Eusociality through conflict dissolution

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Abstract

Eusociality, where largely unreproductive offspring help their mothers reproduce, is a major form of social organization in social insects and other animals. An increasingly documented feature of eusociality is that mothers induce their offspring to help by means of hormones, pheromones, or behavioral displays, with evidence often indicating that offspring help voluntarily. The co-occurrence of widespread maternal influence and voluntary offspring help may be explained by what we call the converted helping hypothesis, whereby helping originally arising from maternal manipulation subsequently becomes voluntary. This hypothesis requires that parent-offspring conflict is eventually dissolved—for instance, if the benefit of helping increases sufficiently over evolutionary time. Here we show that maternal manipulation of offspring help enables the mother to increase her fertility to such extent that parent-offspring conflict is transformed into parent-offspring agreement. Such conflict dissolution mechanism requires that helpers alleviate the total percent life-history trade-off limiting maternal fertility, and results in reproductive division of labor, high queen fertility, and honest queen signaling suppressing worker reproduction, thus exceptionally recovering diverse features of eusociality. This mechanism is widely applicable, thus suggesting a general explanation for the origin of eusociality, the prevalence of maternal influence, and the offspring's willingness to help. Overall, our results explain how a major evolutionary transition can happen from ancestral conflict.

A few major evolutionary transitions in individuality have had vast effects on the history of life. Examples include transitions from prokaryotes to eukaryotes, and from multicellularity to eusociality and interspecific mutualisms. A major transition is said to occur when independently replicating units evolve into groups of entities that can only replicate as part of the group and that show a relative lack of within-group conflict [4, 27, 48]. A transition is envisaged to involve the formation of a cooperative group and its transformation into a cohesive collective [4, 48]. These steps are hypothesized to occur through the evolution of cooperation, division of labor, communication, mutual dependence, and negligible within-group conflict, leading to a higher-level individual [48]. This scheme poses the question of how its various features can arise.

The transition to eusociality has been extensively studied, partly because it has occurred relatively recently. Eusociality is commonly defined as involving groups with reproductive division of labor, overlapping generations, and cooperative work [49]. Additionally, an increasingly documented feature of eusociality is that mothers exert a substantial influence—via various proximate mechanisms—on whether offspring express helper phenotypes. Examples include hymenopteran queen pheromones suppressing worker reproduction [43], termite queen pheromones inhibiting differentiation of new queens [25], naked-mole rat workers becoming more responsive to pup calls after coprophagy of queen's feces containing estradiol [44], and queen presence suppressing gonadal development of females in eusocial shrimp [7]. This pattern suggests that explanations for the transition to eusociality should also account for the prevalence of maternal influence on helpers at the nest.

Two classic hypotheses for the origin of eusociality offer different explanations for the prevalence of maternal influence. On the one hand, the *voluntary helping hypothesis* proposes that helping arises in the evolutionary interests of helpers, in the sense that helping is favored when helpers have unconstrained control of their helping behavior [16]. According to this hypothesis, helping evolves in simple models if $B/C > 1/r$, where B is the benefit given by helping, C is the cost paid for helping, and r is the relatedness of helper toward recipient. In this view, maternal influence on workers would arise as a regulatory mechanism after helping evolves, and the prevalence of such maternal influence would be a consequence of the loss of eusociality without it. On the other hand, the *maternal manipulation hypothesis* proposes that helping arises in the evolutionary interests of

