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NEWS AND VIEWS
PERSPECTIVE

Nepotism absent in insect societies — or is it?

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Abstract

Inclusive fitness theory, put forward by English biologist William Hamilton in 1964, is considered by many as the most important addition to the theory of natural selection since Darwin. One prediction of the theory is that animals should often show a tendency to nepotistically favour close relatives. Goodisman *et al*. (2007) test this theory for the first time using molecular methods in a vespine wasp, the eastern yellowjacket, *Vespula maculifrons*. Somewhat surprisingly, nepotism was found to be absent. This begs the question why nepotism is predicted by theory, yet in a growing list of species is shown to be absent. Is inclusive fitness theory in trouble? As we show, it is not: costs and constraints explain the general absence of queen rearing nepotism, and nepotism in insect societies in fact is well supported in the context of male rearing and manipulation of colony sex ratios.

Hamilton (1964) was the first to successfully explain how advanced social behaviour, such as that seen in insect societies, could be selectively favoured. The key turned out to be genetic relatedness. In his theory of inclusive fitness, Hamilton showed that if individuals help close relatives reproduce, then this can be almost as good a way to transmit genes to future generations than having offspring oneself. Hence, a gene for altruism could spread in the population, even if, in the case of social insect workers, it can cause them to be completely sterile. The theory, however, also had a more sinister side to it. It was suggested that it could also cause individuals to discriminately help only close relatives or harm more distant relatives, a behaviour known as nepotism.

Goodisman *et al*. (2007) test the possibility of nepotism for the first time in a North American vespine wasp, the eastern yellowjacket, *Vespula maculifrons* (Fig. 1). Using microsatellite genotyping, the authors show that, similar to the honeybee, eastern yellowjacket queens mate with several males, five to nine to be exact. The result is that in any one colony several distinct genetic lineages or 'patrilines' are present, each derived from the same father. This forms the basis for a conflict, as each worker should prefer to nepotistically rear more related full-sister queens from its own patriline ($r = 0.75$) over less related half-sisters queens from other patrilines ($r = 0.25$). To test whether such nepotism goes on, Goodisman *et al*. do not directly observe the behaviour of the wasps, but rather use an indirect, genetic method. They argue that if nepotism occurs, nepotism by dominant worker patrilines should result in such patrilines being overrepresented even more among the queen brood. Alternatively, if nepotism were expressed in only a few rare worker patrilines, the adult queen brood should end up belonging particularly to such patrilines. Either way, nepotism should cause the patriline distributions of the worker and queen brood to differ.

By genotyping a total of 581 workers and 397 queens from 11 colonies, and using various statistical techniques, Goodisman *et al*. show that the patriline distributions among the queen brood in fact do not differ from those among the worker brood. Assuming that the nepotism expressed by workers from different patrilines would not tend to cancel out, this means that nepotism is almost certainly absent. It also means that larvae of particular genotypes were reared as queens no more likely than expected by chance. This contrasts with some recent results obtained in the honeybee, where after accidental queen loss certain 'royal' larval genotypes are unusually frequently reared as replacement queens (e.g. Tilley & Oldroyd 1997; Osborne & Oldroyd 1999; Moritz *et al*. 2005).

That such selective rearing of larvae is absent in the eastern yellowjacket is perhaps not so surprising: in vespine wasps, all female eggs laid in large-celled comb are reared as queens, not some special subpopulation. But how can it be explained

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Fig. 1 Workers of the eastern yellowjacket (*Vespula maculifrons*) do not prefer to rear full-sisters over half-sisters as queens. Why is such kin nepotism so markedly absent in insect societies? (Photo credit: Doug Wechsler/naturepl.com)

that nepotism is absent? Certainly, Goodisman *et al*. are not the first to come to this conclusion: in a swathe of species, from the honeybee to stingless bees, ants and polistine wasps, nepotism has been looked for, but has been found to be either weak or absent (Keller 1997; Tarpy *et al*. 2004; Ratnieks *et al*. 2006) and even the best evidence for nepotism so far, in a multiple-queen ant (Hannonen & Sundström 2003), has been disputed by some (Holzer *et al*. 2006). Admittedly, some of the honeybee studies may have suffered from low sample sizes — perhaps unavoidable since the honeybee rears only few queens at any one time. But importantly, this limitation did not apply to the present study: in the eastern yellowjacket, hundreds of new queens are reared in each colony, and so the authors had significant statistical power to identify even relatively mild levels of nepotism. So where does this leave us — is inclusive fitness theory somehow in trouble?

