

NEWS AND VIEWS

PERSPECTIVE

Intergenerational reproductive parasitism in a stingless bee

BENJAMIN P. OLDROYD and MADELEINE BEEKMAN

Behaviour and Genetics of Social Insects Laboratory, School of Biological Sciences, University of Sydney, NSW 2006, Australia

Insect colonies have been traditionally regarded as closed societies comprised of completely sterile workers ruled over by a single once-mated queen. However, over the past 15 years, microsatellite studies of parentage have revealed that this perception is far from the truth (Beekman & Oldroyd 2008). First, we learned that honey bee queens are far more promiscuous than we had previously imagined (Estoup *et al.* 1994), with one *Apis dorsata* queen clocked at over 100 mates (Wattanachaiyingcharoen *et al.* 2003). Then Oldroyd *et al.* (1994) reported a honey bee colony from Queensland, where virtually all the males were sons of a single patriline of workers – a clear case of a cheater mutant that promoted intracolony reproductive parasitism. Then we learned that both bumble bee colonies (Lopez-Vaamonde *et al.* 2004) and queenless honey bee colonies (Nanork *et al.* 2005, 2007) are routinely parasitized by workers from other nests that fly in and lay male-producing eggs that are then reared by the victim colony. There is even evidence that in a thelytokous honey bee population, workers lay female-destined eggs directly into queen cells, thus reincarnating themselves as a queen (Jordan *et al.* 2008). And let us not forget ants, where microsatellite studies have revealed equally bizarre and totally unexpected phenomena (e.g. Cahan & Keller 2003; Percy *et al.* 2004; Fournier *et al.* 2005). Now, in this issue, Alves *et al.* (2009) use microsatellites to provide yet another shocking and completely unexpected revelation about the nefarious goings-on in insect colonies: intergenerational reproductive parasitism by stingless bee workers.

Received 16 July 2009; revision received 21 July 2009; accepted 22 July 2009

Stingless bees (*Meliponini*) are a tribe of tropical eusocial bees that rival honey bees in the size and complexity of their societies (Michener 1974). Queens are generally singly mated (Peters *et al.* 1999; Palmer *et al.* 2002), meaning that, on average, workers are more related to the sons of their

sisters than to the sons of their queen (Fig. 1). Thus, kin-selection theory predicts that worker reproduction is more likely in stingless bees than in polyandrous honey bees, where workers are more related to the sons of the queen than to sons of their numerous half sisters (e.g. Tóth *et al.* 2002a; Ratnieks *et al.* 2006). Yet, microsatellite studies have found rates of worker reproduction to be highly variable among stingless bee species, with workers being responsible for 0–100% of offspring males depending on the species and time of year (e.g. Palmer *et al.* 2002; Tóth *et al.* 2004).

Melipona scutellaris are honey-bee-sized bees that live in colonies of up to 2000 workers (Tóth *et al.* 2004). Nests, usually situated in tree hollows, are widely distributed in northeast Brazil (Fig. 2). Colonies are established by colony fission, and queens are regularly replaced. They are sometimes domesticated for honey and wax production.

Alves *et al.* sampled brood from 37 colonies over a period of 2–24 months for each colony, genotyping workers and males at multiple microsatellite loci. Their sampling straddled 13 queen supersedure events, and these events were detectable by changes in the genotypes of the sampled workers. In line with previous findings with this species (Tóth *et al.* 2002b), about 23% of males were worker-laid. What is striking and new, however, is that of these worker-laid males, 81% were sons of the workers of the previous, superseded, queen and thus aunts of the current generation of workers (Fig. 1).

When an unmated stingless bee worker lays a haploid male-producing egg, this egg comes at the cost of replacing a queen-laid, fertilized, female-producing egg. Laying workers thus trade off sons against sisters. Sisters are more valuable than sons for three reasons. First sister workers work, whereas males do not. Second, large numbers of workers are needed for the colony to swarm, whereas males are not needed for a swarm. Third, it is a sister queen (relatedness, $r = 0.75$; Fig. 1) that will head any swarm the colony produces – a sister queen that heads a swarm that has higher value for a worker than any other individual in the colony. However, after queen replacement, a reproductive worker trades off its sons against less valuable nieces ($r = 0.375$). Furthermore, any costs associated with worker reproduction, such as the reduced incentive to work in the field by reproductively active workers, or increased strife among workers, are borne mainly by the current generation of workers, the nieces of the reproductive workers. Thus any alleles that favour successful worker reproduction by daughters of the old, superseded queen are likely to spread relative to alleles that confer behavioural sterility (Ratnieks *et al.* 2006; Ratnieks & Wenseleers 2008).

