

Cooperation and Competition between Relatives Supplementary Online Information Stuart A. West, Ido Pen & Ashleigh S. Griffin

Here, we expand upon three areas briefly mentioned in the main text. Specifically, we describe: (A) an extreme empirical example of when competition between relatives is so severe that it negates and kin selection for altruism towards relatives – competition for mates between male fig wasps; (B) how the rash generalisations given in the main text may help us explain when kin selection theory hasn't been successful in explaining empirical patterns; (C) how the large body of research on sex allocation (allocation of resources to male and female reproduction) in structured populations relates to the topics discussed in the main text.

Fighting In Fig Wasps

One useful system for the empirical study of kin selection when relatives compete is the level of fighting between male fig wasps (*I*). Fig wasps develop within the fruit of fig trees, and include mutualistic pollinating species as well as parasitic non-pollinating species. In many species the males are wingless, and mate with the winged females before the females disperse from the fruit. At one extreme, males of some non-pollinating species are highly modified for combat with armoured bodies and huge mandibles. These mandibles are used to tear soft tissue and sever body parts, including limbs, head, genitals and abdomen, and can result in extremely high mortality levels. At the other extreme, males of other non-pollinating and all pollinating species show no modifications for combat or aggression.

A crucial aspect of this system is that because males only mate females from their own fruit, it is equivalent to completely local competition ($a=1$) in Frank's (2) model, and the actor being equally related to the beneficiary of their altruism and their competitors ($r_{xy} = r_{xe}$) in Queller's (3) model with $b=c+d$. This is the extreme (limiting or bookend) case when competition between relatives negates any effect of increased relatedness in favouring altruism, and so we would predict no relationship between level of fighting and average relatedness. In this situation, kin selection does not favour altruism and less violent fighting in species where competing males are more related because any advantage gained by a related male would, on average, be paid for by an equally related male. This prediction is easily tested because the number of females that lay eggs in each fruit, and therefore the average relatedness of competing males, varies enormously across species. As predicted, across species, both the mean lifetime injury level and the proportion of individuals severely injured showed no significant relationship with estimated relatedness (*I*).

Further Rash Generalisations

Do these generalisations help us explain when kin selection theory has and hasn't been successful in explaining empirical patterns? Many of the most quantitatively successful areas of kin selection theory represent extreme cases in which competition between

relatives is negligible. In these areas theory has usually ignored competition between relatives of the form we have discussed here, but luckily it turns out that it doesn't matter! For example: (i) models that predict behaviours in social insects such as worker policing (eliminating eggs laid by workers) and offspring sex ratios (proportion male) assume no competition between related reproductives (46), as we have argued is likely to be the case; (ii) theoretical models that predict offspring sex ratios in structured populations typically assume completely local competition between males and no competition for patches between related females, as is the case in species such as fig wasps where there is a striking fit between theory and data (see below). It has yet to be seen to what extent competition between relatives can explain cases where kin selection theory has been less successful. For example, can competition between relatives explain when: (a) the helping behaviour of cooperative breeding vertebrates does not correlate with the relatedness to those they are helping (1, 7); (b) parasite virulence does not correlate with the relatedness between parasites within hosts (810); (c) data on offspring sex ratios and worker policing fit theoretical predictions less strikingly (46)?

Sex Ratios in Structured Populations

There is a considerable literature on the evolution of sex allocation when relatives compete (often due to limited dispersal or population structuring/viscosity), and in which the extent of competition may differ between the sexes (1113). Sex allocation models for these situations rely on the same underlying theoretical principles as those on the evolution of altruism described in the main text (2, 3, 14, 15). Consequently, because these sex allocation models have proved to be relatively easy to test empirically, they have provided considerable support for the underlying logic of how competition between relatives influences kin selection.

Particularly illuminating have been studies of female biased sex allocation due to a process that has been termed local mate competition, LMC (16). Consider a population made up of discrete patches, similar to that of Taylor's limited dispersal model we described in the main text. Each generation, N females lay equal numbers of eggs per patch. The offspring mature, mate on the patch, and then only the females disperse, to start the cycle anew. This provides a particularly clear case because competition between males, for mates, occurs completely locally ($a=1$; $r_{xe} = r_{xy}$), whereas females disperse and compete globally ($a=0$; $r_{xe} = 0$) for new patches (e.g. female fig wasps are likely to compete on patches with females emerging from different trees, let alone relatives (17)). This tends to diminish the marginal fitness gain of producing males (sons) relative to females (daughters), and so favours a female biased sex allocation.

