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Sex allocation and local mate competition in Old World non-pollinating fig wasps

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Abstract The populations of many species are structured such that mating is not random and occurs between members of local patches. When patches are founded by a single female and all matings occur between siblings, brothers may compete with each other for matings with their sisters. This local mate competition (LMC) selects for a female-biased sex ratio, especially in species where females have control over offspring sex, as in the parasitic Hymenoptera. Two factors are predicted to decrease the degree of female bias: (1) an increase in the number of foundress females in the patch and (2) an increase in the fraction of individuals mating after dispersal from the natal patch. Pollinating fig wasps are well known as classic examples of species where all matings occur in the local patch. We studied non-pollinating fig wasps, which are more diverse than the pollinating fig wasps and also provide natural experimental groups of species with different male morphologies that are linked to different mating structures. In this group of wasps, species with wingless males mate in the local patch (i.e. the fig fruit) while winged male species mate after dispersal. Species with both kinds of male have a mixture of local and non-local mating. Data from 44 species show that sex ratios (defined as the proportion of males) are in accordance with theoretical predictions: wingless male species < wing-dimorphic male species < winged male species. These results are also supported by a formal comparative analysis that controls for phylogeny. The foundress number is difficult to estimate directly for non-pollinating fig wasps but a robust indirect method leads to the prediction that foundress number, and hence sex ratio, should increase with the proportion of patches occupied in a crop. This result is supported strongly across 19 species with wingless males, but not across 8 species with winged males. The mean sex ratios for species with winged males are not significantly different from 0.5, and the absence of the correlation observed across species with wingless males may reflect weak selection to adjust the sex ratio in species whose population mating structure tends not to be subdivided. The same relationship is also predicted to occur within species if individual females adjust their sex ratios facultatively. This final prediction was not supported by data from a wingless male species, a male wing-dimorphic species or a winged male species.

Key words Fig wasps · Local mate competition · Sex allocation · Sex ratio · Wing morphology

Introduction

The offspring sex ratio produced by a parent is tightly linked to fitness, and Fisher (1930) first showed that natural selection will favour equal investment in the sexes in a random-mating population. However, an important and highly successful field of evolutionary biology has been the generation and testing of sex ratio models for scenarios that violate the assumptions of Fisher's model. Arguably the best known class of models deals with selection for female-biased sex ratios in structured populations, especially in haplodiploid species where sex allocation decisions are under control of the ovipositing female. Hamilton (1967) first considered the case in which a single foundress colonises a patch, where her offspring then develop and mate amongst themselves before dispersing. Selection favours a highly female biased sex ratio with just enough males to ensure fertilisation of the females. This phenomenon is known as local mate competition (LMC) because brothers compete with each other for matings with their own

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sisters. If the offspring in the patch originate from two foundresses, the marginal value of sons increases because sons have the potential to also mate with the daughters of the other female. Consequently, models predict that the sex ratio (defined as proportion of males) will increase with the number of foundress females ovipositing in a patch (Charnov 1982).

LMC models have been tested in a number of studies, often involving species of parasitic Hymenoptera – either true parasitoids (reviewed by King 1987; Godfray 1994; Godfray and Cook 1997) or pollinator fig wasps (Frank 1985; Herre 1985, 1987; Herre et al. 1997). These studies have provided strong support for the main predictions of LMC theory. However, while the biology of a few species, such as fig-pollinating wasps, conforms to the extreme scenario of all mating occurring in the local patch, in many species a fraction of matings occur after dispersal from the local patch. This mixture of local and non-local mating (reviewed by Antolin 1993; Godfray 1994; Hardy 1994) has been termed *partial LMC* (Hardy 1994) and theoretical models predict that selection will favour less female biased sex ratios (e.g. Uyenoyama and Bengtson 1982; Frank 1986; Nunney and Luck 1988; Greeff 1995).

While partial LMC is thought to be common, it is not easy to study in parasitoid wasps because the degree of pre- and post-dispersal mating is difficult to estimate, and ideally requires genetic data (Kazmer and Luck 1991). Fig wasp species, however, show a range of natural variation that lends itself to such studies (West and Herre 1998). All pollinating fig wasps have wingless males and mate only within the natal patch, providing excellent examples of fully local mating situations (Frank 1985; Herre 1985, 1987; Herre et al. 1997). In contrast, non-pollinating fig wasps are much more morphologically diverse and include species with wingless males, species with winged males, and species with both types of male (Hamilton 1979; Cook et al. 1997). Since wingless males mate only in the natal patch (fig fruit) and winged males generally mate only after dispersal (Hamilton 1979; Cook et al. 1997; but see also West et al. 1996; West and Herre 1998), non-pollinating fig wasps provide natural experimental groups of species ranging from those with full local mating (wingless males), through those with partial local mating (wing-dimorphic males), and on to those with little or no local mating (winged males).

Male morphology has been used as a surrogate for mating structure in two previous studies of New World fig wasp sex ratios. Hamilton's (1979) informal (non-statistical) comparison of sex ratios of species with different males supported the qualitative prediction, while West and Herre (1998) showed that the sex ratios of winged male species were less female biased than those of wingless male species that occurred in the same proportion of fig fruits in a crop (an index of foundress number – described below). However, neither study was able to provide support for this prediction by using phylogenetically independent contrasts.

