Eusociality through conflict dissolution via maternal reproductive specialization

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Major evolutionary transitions have produced higher-level individuals constituting new levels of adaptation with extensive effects on the history of life. How such transitions occur remains an outstanding question. We show that a major transition can happen from ancestral exploitation triggering specialization that eventually dissolves conflict. Specifically, maternal manipulation of offspring help enables the mother to increase her fertility effort, thereby shifting a parent-offspring conflict over helping to parent-offspring agreement. This process of conflict dissolution requires that helpers alleviate maternal life-history trade-offs, and results in reproductive division of labor, high queen fertility, and honest queen signaling suppressing worker reproduction, thus exceptionally recovering diverse features of eusociality. Our results explain how a major evolutionary transition can happen from ancestral conflict.

Major transitions in individuality from ancestral non-clonal groups (e.g., from prokaryotes to eukaryotes, from solitary living to eusociality, and from multicellular organisms to inter-

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specific mutualisms) require a substantial decrease in within-group conflict (*1*). Low conflict is currently sought with factors facilitating cooperation (notably, high relatedness), repressing competition (e.g., through policing or punishment), or aligning group members' interests (e.g., through concomitant reproduction of group members) (*1*). Yet, a key question is how the evolutionary switch from conflict to interest alignment can occur (*2*).

Here we report a process that dissolves conflict, that is, whereby conflict evolves to interest alignment, and that yields a transition to eusociality. In this process, (i) the mother manipulates offspring to become helpers; (ii) while offspring evolve resistance to manipulation, the mother uses available help to become more fertile; (iii) increased maternal fertility increases the benefit of helping to the point of rendering helping voluntary (Fig. 1A,B). To show how this process can occur, we formulate a game theory model and an evolutionary model.

Consider a sequential game between a mother (M) and a female offspring (O) (Fig. 1C). First, M either manipulates O (e.g., behaviorally via differential food provisioning (*3*) or physiologically with hormones (*4*) or pheromones (*5*)) or not. Second, if M manipulates O, then O either resists manipulation or not. If O does not resist, then O 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 sisters are related 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 manipulate 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 ($1 < B/C < 1/r$), selection favors resistance and manipulation does not yield helping—the game has two subgame perfect equilibria, one with resistance and the other without manipulation.

Consider now an extended game where, after O moves, M can choose (e.g., plastically (*9*)) between specializing into reproduction or not (Fig. 1D). If O resists, M pays a cost K for specializing due to a life-history trade-off. If O does not resist, M produces an extra number of

