

⁸¹Department of Biology, 3314 Spieth Hall, University of California — Riverside, Riverside, California 92521, USA.

⁸²ETH Zurich, Institute of Integrative Biology (IBZ), Universitätsstrasse 16, CH.8092 Zürich, Switzerland.

⁸³School of Philosophy, Psychology and Language Sciences, University of Edinburgh, 3 Charles Street, Edinburgh EH8 9AD, UK.

⁸⁴School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK.

⁸⁵William Paterson University of New Jersey, 300 Pompton Road, Wayne, New Jersey 07470, USA.

⁸⁶Department of Anthropology, 101 West Hall, University of Michigan, Ann Arbor, Michigan 48109, USA.

⁸⁷Department of Entomology and Department of Animal Biology, University of Illinois, Urbana, Illinois 61801, USA.

⁸⁸Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland.

⁸⁹Department of Biology, University of Western Ontario, 1151 Richmond Street North, London, Ontario N6A 5B7, Canada.

⁹⁰Department of Anthropology, University of California, Santa Barbara, California 93106-3210, USA.

⁹¹Department of Environmental Science, Policy and Management, 130 Mulford Hall, 3114, University of California Berkeley, Berkeley, California 94720-3114, USA.

⁹²Faculty of Agriculture, University of the Ryukyus, Okinawa 903-0213, Japan.

⁹³Dipartimento di Biologia Evoluzionistica, Università degli Studi di Firenze, via Romana 17, 50125 Firenze, Italy.

⁹⁴Department of Ecology and Evolutionary Biology, University of Tennessee Knoxville, Knoxville, Tennessee 37902, USA.

⁹⁵Department of Entomology, Box 7613, North Carolina State University, Raleigh, North Carolina 27695-7613, USA.

⁹⁶Institute for Theoretical Biology, Humboldt University zu Berlin, Invalidenstr. 43, D-10115 Germany.

⁹⁷Department of Biology, Zoological Institute, K.U. Leuven, Naamsestraat 59, B-3000 Leuven, Belgium.

⁹⁸Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panamá.

⁹⁹Department of Biology, 101 Morgan Building, University of Kentucky, Lexington, Kentucky 40506-0225, USA.

¹⁰⁰Department of Applied Mathematics, University of Western Ontario, 1151 Richmond Street North, London, Ontario N6A 5B7, Canada.

¹⁰¹Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA.

¹⁰²Department of Biology and Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Nevada 89557, USA.

¹⁰³Department of Biology, San Francisco State University, San Francisco, California 94132, USA.

Received 20 September; accepted 17 December 2010.

- Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466**, 1057–1062 (2010).
- Hamilton, W. D. The genetical evolution of social behaviour, I & II. *J. Theor. Biol.* **7**, 1–52 (1964).
- Hamilton, W. D. Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**, 1218–1220 (1970).
- Grafen, A. Optimisation of inclusive fitness. *J. Theor. Biol.* **238**, 541–563 (2006).
- Frank, S. A. *Foundations of Social Evolution* (Princeton Univ. Press, 1998).
- Gardner, A., West, S. A. & Barton, N. H. The relation between multilocus population genetics and social evolution theory. *Am. Nat.* **169**, 207–226 (2007).
- Rousset, F. *Genetic Structure and Selection in Subdivided Populations* (Princeton Univ. Press, 2004).
- Queller, D. C. A general model for kin selection. *Evolution* **46**, 376–380 (1992).
- Krebs, J. R. & Davies, N. B. *Behavioural Ecology. An Evolutionary Approach* 4th edn (Blackwell Scientific, 1997).
- Foster, K. R. A defense of sociobiology. *Cold Spring Harb. Symp. Quant. Biol.* **74**, 403–418 (2009).
- Westneat, D. F. & Fox, C. W. *Evolutionary Behavioral Ecology* (Oxford Univ. Press, 2010).
- Hardy, I. C. W. *Sex Ratios: Concepts and Research Methods* (Cambridge Univ. Press, 2002).
- West, S. A. *Sex Allocation* (Princeton Univ. Press, 2009).
- Queller, D. C. & Strassmann, J. E. Kin selection and social insects. *Bioscience* **48**, 165–175 (1998).
- Boomsma, J. J. Lifetime monogamy and the evolution of eusociality. *Phil. Trans. R. Soc. Lond. B* **364**, 3191–3207 (2009).
- Ratnieks, F. L. W., Foster, K. R. & Wenseleers, T. Conflict resolution in insect societies. *Annu. Rev. Entomol.* **51**, 581–608 (2006).