Probably not — what is often forgotten is that one also needs to consider costs and constraints. If queen nepotism would greatly reduce net colony productivity or if workers frequently make mistakes in discriminating between full- and half-sister queens, then worker nepotism in fact is selected against (Ratnieks & Reeve 1992). Empirical data suggest that recognition information may indeed be limiting. Cuticular hydrocarbons from Vespinae wasps, for example, failed to distinguish reliably among different patrilines (Dani *et al*. 2004). Theory also shows good reasons for information constraint. Discrimination requires considerable underlying genetic variation at the chemical recognition loci. However, the act of discrimination itself selects against rare recognition alleles, thereby reducing information and increasing errors (Ratnieks *et al*. 1992).

So is nepotism one of those beautiful hypotheses, slayed by the ugly facts? In fact, it is not: while the above shows that nepotism in the context of queen rearing is weak or absent, nepotism in insect societies is actually very well documented in two other contexts: male rearing and worker manipulation of colony sex ratios (Ratnieks *et al*. 2006). In the context of male rearing, it has been shown based on an analysis of *c*. 100 species of ants, bees and wasps that workers show a preference to rear the males to which they are most closely related, workers' sons or queen's sons, and that they tend to inhibit the rearing of workers' sons particularly in those species where they are on average more related to the queen's sons (Wenseleers & Ratnieks 2006). Similarly, it has been shown that in many ants, workers bias the colony's sex ratio towards more related sisters, either by killing less related brothers or by rearing more sisters as queens (reviewed in Ratnieks *et al*. 2006). No matter which way you turn it these observations form excellent demonstrations of kin nepotism. In addition, that queen-rearing nepotism generally appears to be absent in no way brings inclusive fitness theory into dispute. While kin selection raises the possibility of such nepotism, it does not say it should occur, as one must also consider costs and possible constraints. For queen-rearing nepotism, it is these, and not the effects of relatedness, which appear to dominate (Ratnieks *et al*. 2006).

References

Dani FR, Foster KR, Zacchi F *et al*. (2004) Can cuticular lipids provide sufficient information for within-colony nepotism in wasps? *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **271**, 745–753.

Goodisman MAD, Kovacs JL, Hoffman EA (2007) Lack of conflict during queen production in the social wasp *Vespula maculifrons*. *Molecular Ecology*, **16**, 2589–2595.

Hamilton WD (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, **7**, 1–52.

Hannonen M, Sundström L (2003) Worker nepotism among polygynous ants. *Nature*, **421**, 910–910.

Holzer B, Kummerli R, Keller L, Chapuisat M (2006) Sham nepotism as a result of intrinsic differences in brood viability in ants. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **22**, 2049–2052.

Keller L (1997) Indiscriminate altruism: unduly nice parents and siblings. *Trends in Ecology & Evolution*, **12**, 99–103.

Moritz RFA, Lattorff HMG, Neumann P *et al*. (2005) Rare royal families in honeybees, *Apis mellifera*. *Naturwissenschaften*, **92**, 488–491.

Osborne KE, Oldroyd BP (1999) Possible causes of reproductive dominance during emergency queen rearing by honeybees. *Animal Behaviour*, **58**, 267–272.

Ratnieks FLW, Foster KR, Wenseleers T (2006) Conflict resolution in insect societies. *Annual Review of Entomology*, **51**, 581–608.

Ratnieks FLW, Reeve HK (1992) Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *Journal of Theoretical Biology*, **158**, 33–65.

Tarpy DR, Gilley DC, Seeley TD (2004) Levels of selection in a social insect: a review of conflict and cooperation during honey bee (*Apis mellifera*) queen replacement. *Behavioral Ecology and Sociobiology*, **55**, 513–523.

Tilley CA, Oldroyd BP (1997) Unequal subfamily proportions among honey bee queen and worker brood. *Animal Behaviour*, **54**, 1483.

Wenseleers T, Ratnieks FLW (2006) Comparative analysis of worker reproduction and policing in eusocial Hymenoptera supports relatedness theory. *American Naturalist*, **168**, E163–E179.

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