

Local mating and sex ratios

Recently, Hardy and Mayhew¹ discussed the interesting topic of partial local mating in organisms that can facultatively adjust their sex ratios. Although straightforward genetic methods for estimating population structure are useful and have been applied to both fig and parasitoid wasps^{2,3}, their article reported the work of West and Herre⁴, who recently inferred fig-wasp population structures using morphological data and applied this to the problem of optimal sex ratios under partial local mating situations. West and Herre⁴ reasoned that winged-male fig wasps would tend to disperse from their natal patches, and those species with winged males should therefore have sex ratios that are less female biased, as theory generally predicts^{5,6}. West and Herre⁴ generally found the predicted sex ratio pattern.

As Hardy and Mayhew¹ subsequently point out, another (and possibly the only) study in which wing size was used to infer population structure was a study by King and Skinner⁷ on the parasitoid wasps *Nasonia vitripennis* and *N. giraulti*. In this study, however, the investigators found just the opposite pattern: the male-winged *N. giraulti* had significantly more female-biased sex ratios than did the male-wingless *N. vitripennis*⁷. Unsure of the factors influencing the observed sex ratios, they proposed several explanations to account for their data⁷.

The reason for this apparent discrepancy is now clear. In a laboratory study using a number of field isolates, Drapeau and Werren⁸ have found that high percentages of *N. giraulti* females are inseminated before they exit their pupal fly host. Female *N. vitripennis* rarely, if ever, mate within the host. Therefore, males who disperse from their natal site are unlikely to find virgin females outside of hosts. Hence, the original prediction – that winged species will tend to disperse and find mates – is probably false. Drapeau and Werren qualitatively confirmed King and Skinner's sex ratio data for both species^{7,8}.

Interestingly, the males of the third species of *Nasonia*, *N. longicornis*, have wings of intermediate size relative to the other two species, and Drapeau and Werren⁸ found that levels of both within-host-mating (WHM) and sex ratios in *N. longicornis* were intermediate to those of *N. vitripennis* and *N. giraulti*. WHM is an exciting behavior because it can rapidly promote barriers to gene flow between sympatric populations.

We may briefly contemplate why *N. giraulti* males have large wings, if male dispersal does not lead to a male fitness advantage. Assuming that WHM does occur in nature (which unpublished field data confirm, see Ref. 8), WHM might have evolved fairly recently, and male wing-size evolution has therefore lagged behind (note that large male wings appear to be the ancestral state of the Pteromalid wasps). Alternatively, selection might be acting on male wing size either directly (i.e. through courtship cues) or indirectly (i.e. through a pleiotropic effect or linkage disequilibrium), keeping the wing size of male *N. giraulti* approximately constant.

As Hardy and Mayhew¹ point out, cross-species data differences could be due to 'other differences between a few taxa which also happen

to differ in male morphology'. This statement appears to be very relevant to the *Nasonia* pattern.

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References

- 1 Hardy, I.C.W. and Mayhew, P.J. (1998) *Trends Ecol. Evol.* 13, 431–432
- 2 Kazmer, D.J. and Luck, R.F. (1991) in *Proceedings of the 3rd International Symposium on Trichogramma and other Egg Parasitoids* (Wajnberg, E. and Vinson, S.B., eds), pp. 107–110, Institut National de la Recherche Agronomique
- 3 Molbo, D. and Parker, E.D., Jr (1996) *Proc. R. Soc. London Ser. B* 263, 1703–1709
- 4 West, S.A. and Herre, E.A. (1998) *J. Evol. Biol.* 11, 531–548
- 5 Hamilton, W.D. (1967) *Science* 156, 477–488
- 6 Nunney, L. and Luck, R.F. (1988) *Theor. Popul. Biol.* 33, 1–30
- 7 King, B.H. and Skinner, S.W. (1991) *Evolution* 45, 225–228
- 8 Drapeau, M.D. and Werren, J.H. (1999) *Evol. Ecol. Res.* 1, 223–234

Reply from I.C.W. Hardy and P.J. Mayhew

We welcome the new information on *Nasonia*: it is just the kind of empirical investigation we advocate, extends the number of species for comparison and appears to account for an anomalous result¹.