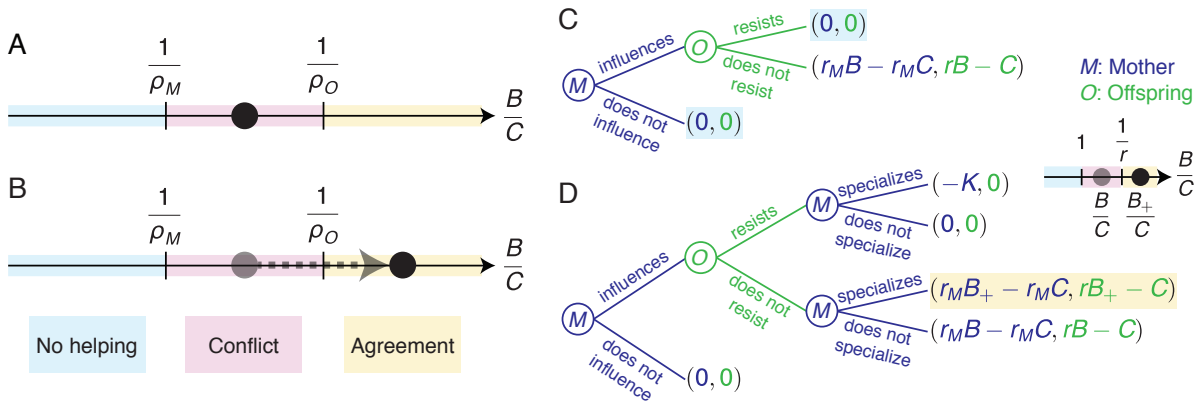

Figure 1: Conflict dissolution. (A,B) Helping is (i) disfavored by mother and offspring if the benefit-cost ratio B/C satisfies $B/C < 1/\rho_M$ (*no helping* zone); (ii) favored by mother and offspring if $B/C > 1/\rho_O$ (*agreement* zone); or (iii) favored by mother but disfavored by offspring if $1/\rho_M < B/C < 1/\rho_O$ (*conflict* zone). Conflict dissolution occurs when (A) B/C starts in the conflict zone but (B) ends in the agreement zone. Helping is favored by actors A when $\rho_A B - C > 0$ (a Hamilton's rule; [16]), where C is the cost to helpers, B is the benefit to help recipients, and ρ_A is the *relative reproductive worth* for actors A of recipients relative to helpers, a reproductive-value weighted measure of relatedness (if all offspring are female, $\rho_M = r_M/r_M = 1$ and $\rho_O = r/1 = r$, where r_M and r are the relatedness of a female to a daughter and a sister, respectively; see SI Appendix, section 3). (C,D) Sequential games modeling conflict and conflict dissolution via maternal reproductive specialization. (C) Without specialization, conflict yields equilibria with no helping (*shaded*); (D) with specialization, conflict is dissolved if $B_+/C > 1/\rho_O$, yielding a unique equilibrium under agreement (*shaded*).

mothers against the evolutionary interests of helpers—that is, there is a parent-offspring conflict over helping [2, 28, 42]. In this case, helping evolves if $B/C > 1$, which is easier to satisfy than the condition for voluntary helping, as long as $r < 1$ [8]. Although the maternal manipulation hypothesis would account for the prevalence of maternal influence by definition, this hypothesis is refuted by increasing evidence suggesting that it is often in the evolutionary interests of offspring to help [19, 20].

A third alternative hypothesis—that we term the *converted helping hypothesis*—proposes that helping initially arises from maternal manipulation but then becomes voluntary. This hypothesis can bring together advantages of both the voluntary helping and maternal manipulation hypotheses without bringing in their disadvantages. First, since it is initially maternally manipulated, helping originates under the easier condition $B/C > 1$ and would be associated to maternal influence. Second, since converted helping is voluntary in the end, the hypothesis is also consistent with evidence that offspring help voluntarily. By considering that manipulated helping becomes voluntary, the converted helping hypothesis requires that there is a switch from conflict to agreement, that is, that *conflict dissolution* occurs (Fig. 1A,B). Hence, it is of substantial interest to identify mechanisms that dissolve conflict and that would give the converted helping hypothesis a basis.

Here we report a widely applicable conflict dissolution mechanism that yields eusociality together with its hallmarks of maternal influence on offspring helping phenotype, offspring voluntary helping, and high maternal fertility. We term this mechanism *conflict dissolution via maternal reproductive specialization*, whereby (i) the mother manipulates offspring (against their inclusive-fitness interests) to become helpers; (ii) while offspring evolve resistance to manipulation, the mother uses available help to become more fertile; and (iii) increased maternal fertility increases the benefit of helping to the point of rendering helping voluntary (i.e., in the inclusive-fitness interest of helpers). The key requirement for this mechanism to work is that helpers alleviate the total percent life-history trade-off limiting maternal fertility in the absence of help—a requirement that is expected to hold widely across eusocial taxa. We show how conflict dissolution via maternal reproductive specialization operates by means of both a game theory model and an evolutionary model.

Results

Game theory model

First, we use a sequential game to show that resistance can prevent manipulation from yielding helping. Consider a game between a mother (M) and a female offspring (O) (Fig. 1C). First, M chooses between either