Alves *et al.* show that some of the laying workers must have been more than 3 months old, an extraordinary age

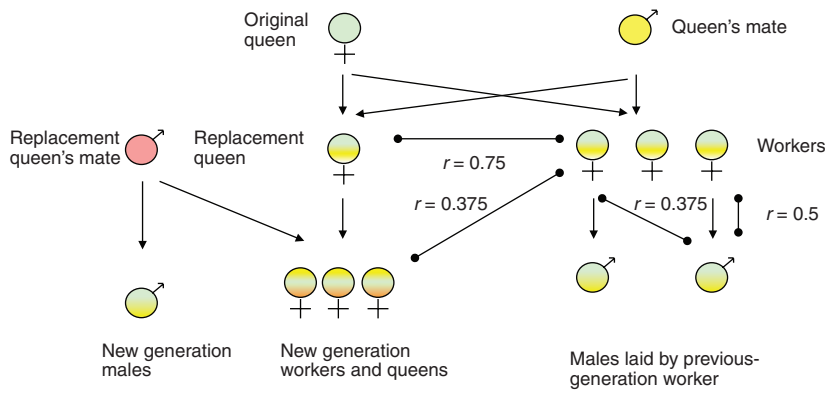


Fig. 1 Relatedness coefficients in stingless bee colonies before and after queen supersedure events.



Fig. 2 Queen and workers of *Melipona scutellaris*. Photo by Denise Alves.

for a worker, and three times the typical age at death for workers in this species. This finding provides further evidence for the hypothesis that reproductively active workers are long-lived, possibly because they avoid providing larval food from their mandibular glands, and avoid foraging (Schmid-Hempel 1990).

It could be argued that Alves *et al.*'s results are just another cute example of the ever-expanding catalogue of underhanded (in the sense that it benefits the reproductive worker at the expense of the other workers) reproductive behaviour initiated by insect workers. Yet we would argue that each fresh example of worker reproduction turned up by 'molecular natural history' (Keller 2007) is important, for it provides an independent test of kin-selection theory, and a better understanding of how relatedness and opportunity interact to determine what the best reproductive strategy is for a worker (Beekman & Ratnieks 2003; Lopez-Vaamonde *et al.* 2004; Wenseleers *et al.* 2004; Beekman & Oldroyd 2008). Based on kin-selection arguments, we have previously predicted that inter-colonial reproductive parasitism is more likely in the stingless bees than it is in honey bees (Gloag *et al.* 2007), and would perhaps be common, as it is in the bumble bee *Bombus terrestris* (Lopez-Vaamonde *et al.* 2004). Alves *et al.* show that, although rare, such parasitism

does indeed occur, although not precisely in the way we thought it might. And this makes an important point. Not only must the relatedness coefficients be right, the details of the reproductive biology of the organism must also favour parasitism – in short there must be opportunity, as well as motive. In this case, opportunity is provided by frequent queen supersedure events and long-lived workers. Without these factors, worker parasitism might not have evolved in *M. scutellaris*, or not in the same way.

Each new instance where worker reproduction has been found, kin-selection theory provides insight into explaining the worker behaviour. Reciprocally, kin-selection theory is made even stronger with these examples. May there be many more.

