eusociality is defined by: (1) Cooperative brood care; (2) Reproductive division of labour; (3) Generational overlap. This definition of eusociality remains popular until today.

In 1995, the Michener-Wilson definition of eusociality has been criticised for its vagueness. Sherman et al.[24] suggested to broaden the scope of the concept of eusociality and apply it to all organisms that exhibit some level of reproductive skew. Consequently, Sherman et al.[24] consider eusociality to be a continuum equalling the amount of reproductive skew in a biological system. Contrarily, Crespi & Yanega[25] proposed narrowing the scope of the concept of eusociality and to only apply it to organisms in which a subfertile group of individuals exhibits helping behaviours and where the subfertile or fully fertile group of individuals lost behavioural totipotency.

A more recent version of the definition by Crespi & Yanega[25] is that of Boomsma[26], who defines (obligate) eusociality as "a breeding system in which all individuals are either designated breeders or unmated workers/soldiers for life, and where castes are always physically distinct and differentially adapted to a specific subset of social tasks so that colony growth and reproduction always require the complementary efforts of all castes. This implies that no caste has retained reproductive totipotency. […]"[26]. Following this definition, eusociality is thus characterised by a lifelong commitment to reproductive or non-reproductive tasks, behavioural and morphological specialisation, and the loss of reproductive totipotency.

The concept of superorganismality, which is related to the concept of eusociality, is another heavily-disputed concept which has been assigned many different meanings[27–31]. However, this issue is beyond the scope of this article.

Fig. 1 | (Eu-)sociality in insects. (a) Many species of ants exhibit extreme caste dimorphism between reproductive queens and non-reproductive workers. In some ant species, as in *Pheidole* sp., also workers differ in body size, belonging to a major and minor worker caste (copyright: Philipp Hönle) **(b)** In honey bees (here *Apis mellifera*), caste is determined by a developmental switch that is regulated by larval nutrition[32]. Here, the queen, surrounded by some of her workers, deposits an egg into an empty brood cell. (copyright: Jan J. Kreider) **(c)** In contrast to the eusocial hymenopterans (bees, wasps and ants), termites (here *Mastotermes dawiniensis*) are diplodiploid, have a queen and a king, and have female and male helpers[33]. (copyright: Cedric Aumont) **(d)** Wasps exhibit a high diversity of social systems. For instance, some species found colonies individually or join solitary foundresses whereas other species found colonies through swarming (here *Polybia occidentalis*) (copyright: Juan José Lagos-Oviedo) **(e)** Some species of bees and wasps are socially plastic, and thus can nest solitarily or socially, sometimes even within the same population[34–36]. Here, a female of the socially plastic sweat bee *Halictus rubicundus* sits in front of her nest entrance. (copyright: Rebecca Boulton) **(f)** Further organisms have been suggested as candidate eusocial species; for instance, two species of mole rats (here *Heterocephalus glaber*)[37,38], one species of ambrosia beetle (*Australoplatypus incompertus*)[39,40], one species of spider (*Anelosimus eximius*)[41], some gall-forming aphids[42], some gall-forming thrips (*Kladothrips* spp.)[43], and some snapping shrimp (*Synalpheus* spp.)[44,45]. (copyright: Chris Faulkes)

1. Commitment to reproductive or non-reproductive tasks

Individuals of eusocial organisms commit to either reproductive or non-reproductive tasks[46]. The evolution of such a reproductive altruism is well-explained by evolutionary theory[5–9,47,48].

Hamilton's[3,4] kin selection theory suggests that reproductive altruism can be evolutionarily favoured if helping behaviours are directed at relatives, because then the altruist's behaviour facilitates the spread of genes in the population, which are shared with the recipient. This is formalized in Hamilton's rule, $rb > c$, in which r is the genetic relatedness between actor and recipient, b is the fitness benefit of the behaviour for the recipient, and c is the fitness cost to the actor. Consequently, commitment to non-reproductive tasks evolves when the relatedness-scaled fitness benefit of helping exceeds its fitness cost. If Hamilton's rule is satisfied due to indirect fitness benefits of helping alone, then lifelong commitment to helping can evolve. However, in some (eu-)social organisms, non-reproductive individuals may also gain direct fitness[49–53] in addition to indirect fitness through helping[54–57]. Due to haplodiploidy, helping females can lay haploid unfertilised eggs and thus produce male offspring[58–63]. Furthermore, in some species without irreversibly determined reproductive and non-reproductive castes, helping can enhance a helper's chance for inheriting the breeder position later in its life[64].

