Reproduction: the almost forgotten currency of fitness

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When an animal behaves in a manner that reduces its Darwinian fitness and increases the fitness of another individual, it is said to behave altruistically. The existence of such altruism in nature is paradoxical because natural selection would normally be expected to eliminate individuals who lower their own fitness. Much theoretical and empirical work is therefore devoted to unravelling the mechanism/s by which altruism may be favoured by natural selection. Social insects such as ants, bees and wasps are at the forefront of this research since their colonies often consist of one or a small number of fertile queens and a large number of apparently sterile workers[1,2]. The European wasp *Polistes dominulus* (Figure 1) has been an especially favourite model system for such studies. *P. dominulus* is one of the most common social wasps in Europe and having been recently introduced into the United States, it has begun to rapidly displace local social wasps there. Its commonness and wide distribution have conferred on it the distinction of being one of the best-studied social wasps, certainly the best-studied *Polistes*. Groups of inseminated females found new nests in the Spring and cooperatively rear brood. The female wasps in a colony organize themselves into a behavioural dominance hierarchy such that only the alpha individual (the queen) reproduces, while the rest appear to function as apparently altruistic, sterile subordinates (workers), building the nest, foraging for food and pulp, feeding and caring for the brood and generally doing all that it takes to keep the nest up and running. But wait a minute, what's in it for the workers? Why should they sacrifice their time and energy helping to rear the queen's brood? Why not go off, found their own nests and rear their own brood – something they are quite capable of? Surely there must be something wrong with our facts. Let us look more closely. Maybe the subordinates lay some of their own eggs after all, at least enough to compensate for the offspring they might have produced in their own nests.

Looking closely is precisely what Leadbeater *et al.*[3,4] have done in a recent study. Using nine microsatellite markers to genotype pupae from 228 natural nests of *P. dominulus* from Spain, they measured the direct reproductive success of 1113 foundresses. Lo and behold, subordinate foundresses were seen to produce more offspring *per capita* than an average solitary foundress who had indeed decided to reproduce on her own. About 32% of the reproduction of subordinates came from sneaking in eggs while the dominant was still alive and 68% came from inheriting the position of the dominant in the nest after the latter had died. Thus the obvious experiment has been done and the expected result has been obtained and, of course, there is no mysterious altruism after all. But then, what is all the fuss about?

Well, I think we should make a great deal of fuss about this study. Indeed, I recommend that this paper[3] be widely read, discussed and emulated. To see why, let us flash back to 1964. That was the year in which Hamilton proposed a radically new theory which is often referred to as kin selection or inclusive fitness theory[5]. Hamilton argued that to deal with the apparent paradox of altruism, we must expand the scope of Darwinian fitness and add to the already existing direct component, gained through personal reproduction, an indirect component gained through aiding close genetic relatives. He dubbed the sum of the direct and indirect components as inclusive fitness. Hamilton went on to derive a rule according to which an altruistic allele will be favoured by natural selection if $rb > c$, where r is the relatedness between the altruist and the recipient of altruism, b is the benefit accrued to the recipient and c is the cost incurred by the altruist. Unfortunately Hamilton's rule has not been put to as rigorous an empirical test as one might have liked – costs and benefits are hard to measure although relatedness has turned out to eminently measurable. When r, b and c have all been measured as in the Indian paper wasp, *Ropalidia marginata*, for example, the importance of all the three parameters has become evident and Hamilton's rule has provided a satisfactory explanation for the evolution of altruism[6]. However, rather than take the trouble of measuring all three parameters, it has often been implicitly or explicitly argued that if b is sufficiently greater than c, then it is r that must drive the evolution of altruism. All this has led willy-nilly to the emergence of the corollary that altruism can evolve if it is nepotistic, i.e. directed to individuals with high genetic relatedness[7]. Although it is clear from Hamilton's rule that what is high relatedness depends on the relative magnitudes of the costs and benefits, it has become customary not to raise your eyebrows at the evidence of altruism, as long as relatedness between