Specifically, for a diploid organism, assuming that males and females are equally costly to produce (as we do from here onwards), the unbeatable (evolutionary stable) sex ratio (proportion males, s) is given by the equation $s=(N-1)/2N$ (16). The sex ratio is predicted to vary from 0 when $N=1$, which is interpreted to mean producing just enough sons to mate her daughters, to 0.5 for large N . For the purpose of this paper, a useful way to think about the female biased sex ratio favoured under conditions of LMC (low N) is as a kin selected trait or kind of altruism. Specifically, female biased sex ratios represent what has

been termed a “weakly altruistic” or a “whole group trait”. The reason for this is that producing a female biased offspring sex ratio increases an individual's fitness (by decreasing the amount of competition for mates between sons, and increasing the number of females that sons can mate), but does so also for the other females laying eggs on the patch (18, 19)]. Lower numbers of females laying eggs per patch (N) means a higher relatedness ($r=1/N$, because females are assumed to disperse completely and so are only related to themselves) between an individual and all the females laying eggs on a patch (including herself), favouring a more female biased (altruistic) sex ratio.

There is an enormous amount of empirical support for LMC theory, both qualitative and quantitative. First, a wide range of organisms whose life history is likely to lead to LMC have female biased sex ratios, including insects, mites, spiders, nematodes, parasitic protozoa and plants (11, 12, 20). Second, variation in the sex ratio across populations and species can be explained by differences in the average number of females laying eggs in a patch (N , or equivalent determinant of the extent of LMC such as the extent of inbreeding; (21,24). Third, in certain species, some or all of the males disperse from the patch after mating has occurred on their own patch (25), leading to competition between males occurring at a scale intermediate between local and global (i.e. $0 < a < 1$). In these species the observed sex ratio is less female biased than in species in which similar numbers of females oviposit per patch (i.e. same N), but in which competition between males is local (24). Fourth, individuals of many species facultatively alter the sex ratio of their offspring in response to the number of females laying eggs on a patch (22, 26, 27). The occurrence of female biased sex ratios, and a lower bias in species where males disperse (points 1 & 3), demonstrates the importance of the scale of density dependent competition (a or the relationship of r_{xe} to r_{xy}). The variation in sex ratios with the number of females laying eggs in a patch (points 2 & 4) demonstrates the importance of within patch relatedness (r).

The influence on the unbeatable sex ratio of limited dispersal by females has also been examined theoretically, with predictions analogous to those of the limited dispersal altruism models discussed in the main text. For example, in the main text we discussed how in certain patch structured models, the amount of dispersal between patches does not effect the evolution of altruism (15, 28). The reason for that is that limited dispersal leads to a higher relatedness between interacting individuals, which favours altruism, but also increased competition between relatives, which opposes altruism, and that these two forces exactly balance one another. The same model had been developed previously for sex ratio evolution, with the analogous prediction that the offspring sex ratio should not depend upon dispersal rates (13, 29,33). In this case, limited dispersal increases the relatedness between individuals laying eggs on a patch, which favours a more female biased sex ratio (to increase the reproductive success of relatives sons), but this is exactly balanced by the fact that limited dispersal also increases competition between related females for patches, favouring a less female biased sex ratio (to increase the reproductive success of your and relatives daughters who do not disperse). Analogous to the work on the evolution of altruism, the predictions of these sex ratio models also depend upon the extent to which resources are limited locally or globally (i.e. if the population is elastic or inelastic) (30). The predictions of these models could be tested by: (i) setting up

experimental populations with different dispersal rates or population structures and examining how the sex ratio evolves (e.g. in a species that shows genetic variability for offspring sex ratios such as *Nasonia vitripennis* (34)), or (ii) collecting observational field data on a species that breeds in discrete patches and where female dispersal rates can be estimated directly by genetic markers, and in which dispersal rates vary.

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