The haplodiploidy hypothesis. Many eusocial organisms have a haplodiploid sex determination system, in which females are diploid and emerge from fertilized eggs and males are haploid and emerge from unfertilized eggs[65,66]. This has led Hamilton[4,67] to suggest that haplodiploid organisms are particularly prone to evolve altruistic behaviours because in outbred populations with randomly mating monogamous females, haplodiploidy causes females to be more closely related to sisters ($r = 0.75$) than to their own offspring ($r = 0.5$; Fig. 2)[68]. However, as Trivers & Hare[69] pointed out, the benefit from raising sisters over own offspring cancels out exactly under even sex ratios because females are less related to their brothers ($r = 0.25$) than to their sons ($r = 0.5$; Fig. 2). Also if female helpers bias sex allocation towards female offspring, haplodiploidy does not favour the evolution of helping behaviours, because this bias also increases the reproductive value of male offspring[70]. Even if some nests specialise on the production of females while other nests predominantly produce male offspring[71], then haplodiploidy does not favour the evolution of reproductive altruism because while helping would be evolutionarily favoured in the nests with female-biased sex allocation, it would also be disfavoured in the nests with male-biased sex allocation[72–74]. However, if haplodiploidy occurs in combination with further preadaptations, such as a partially bivoltine life cycle, then haplodiploidy can favour the evolution of helping behaviours[75–78]. Furthermore, haplodiploidy could facilitate the evolution of reproductive altruism by enhancing the maternal ability for sex ratio adjustments towards the helping sex[79].

The monogamy window hypothesis. Eusocial species have most likely evolved from monogamous ancestors[80,81]. Lifetime monogamy predisposes organisms towards the evolution of reproductive altruism because it causes helpers to be evenly related to their siblings and to their own offspring ($r = 0.5$), both under diplodiploidy and haplodiploidy, assuming even sex ratios[82] (Fig. 2). Boomsma[26,83,84], consequently, suggested that eusocial species had to pass through a "monogamy window" to evolve reproductive altruism. This also implies that eusociality is more likely to evolve from subsocial mother-offspring associations than from semisocial (or parasocial) associations of individuals from the same generation[85–87] because, all else being equal, semisociality results in lower relatedness than subsociality[84] (Fig. 2).

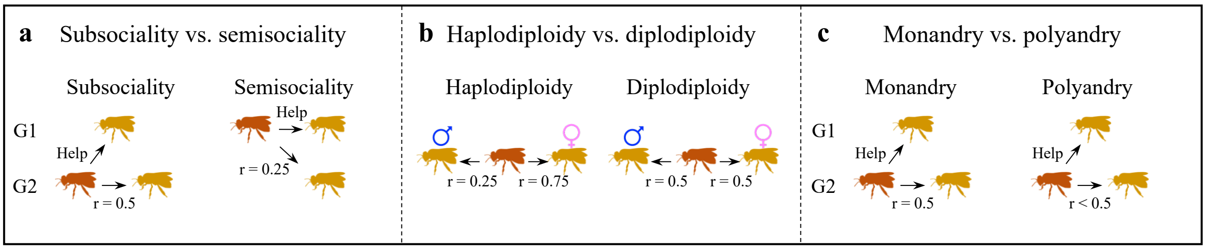

Fig. 2 | Relatedness in different social, sex determination and mating systems. (a) In subsocial systems, the focal female (red) helps her mother (yellow) raise her siblings (yellow; G1 = generation 1; G2 = generation 2). The focal female is related to her siblings by $r = 0.5$, given that offspring is produced at even sex ratios, if the species is haplodiploid, and given that the mother is monandrous. In semisocial systems, the focal female helps another individual from the same generation (in this case, her sister) raise her nephews and nieces. The focal female is related to her nephews and nieces by $r = 0.25$, given that offspring is produced at even sex ratios, if the species is haplodiploid, and given that the mother is monandrous. **(b)** In haplodiploid systems, the focal female (red) is more closely related ($r = 0.75$) to her sisters (yellow) than to her brothers ($r = 0.25$; yellow). Such a relatedness asymmetry does not exist in diplodiploid systems, where the focal female is related by $r = 0.5$ to both her sisters and brothers. **(c)** In monandrous systems, the focal female (red) is related by $r = 0.5$ to her siblings (yellow) that she helps her mother (yellow) to raise, given that offspring is produced at even sex ratios, if the species is haplodiploid. In polyandrous systems, relatedness decreases with the degree of maternal polyandry, and thus the relatedness of the focal female to her siblings is $r < 0.5$.