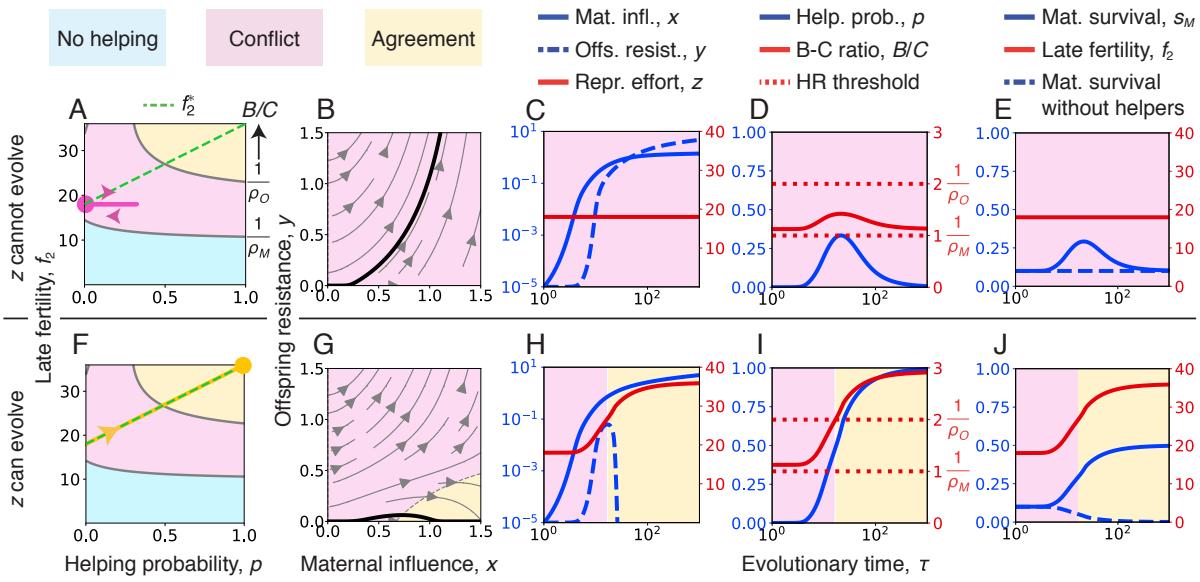

Figure 2: Conflict dissolution via maternal reproductive specialization (evolutionary model). (A-E) Co-evolution of maternal influence x and offspring resistance y when maternal reproductive effort z cannot evolve (i.e., the genetic variance of z, G_z, is zero). (A) Starting from conflict, helping evolves temporarily but is eventually lost due to the evolution of resistance (*circle*). (B) Co-evolutionary trajectory of maternal influence and offspring resistance (*black*). (C-E) Time series of: (C) the evolving traits, (D) the resulting helping probability p and benefit-cost ratio B/C, and (E) the vital rates s_M, f_2, and s_M with zero helpers. (F-J) Analogous plots but now z can evolve as the mother chooses it optimally for the number of helpers she has (i.e., as if $G_z \to \infty$). (F) Starting from conflict, helping emerges and is maintained through the evolution of z yielding agreement (*circle*). (G) Trajectories starting at conflict can converge to agreement. (H) Resistance reversal. (I) B/C evolves and the Hamilton's rule threshold from the helpers perspective is crossed. (J) The mother becomes highly fertile and reliant on helpers for her own survival. The genetic system is diploid, both sexes help, and helping is under shared control with sequential determination of the joint helping phenotype. Here, the life-history trade-off is between parent survival s_M and late fertility f_2, as illustrated in Fig. 3. Second-brood offspring survival s_2 is constant. The remaining details of the functional forms and parameter values used are given in SI Appendix, section 8.

influencing O or not. Second, if M influences O, then O chooses between either resisting the influence or not. If O does not resist, then she helps M produce an extra number B of daughters, at a cost C to herself. If M is related to each daughter by r_M, and if O is related to each sister by r, then M gets an "inclusive-fitness payoff" of $r_M B - r_M C$ while O gets $rB - C$. Otherwise, if M does not influence or if O resists, O does not pay any cost and no extra daughters are produced, yielding payoffs of zero to both players. Under conflict ($1 < B/C < 1/r$), maternal influence constitutes manipulation, in which case selection favors resistance and manipulation does not yield helping: the game has two subgame perfect equilibria, one with resistance and the other without influence.

Let us extend this game to show that reproductive specialization allows maternal influence to yield helping despite possible resistance. Now, after O moves, M can choose between specializing into reproduction or not (Fig. 1D). If O resists, M pays a cost K for exerting more reproductive effort due to a life-history trade-off. If O does not resist, M produces an extra number of daughters B_+ at no cost provided that O alleviates M's trade-off. Importantly, if helping and specialization are synergistic enough that $B_+/C > 1/r$, then there is agreement with specialization although there is conflict without. Thus, influence and specialization yield helping: the game has a unique subgame perfect equilibrium with influence, specialization, and no resistance. This shows that if mothers can use offspring help to increase their fertility sufficiently, the underlying parent-offspring conflict can be dissolved.

Evolutionary model

We now formulate an evolutionary model to show that the evolution of maternal reproductive specialization can increase the benefit of helping to a point where conflict is dissolved. The model is age-, sex-, and genotype-

structured with explicit population and mutant-invasion dynamics, which allows us to derive rather than assume inclusive-fitness payoffs (the model is fully described in the SI Appendix, section 1). We consider a large population with overlapping generations, a fixed number of nesting sites, and a monogamous life cycle with two offspring broods. The genetic system is diploid or haplodiploid, and either both sexes or only females help, which covers the spectrum of known eusocial taxa [36, SI Appendix, Fig. S1]. Young parents produce f_1 first-brood offspring and with probability s_M survive to old age to produce f_2 second-brood offspring. Each first-brood offspring of the helper sex becomes a helper with probability p or disperses with probability $1-p$; the number of helpers h at the nest is hence proportional to p. All second-brood offspring disperse. Dispersing first-brood offspring (resp. second-brood offspring) survive dispersal with probability s_1 (resp. s_2). Surviving individuals mate singly at random and start a nest if nesting sites are available (SI Appendix, Fig. S2). We assume vital rates are such that (i) f_2 increases with maternal reproductive effort z (e.g., number of ovarioles), (ii) there is a trade-off between survival and fertility, so that s_M or s_2 decreases with f_2, and (iii) helpers increase parent or second-brood survival, so that s_M or s_2 increases with h. A couple's expected number of reproductive first-brood (resp. second-brood) offspring is given by the couple's early productivity $\Pi_1 = (f_1 - h)s_1$ (resp. late productivity $\Pi_2 = s_M f_2 s_2$). We analyze the co-evolutionary dynamics of offspring helping probability p and maternal reproductive effort z. We let p be under maternal, offspring, or shared control. Under shared control, p is a joint phenotype [33] that increases with maternal influence x (e.g., pheromone production) and decreases with offspring resistance y (e.g., receptor antagonist production). Reproductive effort z is under maternal control. For the inclusive fitness interpretation of our results, we distinguish between different sets of individuals in a focal nest. In particular, we denote by M the singleton whose only member is the mother, by $O_{a\ell}$ the set of sex-ℓ offspring produced in brood a, and by O_a the set of a-th brood offspring (both male and female). Furthermore, we let $O \equiv O_1$ if both sexes help, and $O \equiv O_{1♀}$ if only females help.