Author Contributions All authors contributed to the planning, writing and/or revising of this paper. Several others who contributed significantly are not listed because they are named on separate comments.

Competing financial interests: declared none.

doi:10.1038/nature09831

Only full-sibling families evolved eusociality

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466**, 1057–1062 (2010)

The paper by Nowak *et al.*¹ has the evolution of eusociality as its title, but it is mostly about something else. It argues against inclusive fitness theory and offers an alternative modelling approach that is claimed to be more fundamental and general, but which, we believe, has no practical biological meaning for the evolution of eusociality. Nowak *et al.*¹ overlook the robust empirical observation that eusociality has only arisen in clades where mothers are associated with their full-sibling offspring; that is, in families where the average relatedness of offspring to siblings is as high as to their own offspring, independent of population structure or ploidy. We believe that this omission makes the paper largely irrelevant for understanding the evolution of eusociality.

Eusociality is not just any form of condition-dependent reproductive altruism as found in cooperative breeders, but the permanent division of reproductive labour. Clades where helpers became irreversibly eusocial (ants, some bees, some wasps, and termites²) are old, radiated into many subclades over evolutionary time, and achieved considerable ecological footprints. A recent comparative study³ showed that all hymenopteran

clades that fit the standard definition of eusociality⁴ evolved from lifetime monogamous ancestors^{5–8}. This implies that high relatedness always preceded or coincided with eusociality, and contrasts with the contention of Nowak *et al.*¹ that eusociality can evolve in any group with parental care, or that high relatedness arises after eusociality.

Given that promiscuity is the most common mating system in animals, strict ancestral monogamy throughout eusocial clades implies that high relatedness was necessary for eusociality to evolve. Nonetheless, necessity does not imply sufficiency. Monogamous lineages may have remained solitary because the benefits of helping at the nest were insufficient to surpass independent breeding. This is elegantly captured by the ratio of the parameters *b* and *c* in Hamilton's rule. In a number of ant, bee and wasp genera the high relatedness condition for eusociality has become secondarily relaxed via evolutionary elaborations such as multiple queen mating, but this has only occurred after worker phenotypes had specialized so that opting out to independent breeding had become selectively disadvantageous or

developmentally impossible³. Claiming (in their Supplementary Information, Part B) that it is far simpler to consider that advanced eusocial species just need more sperm¹ muddles proximate and ultimate explanations^{9,10}; many multiply-mating queens discard most of the sperm they receive^{11,12}, indicating that sperm limitation cannot explain polyandry.

We now also know that departures from high relatedness would almost certainly have prevented the evolution of eusociality if they had happened before sterile castes had become permanent⁸, that is, before reaching the point of no return to breeding independently¹³. A recent comparative study on birds¹⁴ showed that cooperative breeding is an unstable state that predominantly occurs in monogamous clades and is likely to be lost when parents become more promiscuous. This evidence is not merely correlative: differences in ancestral promiscuity between cooperative and non-cooperative species were found even before cooperation arose, illustrating that monogamy preceded the evolution of helping and that helpers leave when relatedness incentives are reduced. This shows that high relatedness among siblings is critical along with the Hamiltonian *b/c* ratio but, as in the insects, relatedness is not sufficient because many monogamous birds are not cooperative breeders.

In light of these reconstructions of the ancestral life histories of numerous social clades, it is surprising that the argument of Nowak *et al.*¹ about eusocial evolution starts by assuming that family structure can be replaced by any form of population structure. This assumption is puzzling given the lack of empirical evidence that this hypothetical 'parasocial' route to eusociality^{1,4} (where same-generation individuals associate independent of relatedness) has produced a single extant clade with obligately eusocial workers. We believe that this renders Part A of the Supplementary Information of Nowak *et al.*¹, and the arguments throughout the first two-thirds of the paper, largely irrelevant to the origin of eusociality. Part C of the Supplementary Information addresses the evolution of sterile workers within monogamous or clonal families, meaning that relatedness in these models is invariant. As a consequence, we believe that these models have nothing to say about the importance of relatedness in the evolution of eusociality beyond showing that costs and benefits are also important. This was already clear from Hamilton's rule nearly half a century ago.

