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## Only full-sibling families evolved eusociality

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The paper by Nowak *et al.*<sup>1</sup> 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.*<sup>1</sup> 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 termites<sup>2</sup>) are old, radiated into many subclades over evolutionary time, and achieved considerable ecological footprints. A recent comparative study<sup>3</sup> showed that all hymenopteran

clades that fit the standard definition of eusociality<sup>4</sup> evolved from lifetime monogamous ancestors<sup>5–8</sup>. This implies that high relatedness always preceded or coincided with eusociality, and contrasts with the contention of Nowak *et al.*<sup>1</sup> 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 impossible<sup>3</sup>. Claiming (in their Supplementary Information, Part B) that it is far simpler to consider that advanced eusocial species just need more sperm<sup>1</sup> muddles proximate and ultimate explanations<sup>9,10</sup>; many multiply-mating queens discard most of the sperm they receive<sup>11,12</sup>, 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 permanent<sup>8</sup>, that is, before reaching the point of no return to breeding independently<sup>13</sup>. A recent comparative study on birds<sup>14</sup> 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.*<sup>1</sup> 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<sup>1,4</sup> (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.*<sup>1</sup>, 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.*<sup>1</sup> 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.

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## Kin selection and eusociality

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Hamilton<sup>1</sup> 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.*<sup>2</sup> 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 kin<sup>3</sup>. (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 siblings<sup>4</sup>. (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