Inclusive-fitness effects

We find that, in agreement with inclusive fitness theory, each evolving trait ζ is favored by selection if and only if its inclusive-fitness effect $\mathscr{H}_\zeta$ is positive (see SI Appendix). More specifically, the selection gradients quantifying the directional selection acting on each trait are

$$\mathscr{S}_x \propto \frac{\partial p}{\partial x}(\rho_M B - C), \tag{1a}$$

$$\mathscr{S}_y \propto \frac{\partial p}{\partial y}(\rho_O B - C), \tag{1b}$$

$$\mathscr{S}_z \propto \frac{\partial \Pi_2}{\partial f_2}, \tag{1c}$$

where the inclusive fitness effect of helping from the perspective of actors A is $\mathscr{H}_p^A \propto \rho_A B - C$ with $A = M$ when helping is under maternal control, and $A = O$ when it is under offspring control. Here, $C = -\mathrm{d}\Pi_1/\mathrm{d}h = s_1$ is the marginal cost of helping, $B = \partial\Pi_2/\partial h$ is the marginal benefit of helping, and ρ_A is what we term the *relative reproductive worth* for a random actor in set A relative to a random candidate helper in set O of a random candidate recipient of help in set O_2. Such ρ_A generalizes Hamilton's life-for-life relatedness [17] to allow for helpers and recipients of both sexes. It depends on the relatedness of actors toward candidate recipients of help, the sex-specific reproductive values of such recipients, and the stable sex distribution of the parents of candidate helpers (SI Appendix, section 3).

Conflict dissolution

Numerical solutions of the evolutionary model show that conflict dissolution via maternal reproductive specialization can occur. If maternal influence x and offspring resistance y co-evolve under conflict but reproductive effort z cannot evolve (i.e., there is no genetic variation for z), resistance may win the ensuing arms race and eliminate helping in the long run (Fig. 2A-E). This matches the standard expectation [21]. Alternatively, if reproductive effort co-evolves with influence and resistance, the benefit-cost ratio can move out of conflict and into the agreement zone (Fig. 2F-J). In this case, the arms race vanishes as manipulated helping becomes voluntary. The final outcome is eusociality where (i) helpers are maternally induced to help and not favored to resist, and (ii) the mother has become highly fertile and reliant on helpers for her own or her offspring's survival. Moreover, ancestral manipulation becomes an honest signal [26]: the resulting maternal influence alters the recipient's phenotype in the recipient's interest (i.e., helpers are induced to help, and they "want" to help); the signaler evolved to produce that effect (i.e., maternal influence evolved to induce helping); and the recipient evolved to attend the signal (i.e., offspring evolved lack of resistance to influence).

Trade-off alleviation

We now show that conflict dissolution via maternal reproductive specialization requires that helpers alleviate the total percent trade-off limiting maternal fertility. Conflict occurs when the mother favors helping (i.e., $\mathscr{H}_p^M > 0$) while offspring disfavor helping (i.e., $\mathscr{H}_p^O < 0$). Conflict dissolves if there is eventual agreement (i.e., $\mathscr{H}_p^M > 0$ and $\mathscr{H}_p^O > 0$ in the end). Hence, for conflict dissolution it is necessary that the inclusive-fitness effect $\mathscr{H}_p^O$ for helping under offspring control increases with evolutionary time τ and changes sign from negative to positive, namely that

$$\frac{\mathrm{d}\mathscr{H}_p^O}{\mathrm{d}\tau} > 0 \text{ for all } \tau \in [\tau_1, \tau_2], \text{ and} \qquad \text{(persuasion condition)}$$

$$\mathscr{H}_p^O = 0 \text{ for some } \tau \in (\tau_1, \tau_2), \qquad \text{(conversion condition)}$$

hold for some evolutionary time interval $[\tau_1, \tau_2]$. By the chain rule, the persuasion condition is equivalent to $\left(\partial\mathscr{H}_p^O/\partial p\right)(\mathrm{d}p/\mathrm{d}\tau) + \left(\partial\mathscr{H}_p^O/\partial z\right)(\mathrm{d}z/\mathrm{d}\tau) > 0$ for all $\tau \in [\tau_1, \tau_2]$. Motivated by this, we say that conflict dissolution via maternal reproductive specialization occurs when $\left(\partial\mathscr{H}_p^O/\partial z\right)(\mathrm{d}z/\mathrm{d}\tau) > 0$ for all $\tau \in [\tau_1, \tau_2]$, a condition that requires helping-fertility synergy (i.e., $\partial\mathscr{H}_p^O/\partial z > 0$; [5]) as reproductive effort increases over evolutionary time.