The limitations of kin selection models for explaining the evolution of eusociality. Kin selection theory is extraordinarily powerful for explaining the evolution of reproductive altruism in eusocial organisms and beyond[5–7,9,88–95]. Many eusocial species with irreversibly determined castes have secondarily evolved multiple mating of queens and consequently Hamilton's rule does not necessarily hold any longer in these species[81,96–98]. In order to avoid a contradiction with kin selection theory, Boomsma[26,27,84], following Wilson & Hölldobler[99], invokes a "point of no return", which eusocial species have passed, and after which reproductive totipotency cannot be regained, even if Hamilton's rule no longer holds. However, it is not clear why a developmental switch that leads to irreversibly distinct reproductive and non-reproductive phenotypes evolves (developmental constraint), why an evolutionary "point of no return" is passed (evolutionary constraint), and why the evolution of developmentally irreversible phenotypes coincides with evolutionary irreversibility. As current kin selection models do not explicitly model genetic architecture and development, they cannot answer these questions, and thus rely on such verbal arguments that are added to the formal models to explain such apparently maladaptive phenomena as multiple queen mating. Consequently, current kin selection models cannot explain all of the three aspects of eusociality, and therefore they are an insufficient explanation for the evolution of eusociality.

2. Behavioural and morphological specialisation

Eusocial organisms exhibit behavioural specialisation between reproductive and non-reproductive tasks, and in some species this reproductive division of labour is accompanied by a queen-worker dimorphism[46]. Furthermore, many eusocial species also exhibit division of labour between workers who, for instance, specialise in foraging, nursing the brood or defending the nest, and might belong to morphologically distinct worker castes[100].

The emergence of division of labour. Models for the emergence of division of labour evaluate whether an assumed mechanism can lead to the emergence of division of labour but typically there is no mutation and selection in them[101]. Thus, these models do not investigate whether the assumed mechanism is adaptive. Response threshold models are the standard approach for modelling the self-organised emergence of division of labour[102–109]. These models assume that individuals have different response thresholds that determine their probability to perform a task when they are confronted with a task stimulus (Fig. 3a). As individuals, that perform a task, reduce the task stimulus, individuals with higher response thresholds are prevented from performing that task. As response threshold models build on interindividual differences, they predict that higher genetic diversity within colonies, for instance, through multiple mating of queens, is advantageous for the efficiency of division of labour[105,107,110,111]. However, interindividual differences in response thresholds could also be caused by other internal or environmental factors[112]; for instance, through differences in body size, that are commonly observed in social insects[113,114]. Some response threshold models and empirical studies, furthermore, predict stronger division of labour with larger group size[106,115,116], although this pattern is not supported unequivocally[117,118]. None of the factors that favour division of labour in response threshold models – multiple mating, large interindividual differences, or large group sizes – are typically considered to have played an important role during the transition to eusociality. However, division of labour can also emerge in small groups of highly similar individuals. For instance, if individuals become more likely to forage as their nutrition level decreases[119–124], then division of labour can emerge through resource sharing between identical individuals[125]. This is because resource sharing delays the onset of foraging in non-foraging individuals while it also prevents foragers from filling up their nutrition levels, thus making them more likely to forage again.