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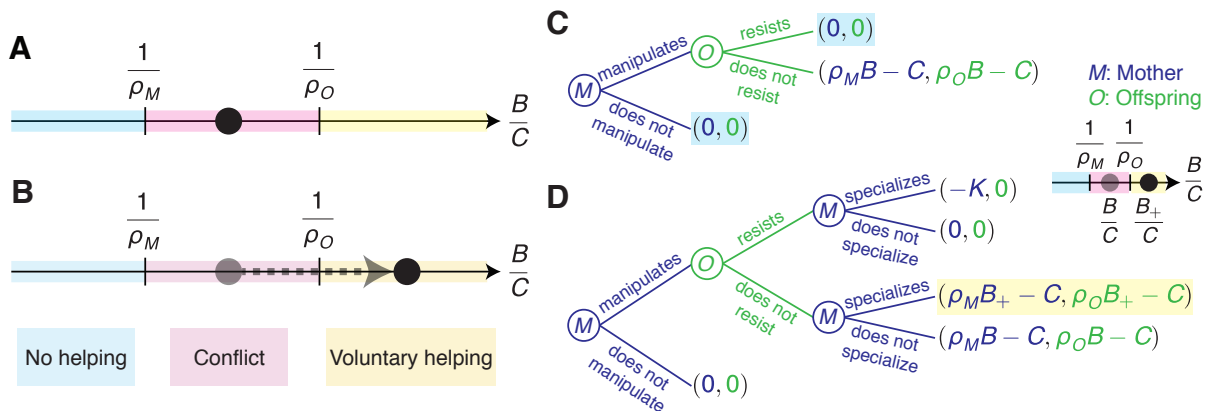Figure 1: Conflict dissolution. (**A,B**) Helping is (i) disfavored by mother and offspring if the benefit-cost ratio B/C satisfies $B/C < 1/\rho_M$ ("no helping" zone); (ii) favored by mother and offspring if $B/C > 1/\rho_O$ ("voluntary helping" zone); or (iii) favored by mother and disfavored by offspring if $1/\rho_M < B/C < 1/\rho_O$ ("conflict" zone). Conflict dissolution occurs when (**A**) B/C starts in the conflict zone and (**B**) ends in the voluntary helping zone. Helping is favored by actors A when $\rho_A B - C > 0$ (a Hamilton's rule; (6)), where C is the cost to helpers, B is the benefit to help recipients, and ρ_A is the "relative reproductive worth" of help recipients for actors A relative to helpers, which generalizes life-for-life relatedness (7) to allow helpers and recipients of both sexes (if all offspring are female, $\rho_M = r_M/r_M = 1$ and $\rho_O = r/1 = r$) (8). (**C,D**) Sequential games modeling conflict and conflict dissolution via maternal reproductive specialization. (**C**) Without specialization, conflict yields equilibria without helping (shaded); (**D**) with specialization, conflict no longer occurs if $B_+/C > 1/\rho_O$, yielding a unique equilibrium with voluntary helping (shaded).

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daughters B_+ at no cost provided the helper alleviates the trade-off. If helping and specialization are synergistic enough that $B_+/C > 1/r$, there is no conflict with specialization although there

42 is without. Thus, manipulation and specialization yield helping: the extended game has a unique subgame perfect equilibrium with manipulation, specialization, and no resistance. This shows that if mothers can use offspring help to increase the benefit sufficiently, the conflict can be

45 dissolved.

We now show, using an evolutionary model, that such evolution of the benefit can occur. The model is class-structured with explicit population and mutant-invasion dynamics, which allows

48 us to derive rather than assume inclusive-fitness payoffs (the model is fully described in (8)). We consider a large population with 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

51 sexes or only females help, which covers the spectrum of known eusocial taxa (10). A mated pair produces f_1 first-brood offspring and with probability s_M survives to old age to produce f_2 second-brood offspring. Each first-brood offspring of the helper sex becomes a helper with

54 probability p or disperses; hence, the number of helpers h of a mated pair is 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 randomly

57 once and start a nest if nesting sites are available. We assume 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 mated-pair or second-brood

60 survival, so that s_M or s_2 increases with h. A mated pair's expected number of reproductive first- or second-brood offspring is given by $\Pi_1 = (f_1 - h)s_1$ and $\Pi_2 = s_M f_2 s_2$, respectively. We study the co-evolutionary dynamics of the offspring helping probability p and the maternal

63 reproductive effort z. We let p be under maternal, offspring, or shared control. Under shared control, p is a joint phenotype (11) that increases with maternal influence x (e.g., pheromone

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production) and decreases with offspring resistance y (e.g., receptor antagonist production). Reproductive effort z is under maternal control.

If maternal influence and offspring resistance co-evolve under conflict while reproductive effort is constant, resistance may win the ensuing arms race and eliminate helping in the long run (Fig. 2A-E). This matches the standard expectation (*12*). Alternatively, if reproductive effort co-evolves with influence and resistance, the benefit-cost ratio can move out of the conflict zone (Fig. 2F-J). In this case, the arms race vanishes as manipulated helping becomes voluntary. The 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 (*13*): the resulting maternal influence alters the recipient's phenotype in recipient's interest (i.e., helpers are induced to help, and they "want" to help); the signaler evolved to produce that effect (i.e., influence evolved to induce helping); and the recipient evolved to attend the signal (i.e., offspring evolved lack of resistance to influence). This process constitutes conflict dissolution via maternal reproductive specialization, which generates eusociality with reproductive division of labor, high queen fertility, and queen suppression of worker reproduction via an honest signal.

