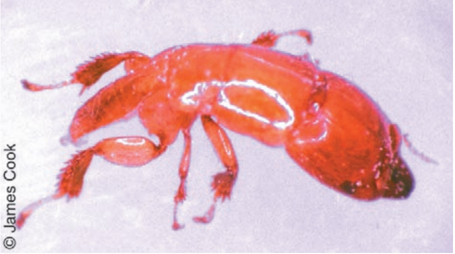
Journal Club

Vicious fig wasps in viscous populations

Understanding when interacting individuals should conflict or cooperate is an enduring topic in evolutionary ecology. Cooperation can be favoured through kin selection when those interacting are genetic relatives. Because high levels of relatedness can be generated in 'viscous' populations, characterized by limited dispersal, it has often been assumed that population viscosity will lead to cooperation. However, the same viscosity might also increase resource competition between relatives, and recent theory predicts that this might oppose the evolution of cooperation. The predicted and opposing influences of relatedness and competition can be difficult to disentangle in practice but a new comparative study on male–male conflicts in fig wasps shows that fighting is correlated with resource competition rather than with genetic relatedness[1].

Fig wasps develop within sycones, which are the closed inflorescences often called 'figs'. The females are always winged but males of many species are wingless and nondispersing. Wingless males mate with females inside the sycone, before the females disperse. Male–male aggression varies greatly among species: in some, males have a 'combat morphology', consisting of armour and large mandibles, whereas, in others, males have no structures for fighting or for defence. The average relatedness of competing males also varies greatly among species, mainly as a result of varying numbers of 'foundress' mothers laying eggs into each sycone (when more mothers contribute offspring, average offspring relatedness decreases). West *et al.* used sex ratio (a known correlate of foundress number) as an index of relatedness and quantified conflict levels across 25 species by assessing physical damage sustained by males during the mating period (scoring 0.5 points for loss of an antenna and the maximum of eight points for decapitation). Controlling for phylogeny, they found no relationship between relatedness and conflict level, but there was a negative correlation between injury level and the mean number of females (mating resource) developing in a fig.



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This study provides the first good support for the prediction that lack of dispersal before resource competition counteracts possible benefits of cooperating with kin. Instead, conflict levels appear to be determined by the importance of fighting for (and mating with) any particular female: when females are rare (small brood sizes) fighting is at its most intense.

West *et al.*'s paper is valuable not only because it tests the alternative predictions but also because it emphasizes the need for empiricists to assess competition, as well as relatedness. Moreover, the scale at which competition operates is important. For fig wasps, the key biological scale is at the sycone level: without male dispersal from the sycone, it appears that kin selection is cancelled by resource competition.

1 West, S.A. *et al.* (2001) Testing Hamilton's rule with competition between relatives. *Nature* 409, 510–513

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Faecal pellets and energy flow in rivers

With the ever-increasing need for water abstraction and power generation, the attention of many researchers interested in freshwater systems has turned to river flow management. However, as a new paper by Björn Malmqvist, Roger Wotton and Yixin Zhang shows, interest in management of anthropogenic changes to ecosystems does not preclude advancement in basic science.

Blackfly larvae (Diptera: Simuliidae) are ubiquitous in most freshwater ecosystems, and their feeding habits result in an unusual transformation of organic matter. Along with several other filter-feeding macroinvertebrates, blackfly larvae remove fine particulate organic matter, and even dissolved organic matter, from the water column and, as a consequence of somewhat poor digestion efficiency, produce large numbers of faecal pellets (FPs). In some ways, this process is analogous to the amalgamation of organic matter into 'marine snow' by marine suspension feeders. However, in flowing water, the process of amalgamation results in increased retention of carbon, whereas in the marine environment and lakes, it results in increased loss of carbon from the upper layers. In streams and rivers, the suspended organic matter captured but not assimilated by the blackfly larvae would otherwise be carried downstream. The 'recycled' organic matter is heavier than its constituent parts and so sinks more rapidly, which, in turn, means that the organic matter contained in the FPs is available to the large contingent of detritus feeders found in flowing waters.

Malmqvist *et al.* show that if these FPs were not produced, the potential energy loss of organic material from large river systems could be immense. For instance, they estimated that for a single river in the period of April 1999 to August 1999, the average daily transport of organic matter in the form of FPs was 69.2 tonnes (dry mass), equivalent to 2.7 tonnes of carbon per day. The authors also sampled a river that had been dammed, and suggest that regulation of rivers by damming could considerably reduce the concentration of FPs in the water, either through negative impacts on blackfly populations via reduction of available habitat, or perhaps through reductions in flow, resulting in more rapid sedimentation of the FPs. However, in terms of carbon retention, these two processes have conflicting effects: loss of habitat means carbon is lost from the system, whereas reduced flow could result in increased carbon retention through increased sedimentation. Hence, the effect of damming on carbon flow is

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