Helping-fertility synergy at an optimal fertility f_2^* (implicitly given by $\partial\Pi_2/\partial f_2|_{f_2=f_2^*} = 0$) is equivalent to the four following statements (SI Appendix, section 5). First, the benefit-cost ratio, B/C, increases with late fertility at an optimal late fertility f_2^*, so $\partial(B/C)/\partial f_2|_{f_2=f_2^*} > 0$. Second, optimal late fertility f_2^* increases with the number of helpers, so $\mathrm{d}f_2^*/\mathrm{d}h > 0$. Third, the late productivity function Π_2 is supermodular, meaning that helping and fertility act as strategic complements, so that $\left(\partial^2\Pi_2/\partial f_2\partial h\right)_{f_2=f_2^*} > 0$ holds. Fourth, helpers alleviate the total percent trade-off at optimal late fertility, so that

$$\left(\frac{\partial}{\partial h}\left[\epsilon_{f_2}(s_M) + \epsilon_{f_2}(s_2)\right]\right)_{f_2=f_2^*} > 0 \qquad \text{(alleviation condition)}$$

holds, where

$$\epsilon_X(Y) = \frac{X}{Y}\frac{\partial Y}{\partial X} = \frac{\partial \ln Y}{\partial \ln X} \tag{2}$$

is the elasticity of Y with respect to X (i.e., the percent change in Y caused by a marginal percent increase in X [40]). The elasticities $\epsilon_{f_2}(s_M)$ and $\epsilon_{f_2}(s_2)$ measure the assumed percent life-history trade-offs and consequently satisfy $\epsilon_{f_2}(s_M) < 0$ or $\epsilon_{f_2}(s_2) < 0$. The quantity $\epsilon_{f_2}(s_M) + \epsilon_{f_2}(s_2) < 0$ thus measures the total percent life-history trade-off (Fig. 3). We conclude that a key requirement for conflict dissolution via maternal reproductive specialization is that the severity of the total percent-life history trade-off faced by mothers at an optimal fertility is marginally decreasing with the number of helpers.

Promoters of conflict dissolution

Conflict dissolution depends on the relative evolutionary speeds of the co-evolving traits, as speeds determine the size of the basin of attraction toward agreement [14]. Conflict dissolution is thus promoted by higher genetic variance of maternally-controlled traits and lower genetic variance of offspring-controlled traits (Fig. 4A,B). The power of mother and offspring on determining the joint phenotype [34] also affects the evolutionary speed (but not the direction of selection) of influence and resistance. Hence, conflict dissolution is promoted by high maternal power (Fig. 4C). Finally, the evolutionary speed depends on whether mother and offspring contest the joint phenotype simultaneously (e.g., behaviorally, through aggression [10, 39]) or sequentially (e.g., physiologically, where the mother alters offspring development through nutrition or hormones transferred before eclosion or birth [24, 37]). Conflict dissolution is promoted by simultaneous contests if resistance is small (Fig. 4D; see SI Appendix, section 7).

Discussion

We have shown that maternal reproductive specialization can dissolve conflict and yield a major transition. Conflict dissolution occurs here because of the evolutionary synergy between offspring help and maternal fertility, whereby the benefit of helping increases to a point that the original parent-offspring conflict shifts to parent-offspring agreement. This provides a widely applicable mechanism for the converted helping hypothesis to explain the origin of eusociality and various hallmarks thereof. This hypothesis, where ancestrally

