Reproduction: the almost forgotten currency of fitness

Raghavendra Gadagkar

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. 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 wasps in Europe and having been reared in the laboratory. Its commonness and wide distribution have conferred on it the distinction of being one of the best-studied

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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. A recent attempt by Nowak et al. has been angrily rebuffed by no less than 150 prominent practitioners of the field. The obvious conclusion to draw from the findings of Leadbeater et al. 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., 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 sympathetic 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.


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