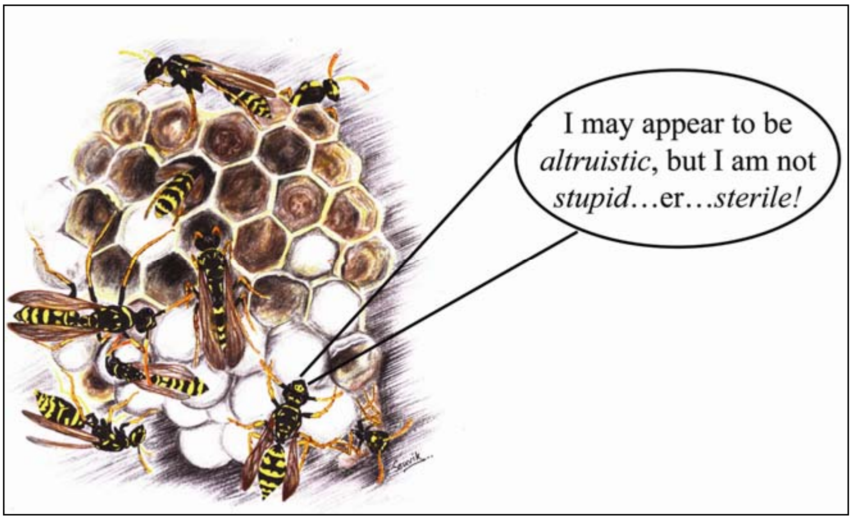

Figure 1. *Polistes dominulus.*

altruist and beneficiary is above the average in the population. I suspect that comfort is implicitly drawn from the knowledge that the relative magnitudes of costs and benefits can potentially rescue any value of non-zero relatedness. Thus the theoretical appeal of kin selection fuelled also by *prima facie* evidence in its favour (on account of non-zero relatedness among interacting individuals) has been so enchanting and magical that it has become hard to criticize it any more[8]. A recent attempt by Nowak *et al*.[9] has been angrily rebuffed by no less than 150 prominent practitioners of the field[10–14].

So, would anything make people suspicious of kin selection? Yes – zero relatedness, for, no amount of playing with costs and benefits can rescue that situation. Fortunately (some might say), zero relatedness has in fact been found. About 35% of the workers in *P. dominulus* colonies have been found to have zero relatedness[15] to their queens and that is what made Leadbeater *et al.*[3] to sit up and take notice (never mind that it took 11 years). As mentioned above, they looked for possible reasons for the apparent altruism of the workers and found that there was no altruism in the first place. The obvious conclusion to draw from the findings of Leadbeater *et al.*[3] is that this does not just clear up the mystery of the unrelated workers. An average worker (and that includes full sisters of the dominant egg-layer) gets enough direct fitness to justify her subordinate role, making kin selection (or indirect fitness) entirely unnecessary for explaining sociality in *P. dominulus*. This seems too heretic even to Leadbeater *et al.*[3], who downplay the enormity of their own findings by saying, 'we do not imply that direct fitness benefits are always the main driver of subordinate behaviour, because our data also show that indirect benefits usually outweigh direct benefits for those subordinates…that are relatives of the dominant wasp'. I think it will take some more time for our community to escape the stranglehold of kin selection so as not to invoke it, at least when it is not necessary.

Whether we like to admit it or not, I think those who work with social wasps or inclusive fitness theory find ourselves in a somewhat embarrassing position. Only when indirect fitness failed us did we look for and find direct fitness – clearly, it should have been the other way around; after all, direct reproduction is the original currency of fitness. And we should not now attempt to explain away our predicament by asserting that the recent advances in molecular techniques were essential to uncover direct reproduction by the subordinate wasps. Long-term observations can do much the same and sometimes do even better; for instance, they would have also told us whether the unrelated subordinates were behaving differently compared to the related subordinates. What a pity that biologists sympatric with interesting species, who can make the long-term observations, do not work often enough on their native fauna and flora. Looking closely would be so much easier, if they did.

1. Wilson, E. O., *The Insect Societies*, The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA, 1971.
2. Gadagkar, R., *Survival Strategies – Cooperation and Conflict in Animal Societies*, Harvard University Press, Cambridge, Massachusetts, USA and Universities Press, Hyderabad, India, 1997.
3. Leadbeater, E., Carruthers, J. M., Green, J. P., Rosser, N. S. and Field, J., *Science*, 2011, **333**, 874–876.
4. Gadagkar, R., *Science*, 2011, **333**, 833–834.
5. Hamilton, W. D., *J. Theor. Biol*., 1964, **7**, 1–52.
6. Gadagkar, R., *The Social Biology of Ropalidia marginata: Toward Understanding the Evolution of Eusociality*, Harvard University Press, Cambridge, Massachusetts, USA, 2001.
7. Sherman, P. W., *Science*, 1977, **197**, 1246–1253.
8. Gadagkar, R., *Curr. Sci.*, 2010, **99**, 1036–1041.
9. Nowak, M. A., Tarnita, C. E. and Wilson, E. O., *Nature*, 2010, **466**, 1057–1062.
10. Abbot, P. *et al*., *Nature*, 2011, **471**, E1–E4.
11. Boomsma, J. J. *et al*., *Nature*, 2011, **471**, E4–E5.
12. Strassmann, J. E., Page Jr, R. E., Robinson, G. E. and Seeley, T. D., *Nature*, 2011, **471**, E5–E6.
13. Ferriere, R. and Michod, R. E., *Nature*, 2011, **471**, E6–E8.
14. Herre, E. A. and Wcislo, W. T., *Nature*, 2011, **471**, E8–E9.
15. Queller, D. C. *et al*., *Nature*, 2000, **405**, 784–787.

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