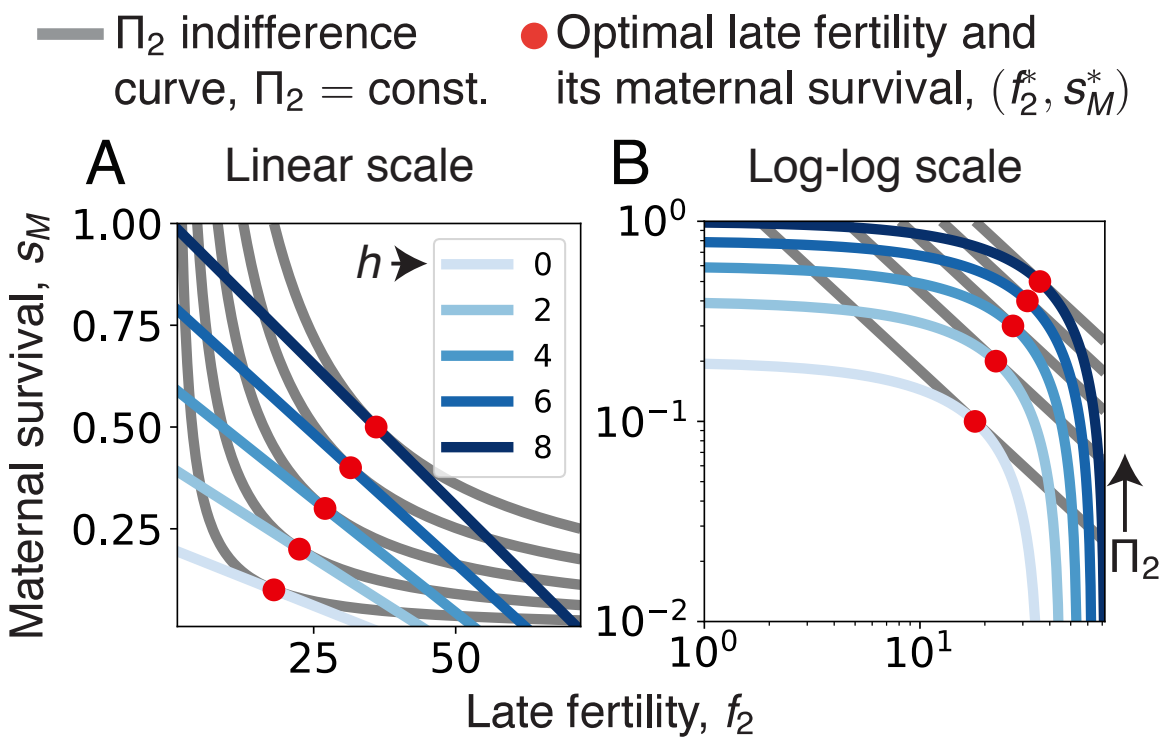

Figure 3: Survival-fertility trade-off alleviation by helpers. Here, parent survival s_M decreases with late fertility f_2 due to the assumed trade-off (*blue lines*; linear trade-off in (A) linear scale or (B) log-log scale) whereas second-brood survival s_2 is constant. For a given number of helpers, h, an optimal late fertility f_2^* occurs when a s_M curve has the same slope as a Π_2 indifference curve (*gray*, where late productivity Π_2 is constant). In log-log-scale, all Π_2 indifference curves have the same slope, namely -1, as $\partial\Pi_2/\partial f_2 = 0$ is equivalent to $\epsilon_{f_2}(s_M) + \epsilon_{f_2}(s_2) = -1$ (see SI Appendix, section 5). Since here $\epsilon_{f_2}(s_2) = 0$, the alleviation condition states that, in log-log scale, the slope of s_M wrt f_2 increases with increasing h at an optimal f_2^*. Equivalently, f_2^* increases with h (*red dots* move to the right as h increases). Functional forms and parameter values are as in Fig. 2.

manipulated helping eventually becomes voluntary, brings together advantages of both the voluntary helping [16] and maternal manipulation [2, 28] hypotheses without bringing in their disadvantages.

The converted helping hypothesis brings advantages in that eusociality arises under less stringent conditions than under voluntary helping, while being supported by the available evidence supporting both voluntary helping and maternal manipulation. First, by being initially manipulated, converted helping requires smaller benefit-cost ratios than voluntary helping at the start of the evolutionary process. Second, converted helping co-occurs with maternal influence. Thus, the converted helping hypothesis is consistent with the widespread maternal influence observed across eusocial taxa. In contrast, widespread maternal influence is not necessarily expected from ancestral voluntary helping. Third, by being eventually voluntary, converted helping requires high relatedness of helpers toward help recipients. Hence, the converted helping hypothesis is consistent with evidence that eusociality originated exclusively under lifetime monogamy [20].

In turn, the converted helping hypothesis does not bring disadvantages in that it is not refuted by the available evidence of voluntary helping refuting the maternal manipulation hypothesis. First, by turning manipulated helping into voluntary helping, conflict dissolution eliminates selection for resistance that would destabilize the eusocial system [21]. Second, since conflict dissolution turns manipulation into honest signaling, the converted helping hypothesis is consistent with evidence in extant taxa that queen pheromones act as honest signals rather than as manipulative control [19, 21, 30, 43].

Although converted helping initially requires smaller benefit-cost ratios than voluntary helping, conflict dissolution is not necessarily straightforward. Indeed, conflict dissolution has additional conditions other than Hamilton's rule (e.g., the persuasion condition and conversion condition) and occurs under restricted parameter combinations (e.g., Fig. 4). This is in principle consistent with the patchy taxonomic distribution of eusociality, including the absence of eusociality in vast numbers of species with high intra-colony relatedness [29].

Our mathematical model is related to previous models showing how the co-evolutionary dynamics of mul-