References

- Alves DA, Imperatriz-Fonseca VL, Franco TM *et al.* (2009) The queen is dead—long live the workers: intraspecific parasitism by workers in the stingless bee *Melipona scutellaris*. *Molecular Ecology*, **18**, 4102–4111.
- Beekman M, Oldroyd BP (2008) When workers disunite: intraspecific parasitism in eusocial bees. *Annual Review of Entomology*, **53**, 19–37.
- Beekman M, Ratnieks FLW (2003) Power over reproduction in the social Hymenoptera. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **358**, 1741–1753.
- Cahan SH, Keller L (2003) Complex hybrid origin of genetic caste determination in harvester ants. *Nature*, **424**, 306–309.
- Estoup A, Solignac M, Cornuet J-M (1994) Precise assessment of the number of patrines and of genetic relatedness in honey bee colonies. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **258**, 1–7.
- Fournier D, Estoup A, Orivel RM *et al.* (2005) Clonal reproduction by males and females in the little fire ant. *Nature*, **435**, 1230–1234.
- Gloag RS, Heard TA, Beekman M, Oldroyd BP (2007) No worker reproduction in the Australian stingless bee, *Trigona carbonaria* Smith (Hymenoptera: Apidae). *Insectes Sociaux*, **54**, 412–417.
- Jordan LA, Allsopp MH, Oldroyd BP, Wossler TC, Beekman M (2008) Cheating honeybee workers produce royal offspring. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **275**, 345–351.
- Keller L (2007) Uncovering the biodiversity of genetic and reproductive systems: time for a more open approach – American Society of Naturalists E. O. Wilson award winner address. *American Naturalist*, **169**, 1–8.

- Lopez-Vaamonde C, Koning JW, Brown RM, Jordan WC, Bourke AFG (2004) Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature*, **430**, 557–560.
- Michener CD (1974) *The Social Behavior of the Bees*. Harvard University Press, Cambridge.
- Nanork P, Paar J, Chapman NC, Wongsiri S, Oldroyd BP (2005) Asian honey bees parasitize the future dead. *Nature*, **437**, 829.
- Nanork P, Chapman NC, Wongsiri S, Lim J, Gloag S, Oldroyd BP (2007) Social parasitism by workers in queenless and queenright *Apis cerana* colonies. *Molecular Ecology*, **16**, 1107–1114.
- Oldroyd BP, Smolenski AJ, Cornuet J-M, Crozier RH (1994) Anarchy in the beehive. *Nature*, **371**, 749.
- Palmer KA, Oldroyd BP, Quezada-Euán JJV, Paxton RJ, May-Itza WD (2002) Paternity frequency and maternity of males in some stingless bee species. *Molecular Ecology*, **11**, 2107–2113.
- Pearcy M, Aron S, Doums C, Keller L (2004) Conditional use of sex and parthenogenesis for worker and queen production in ants. *Science*, **306**, 1780–1783.
- Peters JM, Queller DC, Imperatriz-Fonseca VL, Roubik DW, Strassmann JE (1999) Mate number, kin selection and social conflicts in stingless bees and honeybees. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 379–384.
- Ratnieks FLW, Wenseleers T (2008) Altruism in insect societies and beyond: voluntary or enforced? *Trends in Ecology and Evolution*, **23**, 45–52.
- Ratnieks FLW, Foster KR, Wenseleers T (2006) Conflict resolution in insect societies. *Annual Review of Entomology*, **51**, 581–608.
- Schmid-Hempel P (1990) Reproductive competition and the evolution of work load in social insects. *The American Naturalist*, **135**, 501–526.
- Tóth E, Queller DC, Imperatriz-Fonseca VL, Strassmann JE (2002a) Genetic and behavioral conflict over male production between workers and queens in the stingless bee *Paratrigona subnuda*. *Behavioral Ecology and Sociobiology*, **53**, 1–8.
- Tóth E, Strassmann JE, Nogueira-Neto P, Imperatriz-Fonseca VL, Queller DC (2002b) Male production in stingless bees: variable outcomes of queen-worker conflict. *Molecular Ecology*, **11**, 2661–2667.
- Tóth E, Queller DC, Dollin A, Strassmann JE (2004) Conflict over male parentage in stingless bees. *Insectes Sociaux*, **51**, 1–11.
- Wattanachaiyingcharoen W, Oldroyd BP, Wongsiri S, Palmer K, Paar J (2003) A scientific note on the mating frequency of *Apis dorsata* Fabricius. *Apidologie*, **34**, 85–86.
- Wenseleers T, Hart AG, Ratnieks FLW, Quezada-Euan JVG (2004) Queen execution and caste conflict in the stingless bee *Melipona beecheii*. *Ethology*, **110**, 725–736.

doi: 10.1111/j.1365-294X.2009.04324.x