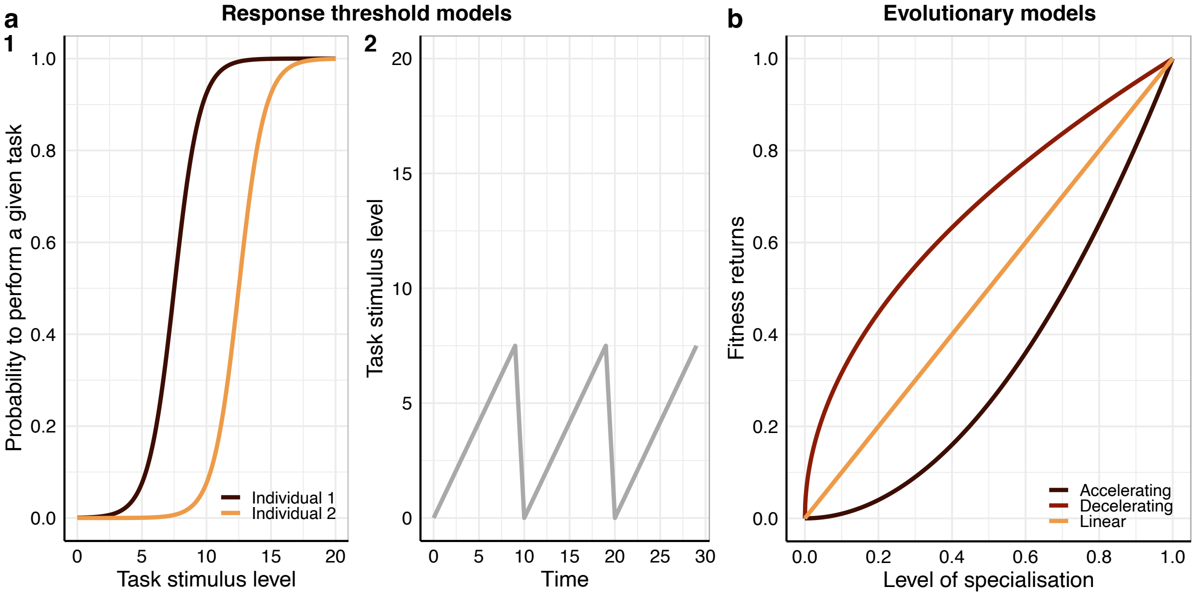

Fig. 3 | The emergence and evolution of division of labour. (a) The emergence of division of labour in response threshold models. **(a1)** Two logistic functions that resemble response thresholds of two individuals. Individual 1 is more likely to start performing a given task under relatively low stimulus levels compared to individual 2. **(a2)** A hypothetical scenario of the change of stimulus levels over time in a response threshold model. The stimulus level increases (in this case linearly) until individual 1 is triggered to perform the task. This reduces the stimulus level. Subsequently, the stimulus level increases again. As individual 2 has a higher threshold level than individual 1, it never performs the task. **(b)** Fitness returns by level of specialisation in evolutionary division of labour models. Division of labour is typically predicted to evolve under accelerating returns but not under linear or decelerating returns of specialisation.

The evolution of division of labour. Evolutionary division of labour models investigate the conditions under which division of labour evolves but usually they do not explicitly consider the mechanisms that regulate division of labour[101]. Evolutionary division of labour models typically predict that division of labour evolves when efficiency benefits increase with higher levels of individual specialisation ("accelerating returns") but not in the absence of efficiency benefits ("linear" or "diminishing returns"; Fig. 3b)[126–129]. However, such an efficiency increase due to specialisation is not always observed in eusocial organisms[130,131]. Furthermore, some recent work has highlighted that division of labour can also evolve under diminishing returns if individuals differ in their efficiency for task performance or if beneficial synergies emerge from division of labour[129,132].

The limitations of division of labour models for explaining the evolution of eusociality. Division of labour models have yielded important insights into the emergence and evolution of division of labour. Duarte et al.[101] have argued for combining mechanistic self-organisation models for the emergence of division of labour with evolutionary division of labour models. This allows for evaluating under which mechanisms division of labour can be evolutionarily fixed. At the same time, it can be evaluated which mechanisms for regulating division of labour evolve[133,134]. Reproductive division of labour is expected to evolve if Hamilton's rule is satisfied. However, also non-reproductive division of labour could play a role for the evolution of reproductive division of labour because benefits could arise from division of labour between helpers. Furthermore, it still remains poorly understood under which conditions specialisation evolves to be purely behavioural and thus reversible, and under which conditions specialisation is not only behavioural but also accompanied by morphological differences that make it irreversible[135]. The evolution of such "sensitive windows" in development is likely to depend on the uncertainty of the environment and the degree to which environmental cues can give information about the environmental state during different life stages of the individual[136]. Investigating these questions in division of labour models requires taking the evolution of mechanisms that regulate behaviour and individual development into account. Just as current kin selection models, current division of labour models cannot explain all of the three aspects of eusociality, and therefore they are an insufficient explanation for the evolution of eusociality on their own.