It should give pause for thought that none of the long-recognized approximations of inclusive fitness theory raised in the paper was important enough to preclude kin selection theory from developing into a well-integrated network of complementary hypotheses with high predictive power for reproductive decision-making in real-world social organisms. In contrast, the abstractions of Nowak *et al.*¹ fail to provide any new predictions or questions; all they apparently have to offer is the truism that helpers are associated with longer-lived, fecund breeders.

Jacobus J. Boomsma¹, Madeleine Beekman², Charlie K. Cornwallis³, Ashleigh S. Griffin³, Luke Holman¹, William O. H. Hughes⁴, Laurent Keller⁵, Benjamin P. Oldroyd² & Francis L. W. Ratnieks⁶

¹Centre for Social Evolution, Department of Biology, University of Copenhagen, 2100 Copenhagen, Denmark.

e-mail: JJBoomsma@bio.ku.dk

²Behaviour and Genetics of Social Insects Lab, School of Biological Sciences A12, University of Sydney, New South Wales, Australia.

³Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

⁴Institute of Integrative and Comparative Biology, Miall Building, University of Leeds, Leeds LS2 9JT, UK.

⁵Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland.

⁶Laboratory of Apiculture and Social Insects, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK.

Received 19 September; accepted 17 December 2010.

1. Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466**, 1057–1062 (2010).
2. Inward, D. J. G., Vogler, A. P. & Eggleton, P. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Mol. Phylogenet. Evol.* **44**, 953–967 (2007).
3. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216 (2008).
4. Wilson, E. O. *The Insect Societies* (Belknap Press of Harvard Univ. Press, 1971).
5. Hamilton, W. D. The genetical evolution of social behaviour, I & II. *J. Theor. Biol.* **7**, 1–52 (1964).
6. Alexander, R. D. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383 (1974).
7. Charnov, E. L. Evolution of eusocial behavior: offspring choice or parental parasitism? *J. Theor. Biol.* **75**, 451–465 (1978).
8. Boomsma, J. J. Kin selection versus sexual selection: Why the ends do not meet. *Curr. Biol.* **17**, R673–R683 (2007).
9. Mayr, E. Cause and effect in biology. *Science* **134**, 1501–1506 (1961).
10. Tinbergen, N. On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–433 (1963).
11. Baer, B. Sexual selection in *Apis* bees. *Apidologie (Celle)* **36**, 187–200 (2005).
12. den Boer, S. P. A. *et al.* Prudent sperm use by leaf-cutter ant queens. *Proc. R. Soc. Lond. B* **276**, 3945–3953 (2009).
13. Wilson, E. O. One giant leap: How insects achieved altruism and colonial life. *Bioscience* **58**, 17–25 (2008).
14. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972 (2010).

Author Contributions J.J.B. took the initiative for this contribution and wrote the first draft. All co-authors provided written and/or oral comments that helped shape the final submission.

Competing financial interests: declared none.

doi:10.1038/nature09832

Kin selection and eusociality

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466**, 1057–1062 (2010)

Hamilton¹ described a selective process in which individuals affect kin (kin selection), developed a novel modelling strategy for it (inclusive fitness), and derived a rule to describe it (Hamilton's rule). Nowak *et al.*² assert that inclusive fitness is not the best modelling strategy, and also that its production has been "meagre". The former may be debated by theoreticians, but the latter is simply incorrect. There is abundant evidence to demonstrate that inclusive fitness, kin selection and Hamilton's rule have been extraordinarily productive for understanding the evolution of sociality.

Below we list a few examples of what has been learned from applying kin selection theory—there are thousands of others. (1) Organisms overwhelmingly direct costly assistance, and all true altruism, towards kin³. (2) Eusociality in insects originated in organisms with parental care and single mating, which means that relatedness among helpers and brood is generally at the level of siblings⁴. (3) Benefits that can make helping more profitable than reproducing independently often take the forms of either fortress defence (termites, naked mole rats, social shrimp, social thrips and aphids, and some ants) or life insurance