We now show that this conflict dissolution process requires that helpers alleviate the trade-offs limiting maternal fertility. Each evolving trait ζ is favored by selection if and only if its inclusive-fitness effect $\mathcal{H}_\zeta$ is positive (*8*). For helping, $\mathcal{H}_p \propto \rho_A B - C$, where $C = -\partial \Pi_1 / \partial h = s_1$, $B = \partial \Pi_2 / \partial h$, and ρ_A depends on relatedness, sex-specific reproductive values, and the stable sex distribution. For reproductive effort, $\mathcal{H}_z \propto \partial \Pi_2 / \partial f_2$. Conflict occurs when the mother favors helping (i.e., $\mathcal{H}_p > 0$ with p under maternal control) while offspring disfavor helping (i.e., $\mathcal{H}_p < 0$ with p under offspring control). Conflict dissolution occurs when there is conflict at the start of the evolutionary process but mother and offspring favor helping at the end (i.e., $\mathcal{H}_p > 0$ with p both under maternal and offspring control). Hence,
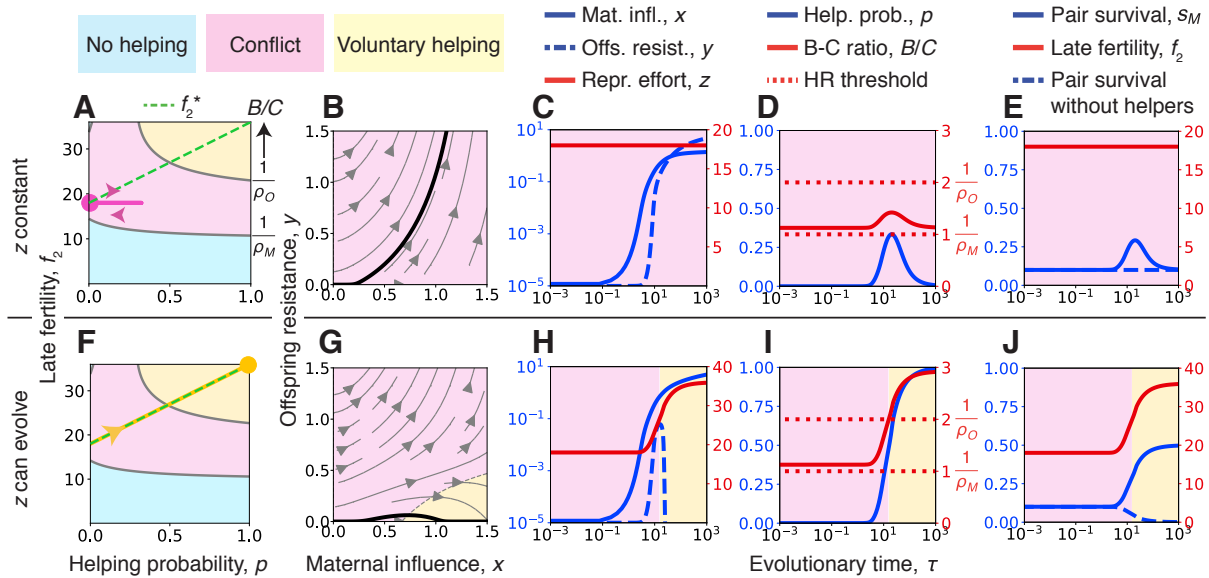
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Figure 2: Conflict dissolution via maternal reproductive specialization (evolutionary model). (**A**-**E**) Co-evolution of maternal influence x and offspring resistance y with constant reproductive effort z (i.e., the genetic variance of z, G_z, is zero), where resistance wins the conflict. (**A**) Starting from conflict, helping increases as maternal influence increases but resistance evolves and helping is lost (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 and benefit-cost ratio, and (**E**) the vital rates. (**F**-**J**) Analogous plots but now reproductive effort evolves as the mother chooses it optimally for the number of helpers she has (i.e., as if $G_z \to \infty$) and resistance disappears. (**F**) Starting from conflict, helping increases as maternal influence increases, and reproductive effort increases yielding voluntary helping (circle). (**G**) Trajectories starting at conflict can converge to voluntary helping. (**H**) Resistance reversal. (**I**) The benefit-cost ratio 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. Functional forms and parameter values used are given in (8).