3. The emergence and evolutionary fixation of a helper-phenotype

Individuals of eusocial organisms either have a helper or a breeder-phenotype. In some (eu-)social organisms, these phenotypes are flexible and helpers can breed later in their life. In other species, individuals belong to morphologically distinct castes, each dependent on the presence of individuals from the other caste for the production of reproductive offspring of both sexes[26]. In such caste-based eusocial organisms, caste is irreversibly determined in individual development[137]. In most cases, caste determination is environmental; for instance, in honey bees, larvae develop into queens or workers depending on whether they are fed with royal jelly[32]. However, also some cases of genetic caste predisposition are known, which probably evolved from ancestral environmental caste determination[138]. Several hypotheses for the evolutionary origin and divergence of helper/worker and breeder/queen-phenotypes have been suggested[139–142]. These hypotheses typically are verbal conceptual models that propose a lineage explanation, i.e. a stepwise explanation for the transformation of one phenotype into another[143], for the evolution of the distinct phenotypes of eusocial organisms. However, some of these models also go beyond providing a lineage explanation. These models are inspired by arguments from evolutionary developmental biology ("evo-devo") that highlight a prominent role of phenotypic plasticity for evolutionary innovation and speciation[144–147]. In these arguments, novel complex traits emerge by phenotypic accommodation, and are thus mutationally or environmentally-induced non-genetic adjustments of the phenotype caused by an adaptive regulatory response[148]. Subsequently, these phenotypic novelties and the ability of the organisms to produce these phenotypes are exposed to natural selection[149]. As phenotypic accommodation precedes genetic change, it could facilitate the evolution of complex traits, such as social behaviours[148,149].

The induction of a helper-phenotype and phenotypic accommodation. The induction of helping behaviours has been suggested to occur by phenotypic accommodation[150]. West-Eberhard's ovarian ground plan hypothesis posits that the reuse of brood cells – induced by mutation or environmental conditions – could lead to nest sharing as a pleiotropic side effect[151,152]. This then leads to a contextual shift of behaviours performed by individuals. For instance, if individuals have an evolved behavioural response to provide parental care when sensing the presence of larvae, then a heterochronous expression of parental care behaviours directed at siblings could be triggered by cues released from the larvae[150,153–156], such as larval begging behaviours[157–160]. As West-Eberhard highlights, the induction of helping could thus happen without any genetic change but as a side effect of a mutation affecting a behaviour or an environmental induction of a behaviour that is not directly related to helping[152]. From her observations of *Zethus miniatus* wasps, West-Eberhard posits a scenario for the emergence of reproductive and non-reproductive roles. In synchronisation with a behavioural cycle of reproductive behaviours (e.g. brood cell building and oviposition) and non-reproductive behaviours (e.g. defending and provisioning brood) ovaries of females could be developed or undeveloped (Fig. 4a). When multiple females share a nest, the behavioural and ovarian cycles could be interrupted, fixing some females into a non-reproductive helping role; for instance, because their ovarian development is restricted due to malnourishment[161–164] or because they experience aggressive behaviours by nest mates that prevent them from reproducing[165,166]. The helper-phenotype, that is induced, can spread through the population and its expression can be maintained as long as the conditions, that induce it, persist[152]. In halictine bees, helping behaviours have been secondarily lost again and some species thus reverted to solitary life[167–169]. If helping is induced environmentally instead of by genetic change, such reversals could easily be explained.

West-Eberhard's ovarian ground plan hypothesis is inspired by the biology of a particular wasp species. However, these details are not crucial. The general principles of pleiotropy, contextual shift, and phenotypic accommodation are the strength of West-Eberhard's explanation, and it is probably possible to formulate similar lineage explanations for other organisms.

Selection on the helper-phenotype and genetic accommodation. The induction of helping by phenotypic accommodation provides the basis for natural selection on the helper-phenotype and on the organism's ability to produce it, thus genetic accommodation[170]. For instance, in the ovarian ground plan hypothesis, gene regulation evolves to dissolve the ovarian and behavioural cycles, though the linkage of non-reproductive behaviours with ovarian deactivation and reproductive behaviours with ovarian activation remains[151,152]. Subsequently, a developmental switch evolves that causes individuals to be irreversibly fixed to perform reproductive behaviours and have activated ovaries or to perform non-reproductive behaviours and have deactivated ovaries[151,152] (Fig. 4a).

