SOCIAL EVOLUTION

Family matters

New details of the social and sex lives of platypodine ambrosia beetles support a controversial link between parental monogamy and complex animal societies.

Nicholas G. Davies

How does cooperation evolve? Biologists interested in this fundamental question often look to the eusocial insects, whose complex societies require extraordinary acts of reproductive altruism to function. Writing in *Nature Ecology & Evolution*, Smith and colleagues[1] report on the eusocial ambrosia beetle *Austroplatypus incompertus*, providing both a fascinating account of natural history and crucial evidence for the role of relatedness in the evolution of social behaviour.

The eusocial insects are famous for their sterile workers, who forgo mating and reproduction in order to stay at home and help feed, house and protect their younger nestmates. But most theories about what drives eusociality are inspired by the charismatic and widespread social Hymenoptera (bees, wasps and ants), while less-familiar insect societies tend to be neglected. This focus on hymenopterans has made it difficult to pinpoint which ecological factors are truly important for eusociality, and which just happen to be found in the best-studied examples. Smith et al.'s study of *A. incompertus* — a beetle rather than a hymenopteran — is thus especially illuminating.

These 6 mm Australian beetles lead remarkable lives. After mating, the female founds a colony by burrowing into a eucalyptus tree, first digging an entrance gallery and then slowly excavating two curved tunnels to either side, tracing along the tree's growth rings. At the same time, she plants and tends gardens of the ambrosia fungus *Ambrosiella*, which provide a food source for her and her offspring; she defends the gallery from predators, blocking the entrance with her abrupt, spiny 'elytral declivity' (i.e., bum); and she keeps the gallery clear of kino, a quick-hardening gum exuded by the host tree, floods of which could otherwise spell the colony's doom. She toils at these tasks single-handedly for three years, until her firstborn clutch of larvae are old enough to start pitching in. Another year later, her first offspring reach adulthood, and most leave home to mate. A few daughters stay home to work full-time, assisting their mother with her many duties, including that of extending the increasingly labyrinthine gallery system. (Work is a thankless task: Smith et al. note that workers are sometimes shoved out of the nest by their overeager siblings dispersing to mate[1].) Thanks to her spermatheca, an organ specialized for sperm storage, the mother can lay eggs for a staggering 30–40 years, producing hundreds of offspring without ever needing to mate again before she dies.

Smith et al. report two major findings that deepen our understanding of this fascinating beetle. First, they establish that *Austroplatypus* workers commit to work for life, rather than working for a short time and leaving the nest to mate afterwards as some other ambrosia beetle species do. Work is permanent because adult workers rapidly lose their claws and tarsal segments through wear and tear as they perform gallery maintenance and excavation. As a result, they can no longer cling to vertical surfaces in the outside world. Their confinement to the colony's tunnels precludes workers from mating and colony founding: sex in this species takes place on the sheer slopes of tree trunks, and females need to be able to cling to trees in order to start excavating a nest of their own. Even mating with their brothers — common practice in some other ambrosia beetles — does not seem to be an option, as no workers with filled spermathecae were found. Workers' commitment to permanently forgo mating is considered to be a crucial feature of obligate eusociality[2,3], so it seems that *Austroplatypus* is the real deal.

The second major finding concerns whether *Austroplatypus* mothers are monogamous — that is, whether they mate with one male or several males before starting a colony — and may help to settle one of the biggest controversies in social evolution of the past decade. When Darwin wondered how natural selection could hone the behaviour of sterile workers when they leave no descendants, he reasoned that selection must act through worker-like tendencies carried, but not expressed, by their reproductive relatives[4]. A century later, W. D. Hamilton's inclusive-fitness theory[5] formalized this insight, identifying the importance of genetic correlations between relatives for the evolution of social adaptations. Put simply, inclusive-fitness theory recognizes that workers raising siblings is in some ways equivalent to them raising descendants. As siblings and offspring both share genes with the worker, either way the worker is helping to pass on its genes. In particular, when nestmates are full siblings rather than half-siblings, a potential worker is, on average, as related to a sibling as they would be to an offspring. This suggests that strict monogamy — which gives rise to full siblings, but is comparatively rare in the animal kingdom — should favour the emergence of eusociality[3].

This 'monogamy hypothesis'[3] has been criticized, most notoriously by a *Nature* paper suggesting that relatedness is unimportant to the evolution of eusociality[6]. This study also argued that the strongest evidence available at the time — focusing mostly on the social Hymenoptera[7] and, to a lesser degree, termites[3] — only demonstrated correlation between monogamy and eusociality, not causation[6]. Because these claims were made in an article more generally disputing the validity of inclusive-fitness theory, which underpins a substantial swath of research in ecology and evolution, the question of monogamy and eusociality became a flashpoint for debate.

However, Smith et al.[1] have indeed found evidence for strict monogamy in *Austroplatypus*. Moreover, they show that monogamy pre-dated the evolution of eusociality in this species, lending further empirical support to the monogamy hypothesis. Together with formal mathematical models supporting a causal link between monogamy and eusociality[8], and an association between monogamy and sibling care in birds[9] and mammals[10], the monogamy hypothesis can now claim both theoretical backing and widespread empirical support.

Cooperation is fundamental to complexity in nature, because living systems are built from a patchwork of alliances at the genetic, cellular and individual level. But cooperation also poses a puzzle, as it stands

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

in apparent opposition to the Darwinian dictum that self-promotion is the sole currency of genetic success. In this new study, Smith et al.[1] help shed light on this most compelling phenomenon. ❒

Nicholas G. Davies
London School of Hygiene and Tropical Medicine, London, UK.
e-mail: Nicholas.Davies@lshtm.ac.uk

Published online: 23 April 2018
https://doi.org/10.1038/s41559-018-0541-3

References

1. Smith, S. M., Kent, D. S., Boomsma, J. J. & Stow, A. J. *Nat. Ecol. Evol.* https://doi.org/10.1038/s41559-018-0533-3 (2018).
2. Crespi, B. J. & Yanega, D. *Behav. Ecol.* **6**, 109–115 (1995).
3. Boomsma, J. J. *Phil. Trans. R. Soc. B* **364**, 3191–3207 (2009).
4. Darwin, C. R. *On the Origin of Species* (John Murray, London, 1859).
5. Hamilton, W. D. *J. Theor. Biol.* **7**, 1–52 (1964).
6. Nowak, M. A., Tarnita, C. E. & Wilson, E. O. *Nature* **466**, 1057–1062 (2010).
7. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. *Science* **320**, 1213–1216 (2008).
8. Davies, N. G., Ross, L. & Gardner, A. *Ecol. Lett.* **19**, 862–872 (2016).
9. Lukas, D. & Clutton-Brock, T. *Proc. R. Soc. B* **279**, 2151–2156 (2012).
10. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. *Nature* **466**, 969–972 (2010).

Competing interests

The author declares no competing interests.

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.