Partial local mating and the sex ratio: indirect comparative evidence

W.D. Hamilton has described his theory of local mate competition[1] as the contribution of which he is the most proud[2]. It is indeed an outstanding accomplishment: as a cornerstone of sex ratio theory, his model has spawned multitudes of interrelated theoretical and empirical studies that constitute perhaps the most successful area of evolutionary biology.

The crucial consideration of the theory of local mate competition was mating structure. Theory by R.A. Fisher[3] had already explained the unbiased sex ratios of many animals. Fisher assumed that an individual's mates are drawn from the pool of the whole population, an outbreeding situation termed 'panmixis'. Hamilton, however, considered species that inhabit discrete and ephemeral resource-patches, inbreed and have female-biased sex ratios. Formally assuming that *all* mating occurs within such local groups before mated female offspring disperse to found new groups, Hamilton's model[1] predicts that when one or a few females contribute offspring, highly female-biased sex ratios are favoured, as these reduce the competition for mates among their sons. As the number of mothers contributing offspring increases, the optimal progeny sex ratio of each becomes progressively less biased, approaching the unbiased sex ratios predicted by Fisher[3]. This convergence makes intuitive sense, because in the extreme – and abstract – case where a patch is founded by all females in a population, the distinction between panmixis and local mating evaporates. Many tests have employed fig wasps or other Hymenoptera to test the prediction both within and across species: the theory is broadly supported[4,5].

Two paths to panmixis

An increase in foundress number is, however, only one of two possible ways to approach panmixis. A number of models have considered the possibility that some mating occurs away from the natal patch, a situation termed 'partial local mating' (review in Ref. 6). These predict that, for a given number of foundresses, optimal sex ratios will become less female-biased as the likelihood of non-local mating increases (Fig. 1). Such models are of more than just mathematical interest since species with *fully* local mating are probably a minority among those with some degree of local mate competition[6]. However, their predictions have remained virtually untested because assessing the degree of non-local mating usually presents formidable practical challenges: Hymenoptera are small and the procreative successes of dispersed individuals are generally difficult to observe.

Recent advances in genetic techniques offer one solution because mating structures can be estimated without observing behaviour[7,8], but obtaining estimates from more than a few species or populations is usually impractical. Alternatively, more readily measurable features may serve as mating structure proxies and relationships between these and the sex ratio can be examined. This indirect approach has been taken by West and Herre[9] in a new field study that tests simultaneously the influences of foundress number and non-local mating on the sex ratios of non-pollinating fig wasps.

Fig wasp foundress numbers: direct and indirect estimates

Fig wasps are only able to develop within figs. They come in two types: pollinating and non-pollinating wasps. In pollinator species, (winged) females enter the fig, lay eggs and die, their corpses usually remaining as convenient evidence of foundress number. Males are wingless and unable to disperse from the natal fig – equally convenient evidence for the absence of non-local mating. Pollinator sex ratios thus provide remarkably neat data for testing Hamilton's prediction[1], which they support[5].

Non-pollinator species are more diverse and less well known[5]. In the species studied by West and Herre[9], females inject eggs into the fig from the outside, have wings and may visit a number of different figs during their lives. Consequently the number of foundresses contributing offspring to a particular fig is much less apparent than in pollinator species.

West and Herre[9] resorted to a model to predict foundress number. Considering three possible distributions (random, aggregated and even) of foundresses foraging for egg-laying opportunities among figs, they predict (for all three scenarios) that the proportion of figs in which a wasp species occurs is positively correlated with the average number of females that lay eggs into each fig. This proportion can thus be used as an indirect estimate of foundress number. Since the latter is also predicted to be related to sex ratio[1], there should be a positive correlation between the proportion of figs containing wasps of a particular species and the sex ratio of that wasp species[9].

Sex ratios under full and partial local mating

Armed with their model, West and Herre[9] sampled 17 species of non-pollinator fig wasps in Panamanian figs. They found a positive relationship between the proportion of figs in which a species occurred and its sex ratio, as predicted. Reassuring though this is, such relationships between sex ratio and foundress number were already shown, and more directly, across pollinator species[5]. What makes the new study particularly interesting is that males in ten of these non-pollinator species are, like those of pollinators, wingless while in the other seven species males have wings. Both types mate within the natal fruit[9], but winged males disperse concurrently with the females, presumably to forage for non-local mating opportunities. For a given estimated foundress number, the sex ratios of species with winged males were less biased than those of wingless-male species[9] – a result consistent with predictions of theory considering partial local mating[10] (Fig. 1).