Another scenario that does not require the evolution of a developmental switch is suggested by the diapause ground plan hypothesis[34,171]. This hypothesis builds on the pre-existing differences between the offspring from the first and second brood of a partially bivoltine life cycle. Gene regulation could be modified so that females from the first brood evolve a helper-phenotype whereas females from the second brood evolve a breeder-phenotype[34,171]. These pre-existing differences between the two broods could be based on maternal manipulation[172–174] of offspring nutrition or body size due to which offspring from the first brood could have a restricted fecundity, and might thus evolve to stay at the natal nest to become a helper[175,176]. Caste would thus be determined by a nutrition-dependent developmental switch which could have been exapted from a nutrition-dependent developmental switch for regulating diapause[34,171,177–179] (Fig. 4b).

Empirically, a role of phenotypic plasticity for the production of helping and breeding-phenotypes is well-supported by gene expression differences between helpers and breeders in various species of social wasps and bees[180–185]. However, the phenotypic divergence of breeders and helpers must also initially be restricted by genetic correlations because breeders and helpers might express the same genes[153,186–190]. Additionally, this divergence must be restricted in species where helpers have the ability to become the breeder at some point in their life.

The evolution of irreversibly determined castes has been suggested to occur by genetic assimilation[150]. Genetic assimilation could indeed play a role for the evolution of a permanent helper-phenotype by reducing opportunities for expressing a solitarily breeding phenotype. However, caste is typically determined by environmental cues and phenotypic differences between castes are a result of caste-specific gene expression[138,191–195]. Even if irreversible, these different phenotypes originate from developmental plasticity. Consequently, there is no loss of plasticity in the evolution of irreversibly determined castes, which would be required to qualify this evolutionary process as genetic assimilation[196]. Genetic assimilation would apply where caste determination evolved to be genetic[197], but this only happened in some eusocial insects[138].