King and Skinner's¹ and West and Herre's² studies are, in fact, not the only ones to have used wing size, or other morphological variables, to infer population structure. As with much else in this field, investigations of potential correlations between wing morphology and mating system can be traced at least back to the work of W.D. Hamilton^{3,4}. Here, we provide brief summaries of two very recent comparative studies, both akin to the work of West and Herre² that we discussed previously⁵ (see also Refs 6,7).

Fellowes *et al.*⁸ examined sex ratios of 44 species of Old World non-pollinating fig wasps, which included eight species in which all males are winged, 32 in which all males are wingless and also four species in which males are dimorphic. In accordance with theoretical predictions, the mean sex ratio of wingless-male species was lower (more female biased) than the mean sex ratio of male-dimorphic species, which was in turn lower than that of the winged-male species. The result that sex ratio is positively related to 'wingedness' was also found using phylogenetically based analysis, despite an incompletely resolved estimate of phylogeny.

General morphology was used by us⁹ to infer mating structure in 19 species of bethylid wasps (parasitoids of Coleoptera and Lepidoptera).

Offspring groups are usually produced by a single mother, so a marked influence of non-local mating on sex ratio is expected. Although local mating almost certainly predominates, males and unmated females in some species disperse^{9,10} and some non-local mating seems likely. In the absence of direct estimates of mating structure, or a winged-wingless dimorphism, we used sexual dimorphism in body size as an estimator of male dispersal ability relative to females (which must disperse from the natal site to find fresh hosts) as a potential correlate of non-local mating.

Across species, sex ratios were less female biased in species with relatively larger males, as expected. However, a poorly resolved phylogeny resulted in only eight independent contrasts and, like West and Herre², we failed to confirm the relationship with phylogenetically based analysis. Our cross-species result is due mostly to differences between two bethylid subfamilies, one with large males and high sex ratios, and one with small males and low sex ratios. Although the species values are consistent with our adaptive hypothesis, differences between the two subfamilies not considered might also account for the cross-species trend.

Thus, only Fellowes *et al.*'s study⁸ currently escapes the dilemma of interpreting inconsistent results from different comparative methodologies (although it does not control for possible confounding variables, unlike the other studies^{2,9,11}). In pleasing support of our previous conclusions⁵, comparison of larger numbers of species⁸ has borne fruit, as has direct examination of mating structure components¹¹.

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References

- 1 King, B.H. and Skinner, S.W. (1991) *Evolution* 45, 225–228
- 2 West, S.A. and Herre, E.A. (1998) *J. Evol. Biol.* 11, 531–548
- 3 Hamilton, W.D. (1967) *Science* 156, 477–488
- 4 Hamilton, W.D. (1979) in *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.A., eds), pp. 167–220, Academic Press
- 5 Hardy, I.C.W. and Mayhew, P.J. (1998) *Trends Ecol. Evol.* 13, 431–432
- 6 Cook, J.M. *et al.* (1997) *Proc. R. Soc. London Ser. B* 264, 747–754
- 7 Hardy, I.C.W., Ode, P.J. and Siva-Jothy, M. in *Insect Natural Enemies: Practical Approaches to their Study and Evaluation* (2nd edn) (Jervis, M. and Kidd, N., eds), Kluwer Academic Publishers (in press)
- 8 Fellowes, M.D.E., Compton, S.G. and Cook, J.M. *Behav. Ecol. Sociobiol.* (in press)
- 9 Hardy, I.C.W. and Mayhew, P.J. (1998) *Behav. Ecol. Sociobiol.* 42, 383–395
- 10 Hardy, I.C.W. *et al.* (1999) *Ethology* 105, 57–72
- 11 Drapeau, M.D. and Werren, J.H. (1999) *Evol. Ecol. Res.* 1, 223–234