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conflict dissolution requires that selection for helping under offspring control increases with evolutionary time τ, that is, $\mathrm{d}\mathcal{H}_p/\mathrm{d}\tau > 0$ for p under offspring control, which is equivalent to $\partial\mathcal{H}_p/\partial p\,\mathrm{d}p/\mathrm{d}\tau + \partial\mathcal{H}_p/\partial z\,\mathrm{d}z/\mathrm{d}\tau > 0$. Conflict dissolution via maternal reproductive specialization occurs when $\partial\mathcal{H}_p/\partial z\,\mathrm{d}z/\mathrm{d}\tau > 0$, and thus requires helping-fertility synergy ($\partial\mathcal{H}_p/\partial z > 0$; (*14*)) as reproductive effort increases. Moreover, at an optimal fertility f_2^* (implicitly given by $\partial\Pi_2/\partial f_2|_{f_2=f_2^*} = 0$), helping-fertility synergy is equivalent to helping and fertility acting as strategic complements (i.e., $\partial^2\Pi_2/\partial f_2\partial h|_{f_2=f_2^*} > 0$), which in turn can be written as

$$\left(\frac{\partial\epsilon_{f_2}(s_M)}{\partial h} + \frac{\partial\epsilon_{f_2}(s_2)}{\partial h}\right)\Bigg|_{f_2=f_2^*} > 0, \tag{1}$$

where $\epsilon_X(Y) = (X/Y)\partial Y/\partial X = \partial\ln Y/\partial\ln X$ is the elasticity of Y with respect to X (i.e., the percent change in Y caused by a marginal percent increase in X (*15*)). From our assumptions, $\epsilon_{f_2}(s_M) < 0$ or $\epsilon_{f_2}(s_2) < 0$, so inequality (1) states that helpers alleviate the trade-offs, which is then required for conflict dissolution via maternal reproductive specialization (Fig. 3).

Conflict dissolution depends on the relative evolutionary speeds of the traits, as they determine the size of the basin of attraction toward voluntary helping (*17*). Conflict dissolution is thus promoted by higher genetic variance in maternally-controlled traits and lower genetic variance in offspring-controlled traits (Fig. S13A,B). The power mother and offspring have on determining the joint phenotype (*18*) also affects the evolutionary speed (but not the direction of selection) of influence and resistance (*8*). Hence, conflict dissolution is promoted by relatively high maternal power (Fig. S13C). The evolutionary speed also depends on whether mother and offspring contest the joint phenotype simultaneously (e.g., behaviorally, through aggression (*19, 20*)) or sequentially (e.g., physiologically, where the mother alters offspring development through nutrition or hormones transferred before eclosion or birth (*3,4*)) (*8*). Conflict dissolution is promoted by simultaneous contests (Fig. S13D).