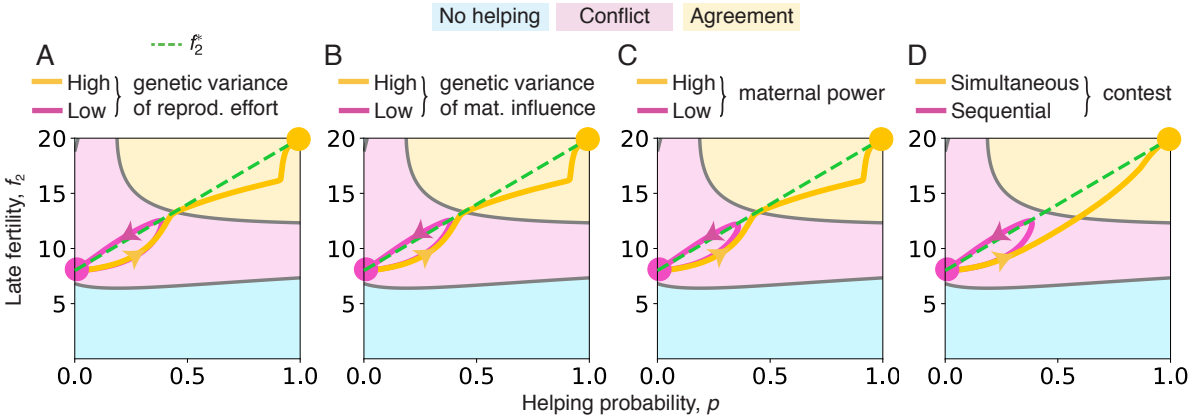

Figure 4: Promoters of conflict dissolution. Resistance wins (trajectory ending at the *purple circle*) or conflict dissolution occurs (trajectory ending at *yellow circle*), respectively for (A) low or high genetic variance of reproductive effort, (B) low or high genetic variance of maternal influence, (C) low or high maternal power, and (D) sequential or simultaneous determination of the joint helping phenotype. The genetic system is diploid and both sexes help. Functional forms and parameter values are as in Fig. 2 except as follows. For A, $G_z = 225$ for low genetic variance of z and $G_z = 250$ for high genetic variance of z. For B, $G_x = 0.9$ for low genetic variance of x and $G_x = 1$ for high genetic variance of x (and $G_z = 250$ for both). For C, $\chi = 0.9$ for low maternal power and $\chi = 1$ for high maternal power (and $G_z = 250$ for both). For D, sequential contest and simultaneous contest (and $G_z = 225$ for both). High genetic variance of z is used here for visualization, but is not necessary for conflict dissolution (cf. SI Appendix, Fig. S14).

tiple traits can make manipulated helping become voluntary [14, 15] (see also [1, 35, 38] for similar ideas in other systems). These models show that maternal manipulation can trigger not only the evolution of helper resistance but also the evolution of helper efficiency [14] or of the reduction of maternal care [15]. The evolution of these traits can make the benefit-cost ratio increase sufficiently over evolutionary time for voluntary helping to become favored. In a similar vein, we have shown that manipulation can trigger the evolution of maternal reproductive specialization, which can make the benefit increase sufficiently for conflict to shift to agreement. The key requirement of our mechanism is that helpers alleviate the total percent life-history trade-off limiting maternal fertility (i.e., the alleviation condition). This requirement is likely to hold widely across eusocial taxa—indeed, trade-off alleviation is thought to be key to explain queens' extraordinary fertility and longevity [23]. This contrasts with the more limited applicability of previously reported conflict dissolution mechanisms [14, 15], which did not yield high maternal fertility and had more restrictive requirements, namely costly helping inefficiency [14] or better help use by maternally neglected offspring [15].

We distinguish conflict *dissolution* (the switch from conflict to agreement) from conflict *resolution* (the outcome of conflict even if conflict persists [13]). Conflict resolution is a static concept where it is enough to study evolutionary equilibria (e.g., evolutionarily stable strategies—ESSs), whereas conflict dissolution is a dynamic concept that requires an explicit consideration of the evolutionary dynamics. To establish that conflict dissolution has occurred, it is not sufficient to know that a population is at an agreement equilibrium, as the population may or may not have arrived to the equilibrium from the conflict zone. Instead, one must consider initial conditions and the basins of attraction to agreement. For instance, the observed worker reproduction in *Melipona* bees matches the predicted optimum from the worker's perspective rather than the queen's perspective (Fig. 4 in [30]). However, while the match between conflict resolution models and data suggests that helping is voluntary at present, this is insufficient to rule out that helping was originally manipulated and only later became voluntary. In this sense, conflict dissolution depends on the evolutionary history, whereas conflict resolution is independent of it.

Empirical inference of conflict dissolution may use its dependence on evolutionary history. In particular, conflict relics may be indicative of conflict dissolution [15]. For instance, the complex chemical composition of honeybee queen mandibular pheromone (QMP; which inhibits worker reproduction) suggests that it resulted from an arms race [18] that seemingly halted since (i) worker reproduction follows the workers' inclusive-fitness interests [30, 45], (ii) QMP behaves as an honest signal [19, 50], and (iii) QMP composition is similar among related species [30, 31]. By stemming from a halted arms race, QMP may be a conflict relic suggesting that conflict dissolution occurred.

Eusociality through conflict dissolution via maternal reproductive specialization contains all the ingredi-

ents of a major transition [48]. First, cooperation evolves, specifically under relatively lax conditions because it is triggered by maternal manipulation. Second, division of labor evolves as the mother specializes in reproduction while offspring help in tasks such as colony defense, brood care, and foraging. Third, honest communication evolves due to conflict dissolution as manipulation becomes honest signaling. Fourth, mutual dependence evolves as the queen becomes unable to survive or reproduce without helpers (Fig. 2J). Fifth, negligible within-group conflict evolves since dissolution eliminates the parent-offspring conflict. Yet, we did not let adults reproduce asexually in their natal nest. Such a conflict might persist in haplodiploids but can be removed by subsequent evolution of multiple mating and worker policing (as reviewed in [48]).

