Only full-sibling families evolved eusociality

BRIEF COMMUNICATIONS ARISING

The paper by Nowak et al. 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. 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) are old, radiated into many subclades over evolutionary time, and achieved considerable ecological footprints. A recent comparative study showed that all hymenopteran clades that fit the standard definition of eusociality evolved from lifetime monogamous ancestors. This implies that high relatedness always preceded or coincided with eusociality, and contrasts with the contention of Nowak et al. 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. 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 indecisive.

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Kin selection and eusociality


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 siblings. (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.