We have shown that maternal reproductive specialization can dissolve conflict and yield a
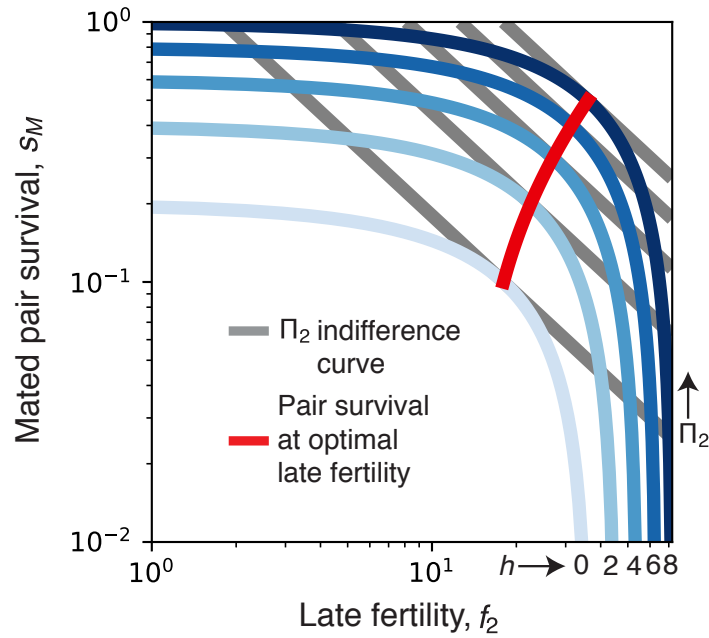
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Figure 3: Helping-fertility synergy as trade-off alleviation. Mated pair survival decreases with late fertility due to the assumed trade-off (blue lines; linear trade-off in log-log scale; cf. Fig. S11). Mated pair survival at an optimal late fertility occurs when a blue line has the same slope as a Π_2 indifference curve (gray, where Π_2 is constant), namely -1, since $\partial \Pi_2 / \partial f_2 = 0$ is equivalent to $\epsilon_{f_2}(s_M) + \epsilon_{f_2}(s_2) = -1$ (cf. (16)). In this example, mated pair survival at an optimal late fertility increases as the number of helpers increases (i.e., the red line has positive slope), meaning that helpers alleviate the trade-off (i.e., (1) holds). Functional forms and parameter values are as in Fig. 2.

114   major transition. While conflict *resolution* refers to the conflict outcome even if conflict persists (*21*) (thus, it is an equilibrium concept), we have defined conflict *dissolution* as the switch from conflict to no conflict (thus, it is an out-of-equilibrium concept). By transforming ma-

117   nipulated helping into voluntary helping, conflict dissolution unifies classic hypotheses for the origin of eusociality from voluntary (*6*) or manipulated (*22*) helping. On the one hand, dissolution makes evidence that queen pheromones are honest signals in extant taxa (*5, 12, 23, 24*)

120   consistent with manipulation at the origin of eusociality. On the other hand, dissolution requires that Hamilton's rule is eventually met from the offspring perspective, which is facilitated by high relatedness. Thus, dissolution also makes evidence that eusociality originated exclu-

123   sively under lifetime monogamy (*25*) consistent with manipulation at the origin of eusociality. The fact that dissolution has additional conditions (e.g., (*1*)) and occurs under restricted parameter combinations (Fig. S11) is in principle consistent with the patchy taxonomic distribution of

126   eusociality, including the absence of eusociality in vast numbers of species with high relatedness (*26*). Moreover, dissolution helps explain the widespread occurrence of maternal influence on workers across the diverse eusocial taxa, which seems more difficult to explain from ances-

129   tral voluntary helping.

    Crucially, the process of conflict dissolution we identify requires that helpers alleviate trade-offs limiting maternal fertility. Such trade-off alleviation is feasible across eusocial taxa—

132   indeed, it is thought to be key to explain queens' extraordinary fertility and longevity (*27*). This contrasts with previously reported conflict dissolution processes (*17, 28*), which did not yield high maternal fertility and had more restrictive requirements, namely costly helping inefficiency

135   (*17*) or better help use by maternally neglected offspring (*28*).

    Empirical inference of conflict dissolution may use its dependence on evolutionary history. In particular, conflict relics may be indicative of conflict dissolution (*28*). For instance,

138   the complex chemical composition of honeybee queen mandibular pheromone (QMP; which

inhibits worker reproduction) suggests that it resulted from an arms race (*29*) that seemingly halted since (i) worker reproduction follows the workers' inclusive-fitness interests (*23, 30*), (ii) QMP behaves as an honest signal (*24, 31*), and (iii) QMP composition is seemingly similar among related species (*23, 32*). By seemingly stemming from a halted arms race, QMP may be a conflict relic suggesting conflict dissolution.

