

BRIEF COMMUNICATIONS

Enforced altruism in insect societies

Cooperation among workers and their seeming altruism result from strict policing by nestmates.

Workers of many species of ant, bee and wasp do not lay eggs, despite having functional ovaries¹, but the selective causes of this extreme form of altruism are unclear^{2–7}. Here we show that workers forego reproduction in response to the threat of their eggs being killed, or 'policed', by nestmates. Our results indicate that social coercion helps to explain worker altruism and cooperation in modern-day insect societies^{3–5}.

Why, in some species, do most workers forego direct reproduction? One possibility is that worker altruism is voluntary: in this scenario, high genetic relatedness should drive the evolution of altruism^{2–7} and worker sterility⁷ because higher relatedness increases the indirect benefit of working. Theoretically, however, worker altruism could also be 'enforced' and may have evolved in response to social sanctions^{4–6}. In many species, worker-laid eggs are killed by the queen or by other workers^{1,8,9} and, if these sanctions are effective, the advantage to workers of laying eggs is reduced. As a result, more would be selected to work altruistically, rather than to lay eggs⁶.

The role of sanctions in promoting worker sterility has long been suspected^{8,9}, but has never been tested in a comparative study. We therefore studied ten single-queen species, nine Vespidae wasps (for example, see Fig. 1) and the honey-



Figure 1 | The wasp *Vespa crabro*.

bee *Apis mellifera*. These are the only species for which there are data to quantify both the proportion of non-egg-laying workers, a measure of worker altruism, and two key predictor variables: relatedness among workers, which depends on the frequency of queen mating, and the effectiveness with which worker-laid eggs are policed by nestmates^{1,8,9}. We analysed the data by using individual species as data points and by phylogenetically independent contrasts (PICs) to control for phylogenetic non-independence. (See supplementary information.)

Figure 2 shows that, as predicted, fewer workers reproduce when the effectiveness of policing worker-laid eggs is higher ($P = 0.00004$, Fig. 2a; using PICs: $P = 0.000006$, see supplementary information). This supports the hypothesis that worker altruism is enforced. Contrary to the voluntary-altruism hypothesis⁷, however, higher relatedness does not lead to increased altruism. In fact, the reverse is true — a larger proportion of the workers reproduce in species where relatedness is high ($P = 0.004$, Fig. 2b; using PICs: $P = 0.04$; see supplementary information). However, this is predicted by policing theory, because low relatedness more strongly selects for workers to police each others' reproduction^{1,8}.

Our results also show that policing effective-

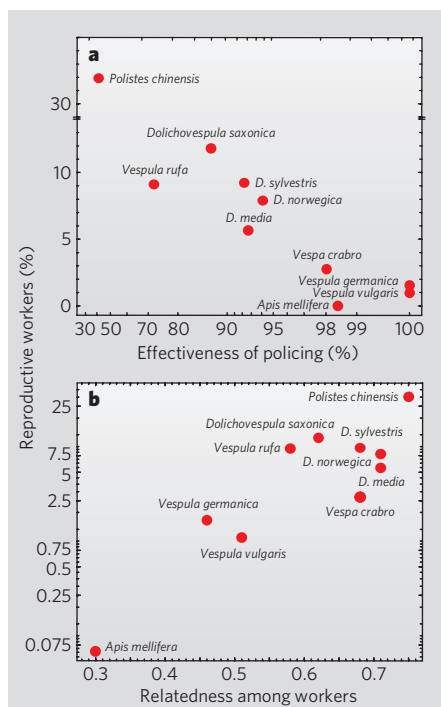


Figure 2 | Effect of sanctions and relatedness on worker altruism in social insects. **a**, If altruism is enforced, more workers should remain sterile when their reproduction is more effectively policed by nestmates, which is what occurs ($R = -0.94$, $P = 0.00004$; effectiveness of policing is reverse \log_{10} -transformed). **b**, If altruism is voluntary, greater altruism and less worker reproduction should be seen when relatedness is high, but the opposite occurs ($R = 0.82$, $P = 0.004$; percentage of reproductive workers is \log_{10} -transformed). The effectiveness of policing is defined as the probability of worker-laid eggs being killed relative to queen-laid eggs; reproductive workers are shown as the percentage of workers with active ovaries (see supplementary information).

ness is negatively correlated with relatedness ($R = -0.60$, one-tailed $P = 0.03$; using PICs: $F(1,8) = 4.69$, one-tailed $P = 0.03$); this contrasts with our results from queenless colonies, in which the relationship is reversed and higher relatedness results in a smaller proportion of the workers laying eggs ($R = -0.79$, $P = 0.007$; using PICs: $P = 0.03$; see supplementary information). This is as expected from theory, as in queenless colonies policing does not occur and its inhibitory effect is lost⁷. However, the effect of relatedness in promoting altruism remains⁷.

The key role of relatedness in the evolution of self-sacrificing behaviour is widely recognized^{2,5}. The origin of insect societies is one of the most cited examples, and high relatedness was probably required for worker behaviour first to evolve^{2,5}. Nevertheless, our results show that in modern-day insect societies it is mainly social sanctions that reduce the numbers of workers that act selfishly. In this, they provide evidence for something that has proved notoriously hard to demonstrate in human society: that better law enforcement can lead to fewer individuals behaving antisocially¹⁰.

Tom Wenseleers*†, Francis L. W. Ratnieks*‡

*Institute for Advanced Study, 14193 Berlin, Germany

†Present addresses: Zoological Institute, Catholic University of Leuven, 3000 Leuven, Belgium (T.W.); Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK (F.L.W.R.)

e-mail: tom.wenseleers@bio.kuleuven.be

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