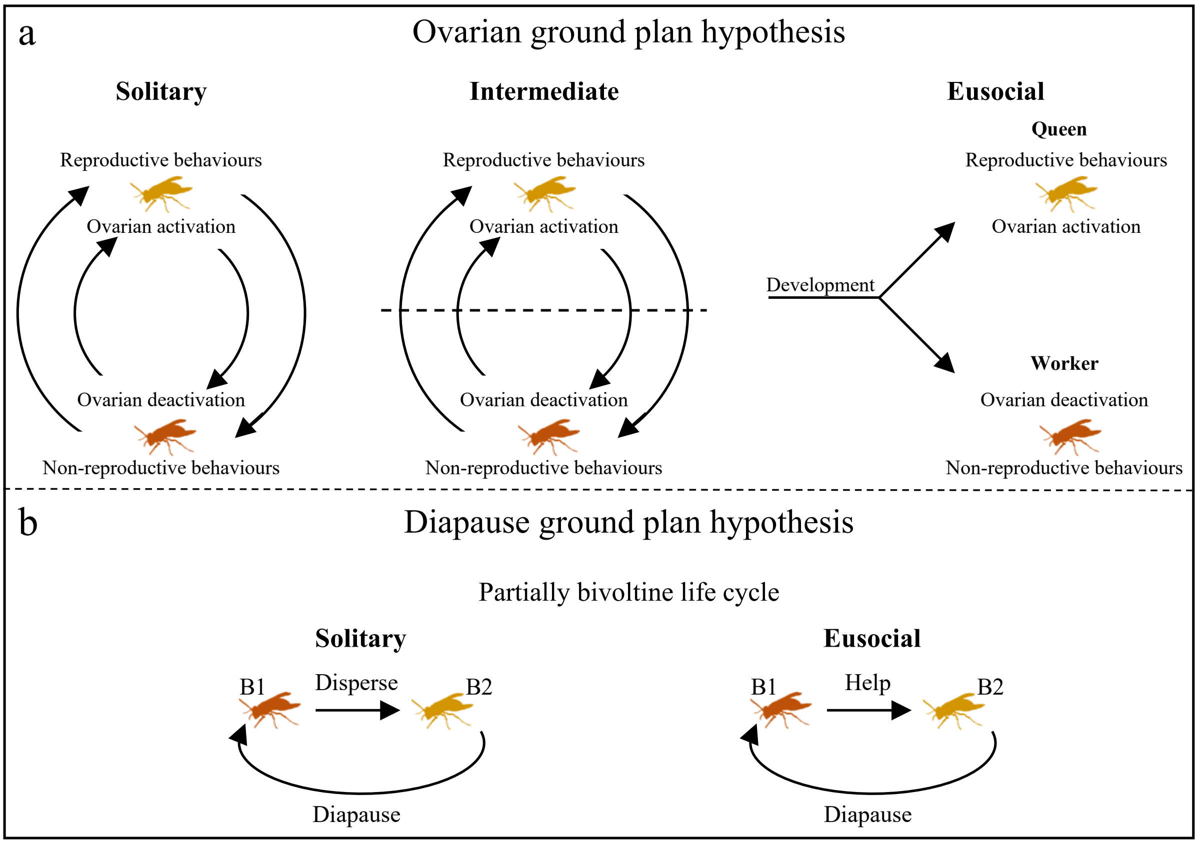

Fig. 4 | The ovarian and diapause ground plan hypotheses. (a) West-Eberhard's ovarian ground plan hypothesis assumes a solitary species that cycles through reproductive behaviours, associated with ovarian activation, and non-reproductive behaviours, associated with ovarian deactivation. This ovarian cycle could become interrupted in shared nests due to various contextual changes and social interactions (dashed line). A developmental switch for caste determination evolves. Queens permanently perform reproductive behaviours and have activated ovaries. Workers permanently perform non-reproductive behaviours and have deactivated ovaries. Figure inspired by West-Eberhard[152]. **(b)** The diapause ground plan hypothesis builds on a partially bivoltine life cycle. In a solitary ancestor, offspring from the first brood disperses, breeds and dies before hibernation. Offspring from the second brood enters diapause and hibernates to breed in the next season. An annual eusocial life cycle can evolve if offspring from the first brood evolves to be philopatric and helps, thus becomes a worker caste, and if offspring from the second brood still enters diapause and hibernates to breed in the next season, becoming foundresses of new colonies, thus queens.

The limitations of evo-devo models for explaining the evolution of eusociality. The conceptual evo-devo models provide a changed perspective on the evolution of eusociality. In kin selection models, helping occurs by mutation in a gene for the helping tendency of an individual. However, in the evo-devo models helping can occur as a side effect of an environmental or mutational induction of another behaviour[152]. Helping could initially be facultatively expressed leading to plasticity between solitary and social breeding, as in a number of wasps and bees[11,12,169]. Such social plasticity could facilitate the evolution of eusociality as the helper-phenotype could become refined by genetic accommodation before it gets fixed by natural selection. The main weakness of the evo-devo models is that they are neither tested in formal models nor formally linked with kin selection and division of labour models. However, also the evo-devo models require kin selection for the evolutionary fixation of helping. Consequently, just as kin selection and division of labour models, also the evo-devo models cannot fully explain the evolution of eusociality on their own.

Conclusions

We here identified three approaches to the study of the evolution of eusociality: (1) Kin selection models; (2) Division of labour models; (3) Conceptual evo-devo models. These three approaches are not mutually exclusive but complementary. Drawing interrelations between them could yield valuable insights into the evolution of eusociality. Particularly the evo-devo models could change our perspective on the evolution of eusociality. If a complex beneficial helper-phenotype emerges through phenotypic accommodation, this could alter benefit-cost ratios in Hamilton’s rule more extremely than previously imagined, leading to the emergence of high levels of division of labour and relaxing the requirement of, for instance, lifetime monogamy for the evolution of eusociality. This could dramatically shift our perspective on the evolution of eusociality in several ways: (1) It would shift the focus from the genetic relatedness term in Hamilton’s rule to the benefit-cost ratio; (2) It would open up the possibility for a rapid rather than a gradual evolutionary transition to eusociality; (3) It would no longer only be mating and sex determination system but also the details of genetic architecture, behavioural expression and developmental regulation that would explain why the evolution of eusociality might have been facilitated in some taxa but not in others. More mechanistic developmental models of the evolution of eusociality could also fill current explanatory gaps for the evolution of irreversibly determined castes (developmental irreversibility) and help answer the question why some eusocial species might have passed a “point of no return” (evolutionary irreversibility). Enhancing our understanding of the effects of phenotypic plasticity in social evolution would ensure research on eusocial organisms a role that it already has for a long time – to be a driving force for the development of evolutionary biology[198].

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Author contributions

JJK wrote a first draft of the manuscript and made the figures. IP gave feedback and edited the manuscript.

Competing interests

The authors declare no competing interests.

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