To conclude, our results offer a unified hypothesis for the origin of eusociality and diverse features thereof, and suggest a reinterpretation of available evidence. More generally, conflict dissolution via analogous processes occurring during evolutionary, cultural, or behavioral timescales may help understand how agreement arises.

References

1. S. A. West, R. M. Fisher, A. Gardner, E. T. Kiers, *Proc. Natl. Acad. Sci. USA* **112**, 10112 (2015).

2. E. Akçay, *Am. Nat.* **195**, 315 (2020).

3. S. P. Lawson, S. L. Helmreich, S. M. Rehan, *J. Exp. Biol.* (2017).

4. T. Schwander, *et al.*, *Curr. Biol.* **18**, 265 (2008).

5. A. Van Oystaeyen, *et al.*, *Science* **343**, 287 (2014).

6. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).

7. W. D. Hamilton, *Ann. Rev. Ecol. Sys.* **3**, 193 (1972).

8. Materials and methods are available as supplementary material online.

9. K. M. Kapheim, *et al.*, *Proc. Natl. Acad. Sci. USA* **117**, 13615 (2020).

10

10. L. Ross, A. Gardner, N. Hardy, S. A. West, *Curr. Biol.* **23**, 2383 (2013).

11. D. C. Queller, *Phil. Trans. R. Soc. B* **369**, 20130423 (2014).

12. L. Keller, P. Nonacs, *Anim. Behav.* **45**, 787 (1993).

13. J. Maynard Smith, D. Harper, *Animal Signals* (Oxford Univ. Press, New York, 2003).

14. S. P. Brown, P. D. Taylor, *Proc. R. Soc. B* **277**, 415 (2010).

15. K. Sydsæter, P. Hammond, A. Strom, A. Carvajal, *Essential Mathematics for Economic Analysis* (Pearson Education Limited, Harlow, UK, 2016), fifth edn.

16. E. L. Charnov, *Nature* **387**, 393 (1997).

17. M. González-Forero, *Evolution* **68**, 2038 (2014).

18. D. C. Queller, J. E. Strassmann, *Annu. Rev. Ecol. Evol. Syst.* **49**, 73 (2018).

19. A. A. Smith, B. Hölldobler, J. Liebig, *Naturwissenschaften* **98**, 237 (2011).

20. B. Dantzer, *et al.*, *Proc. R. Soc. B* **284** (2017).

21. H. C. J. Godfray, *Nature* **376**, 133 (1995).

22. R. D. Alexander, *Ann. Rev. Ecol. Syst.* **5**, 325 (1974).

23. C. A. Oi, *et al.*, *BioEssays* **37**, 808 (2015).

24. L. Holman, *Behav. Ecol.* **29**, 1199 (2018).

25. W. O. H. Hughes, B. P. Oldroyd, M. Beekman, F. L. W. Ratnieks, *Science* **320**, 1213 (2008).

26. M. Nowak, C. Tarnita, E. Wilson, *Nature* **466**, 1057 (2010).

11

177 27. B. H. Kramer, G. S. van Doorn, F. J. Weissing, I. Pen, *Curr. Opin. Insect Sci.* **16**, 76 (2016).

28. M. González-Forero, *J. Evol. Biol.* **28**, 2208 (2015).

29. A. Hefetz, T. Katzav-Gozansky, *Apiacta* **39**, 44 (2004).

180 30. T. Wenseleers, H. Helanterä, D. A. Alves, E. Dueñez-Guzmán, P. Pamilo, *Biol. Lett.* **9**, 20130334 (2013).

31. M. L. Winston, *et al.*, *Ins. Soc.* **36**, 15 (1989).

183 32. E. Plettner, *et al.*, *J. Chem. Ecol.* **23**, 363 (1997).

Acknowledgments

Supplementary materials

Materials and Methods

Table S1

Fig. S1-S16

References *(33-65)*

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