Having or not having wings is a categorical difference, but the proportion of non-local mating may vary between winged species. Calculations[9] suggest a range of 0.43 to 0.95 but, because of aggregation of foundresses and finite brood sizes, these are likely to be overestimates. Indeed, applying the same methods to the wingless species gives proportions of non-local mating ranging from 0.28 to 0.49, rather than the expected value of zero[9]. Although these ranges overlap, it

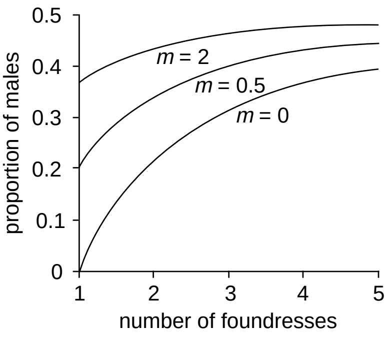

Fig. 1. Increasing foundress numbers and increasing non-local mating: two routes towards panmixis and an unbiased sex ratio. This model[10] assumes haplodiploid genetics and that, after all females in the natal patch are mated, males disperse to seek virgin females in other patches. The degree of non-local mating is represented by '*m*', the number of patches found by a dispersing male. *Reproduced, with permission, from Ref. 10.*

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is at least encouraging that winged species are mostly estimated to have higher proportions of non-local mating. Application of genetic techniques[7,8] would help to improve the accuracy of these estimates.

Phylogenetic awareness

Because of phylogenetic relatedness, differences in species characteristics may not represent independent evolutionary events. So, West and Herre[9] supplemented cross-species analyses with phylogenetically based methods that offer a more valid approach to testing for correlated evolution amongst traits[11]. An incompletely resolved phylogeny reduced the data set to nine independent contrasts[12], but the significance of foundress number survived the loss in power. However, no significant effect of male morphology was shown using these methods. This makes interpreting the data more difficult, because the cross-species result could be due to other differences between a few taxa which happen also to differ in male morphology. Particularly worrying is that the relationship between the proportion of figs colonized and foundress number may differ between these taxa.

Prospects: more resolution, more breadth and more depth

Employing morphology to estimate partial local mating in Hymenoptera is not entirely new. In this vein, King and Skinner[13] compared sex ratios of two *Nasonia* species, one with fully winged males and one with wing-reduced males: the fully winged species had the more female-biased sex ratio. Although this is contrary to expectation, two-species comparisons lack the power for reliable interpretation. Comparisons of more species and resolving phylogenies are two avenues for future research. The other half of the two-pronged empirical attack on understanding sex ratios under partial local mating – examining mating structures directly and in depth[7,8] – will inevitably advance more slowly but with greater force.

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A moveable feast: the evolution of resource sharing in plant–fungus communities

Forty years ago, Erik Bjorkman injected labeled glucose into the phloem of three Norway spruce trees and measured its transfer to nearby individuals of the achlorophyllous plant, *Monotropa hypopitys*[1]. Many similar experiments have since been done with various plant combinations (although all with chlorophyll since Bjorkman), using isotopes of carbon, phosphorus, nitrogen and calcium[2–7]. With a single exception, isotopes have been found to move from one plant to another as long as the plant species in question share mycorrhizal fungi. This finding supports Bjorkman's original hypothesis that movement is predominantly via mycorrhizal hyphae. In the one exception, ^{32}P applied to mycorrhizal hyphae was distributed amongst tree seedlings linked to the hyphal network (two pine species), but when applied to the seedlings did not move into the network, suggesting movement along gradients of relatively high to relatively low concentration[8].

The importance of source–sink gradients, at least for the transfer of carbon and nitrogen, has been confirmed by studies that have experimentally manipulated light (via shading) and nutrients (via fertilization), or used nodulated plants as donors and nonnodulated ones as receivers[7,9,10]. Until recently, the ecological significance of the extent to which an element transfers between plants was uncertain because (among other things) all measures had been one way (donor to receiver) and, therefore, the degree of net transfer was unknown. Simard *et al.*[7] used dual carbon isotopes to show net transfer between paper birch (*Betula papyrifera*) and Douglas-fir (*Pseudotsuga menziesii*). The fir seedlings received up to 10% of their fixed carbon from birch over a 9-day period. Simard *et al.* pointed out that the 10% value is comparable to the amount of carbon transferred from clonal parent-plants to connected ramets, an amount believed to contribute significantly to the survival of the ramets.

Research on element transfers, in conjunction with a larger body of work on the beneficial interactions within plant communities, reflects a growing interest among ecologists and evolutionary biologists in plant–fungi cooperation (and other forms of positive feedback), their implications for ecological function, and how