Conflict dissolution suggests manipulation might play a role in explaining the empirically observed relevance of how groups are formed. Major transitions are envisaged to involve two steps, namely group formation and group transformation [4, 48]. How group formation occurs is thought to be key for major transitions to ensue, since both obligate multicellularity and eusociality have occurred by the staying together, and not the coming together, of lower-level entities [48]. Group formation matters in that staying together typically leads to higher relatedness relative to coming together, yet coming together can lead to high relatedness [12] but has seemingly not led to a major transition. This suggests high relatedness alone is insufficient to explain why group formation is crucial. A contributing factor may be that staying together provides a stage for manipulation: the maternal entity has a monopolistic power asymmetry in the group, at the very least by being there first. Even in clonal groups which lack genetic conflict between group members, such power asymmetry may be exploited by parasitic genetic elements seeking to promote their own transmission (due to different transmission patterns among transposons, nuclear genes, and cytoplasmic genes, or due to different relatedness coefficients [47]). A parasitic genetic element might gain control of the division machinery of its host cell, keep daughter cells together, and exploit them to its own benefit. This might occur against the interests of the host cell (i.e., with $B < C$ from the cell's perspective), possibly releasing an arms race [22]. However, in analogy to our results, such manipulation might also release the evolution of some form of specialization, eventually dissolving conflict between host and parasite, yielding a mutualism.

Although group formation and transformation are seen as occurring sequentially [48], our results indicate that they may reinforce each other. Group formation is seen as occurring first, whereby conflict is reduced [48]. Subsequently, group transformation, involving the evolution of division of labor, is seen as following [48]. In contrast, our model shows that after some incipient group formation via manipulation, group transformation can ensue via maternal reproductive specialization, which can then feed back to increase selection for helping. This positive feedback between helping and division of labor triggered by manipulation can dissolve conflict and generate a major transition from solitary living to eusociality.

Our results suggest how other major transitions might occur via similar mechanisms. Both the possibility of manipulation and the alleviation by manipulated parties of trade-offs faced by manipulating parties can occur in multiple settings. Additionally, subsequent interest alignment may occur not only through kin-selected benefits, but also through direct benefits. Thus, conflict dissolution may not only apply to fraternal but also to egalitarian major transitions [32]. Further, conflict dissolution is likely to be important in cultural evolution. For instance, tax in its earliest forms constituted enforced labor [6], although tax compliance is now voluntary to a large extent in developed economies [46]. Voluntary tax compliance might stem from initial exploitation by monopolist rulers, triggering cultural evolution (e.g., of societal benefits) that dissolved conflict to some extent (e.g., as personal ethics evolve leading many subjects to eventually want to pay tax).

We have obtained our results using a rigorous derivation of the selection gradients from an underlying genetic and demographic model. This contrasts with common heuristic approaches where verbal arguments informed by inclusive fitness theory are given in place of derivations. By avoiding derivations, heuristic approaches may lead to error. For instance, the monogamy hypothesis proposes that eusociality requires lifetime monogamy because it makes helpers value equally an offspring or a sibling [3, 4, 11, 48]. More specifically, it is heuristically argued that helping evolves if $Br_{\mathrm{h}} > Cr_{\mathrm{o}}$ where r_{h} and r_{o} are the relatedness of a helper toward the offspring of the helped individual and toward the offspring of the helper, respectively. Under lifetime monogamy, $r_{\mathrm{h}} = r_{\mathrm{o}} = 1/2$, and the condition becomes $B > C$ [3, 4, 11, 48]. However, this condition does not emerge from our model and other previous models (e.g., [8], where C is weighted by relatedness to self, not to one's offspring). Thus, although lifetime monogamy facilitates eusociality by increasing within-colony relatedness, as supported by empirical evidence, the logic proposed to justify the monogamy hypothesis is not supported by our results. We suggest that potential error along these lines can be avoided by complete models. While complete models require more work to derive, they need not be derived from scratch every time and can instead be built upon.

Our approach also departs from influential approaches to build kin selection models. In particular, the approach of Taylor and Frank [41] (hereafter, TF) verbally argues that the selection gradient of a social trait can be derived as the total derivative of personal fitness, which is assumed to be a function of the breeding value of

a focal individual and of the least-square predicted breeding value of social partners with respect to the focal's breeding value. TF's approach does not prove what such personal fitness is, leaving this to a subjective choice that can lead to error. Moreover, with TF's approach, one has to decide who the help recipient is to calculate relatedness (thus, the approach is unable to identify the logic problem of the monogamy hypothesis). If helpers help the mother, relatedness would reasonably be toward mothers, but this is not what we find (relatedness is toward siblings even if help is toward mother). Additionally, with TF's approach, relatedness is treated as a parameter or endogenised a posteriori by so-called closed models [9], which however cannot address the underdetermination of the used fitness measure. Finally, TF's approach takes a direct fitness perspective, where the benefit of helping refers to the helping *received* by helpers, rather than an inclusive fitness perspective, where the benefit of helping refers to the helping *given* by helpers. In contrast, our approach follows standard invasion analysis techniques, proves what the relevant fitness measure is given our assumptions (parent's productivity), and proves a relationship between selection gradients and inclusive-fitness effects, which offer an inclusive rather than a direct fitness perspective. Importantly, we prove which relatedness measure is relevant, with which associated weights, and do not rely on a priori choices of who recipients of help are or a posteriori decisions typical of closed models.

To conclude, our results offer a widely applicable mechanism for a unified hypothesis for the origin of eusociality and diverse features thereof, and suggest a reinterpretation of available evidence. More generally, analogous mechanisms of conflict dissolution operating during evolutionary, cultural, or behavioral timescales may help understand how agreement can arise from conflict.

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