The other, and better-known, cause of sex ratio variation in fig wasps is the number of foundresses per patch. This can be estimated directly in some fig-pollinating wasps (Herre 1985, 1987) because the cadavers of foundress females remain in the patch where the offspring will emerge. However, most non-pollinating fig wasps oviposit through the wall of the fig fruits from the outside and may lay a small to moderate number of eggs in each of many different fig fruits (Cook et al. 1997; Herre et al. 1997). Consequently, foundress number cannot be estimated directly, unless genetic markers are used (see Molbo and Parker 1996 for an example with parasitic wasps). To obtain an indirect estimate of foundress number in non-pollinating fig wasps, West and Herre (1998) developed a model of oviposition patterns with different distributions of foundresses over available patches. They showed that, for a variety of different patterns of wasp aggregation (random, even, clumped) across patches, the proportion of fig fruits attacked in a crop is a viable surrogate measure of the average foundress number within patches. Their model makes a robust prediction that foundress number and hence sex ratio should increase with the proportion of fruit in a crop attacked by a wasp species. Data from both winged and wingless species of Panamanian non-pollinating fig wasps strongly supported this conclusion, and we further consider their results in the discussion.

In this study, we test the predictions of LMC models using a large data set from 44 Old World non-pollinating fig wasp species. Importantly, this is the first study to include data from species in all three male morph categories (winged, wingless, wing-dimorphic). Specifically, we test the following predictions: (1) across species the order of average species sex ratios should be wingless male species $<$ wing-dimorphic male species $<$ winged male species; (2) between species of each discrete category (e.g. wingless males), the proportion of males should increase with the prevalence of the wasp species (percent figs occupied in a crop); (3) within a given species, the proportion of males should increase with prevalence of wasps in a crop of fruit. This last relationship is only predicted if female wasps are able to facultatively adjust the sex ratio of their offspring in order to meet local circumstances. We first address these issues ignoring phylogeny, and then, where possible, examine them more rigorously with comparative analyses by independent contrasts, which serve to reduce any possible phylogenetic biases (Felsenstein 1985; Burt 1989; Harvey and Pagel 1991).

Fig wasp natural history

The interaction between figs (*Ficus* spp., Moraceae) and their pollinator wasps (Hymenoptera, Agaonidae) is a classic case of an obligate mutualism (Janzen 1979; Bronstein and McKey 1989). Most of the 700 or so fig species are pollinated by their own unique species of pollinator wasp (Agaonidae, subfamily Agaoninae). The female wasps enter receptive young fig fruits, where they both pollinate flowers and lay eggs. The foundress females die inside the fig fruit cavity and their cadavers may still be detectable several weeks later when the next generation of wasps emerge and mate inside the fig fruit. At this time the male fig flowers liberate their pollen and the female fig wasps transport the pollen to the next crop of receptive figs. Since all pollinating fig wasp matings occur inside the natal fig fruit, foundress number is the key determinant of sex ratio.

Each species of fig is also attacked by a number of non-pollinating fig wasps (up to 29 species have been recorded from one tree species: Compton and Hawkins 1992), and most of these also belong to the family Agaonidae (Boucek 1988). Their offspring either feed on the developing fig seeds (West and Herre 1994), induce galls (Godfray 1988; Cook and Power 1996; West et al. 1996) or parasitise other fig wasps (Godfray 1988; West et al. 1996). Most non-pollinating fig wasp females do not enter the syconium (fig fruit) to oviposit, instead using their long ovipositors to penetrate the syconium wall from the outside. The morphologies and mating strategies of the non-pollinating fig wasps are diverse: some species have wingless males, some have winged males, and some have both types of male (Hamilton 1979; Cook et al. 1997). While wingless males are constrained to mate within the confines of the natal syconium (as in pollinating fig wasps), the winged males generally mate after dispersing from the natal fig fruit. Consequently, wingless males contribute to local mating while winged males contribute to non-local mating and species with different types of male form natural experimental groups for the study of sex ratios.

Methods

Data collection

Data for 44 species of externally ovipositing non-pollinating fig wasps (Table 1) were collected from Australia (by J.M.C.), South Africa (by S.G.C.), Malaysia (Murray 1990) and Papua New Guinea (Godfray 1988). The methods used in collection are described in detail elsewhere (Godfray 1988; Compton and Nefdt 1990; Murray 1990; Cook and Power 1996). In summary, figs were collected just before fig wasp emergence was expected. These were preserved in alcohol until required for detailed dissection, when all the wasps from each fig fruit were identified and counted. Where necessary, voucher specimens were sent to taxonomic experts for definitive identification.

Statistical analysis

The data were analysed in two ways. First, we performed phylogeny-free analyses of the between-species, as well as the within-species predictions. The number of data points used in the different phylogeny-free analyses varies because for some species we do not have records of the proportion of fig fruits occupied. While phylogeny-free analyses are suitable for correlations within species, it is often inappropriate to treat species as independent data points when testing predictions between species (Felsenstein 1985) because species are not independent of their evolutionary history and closely related species are more likely to share traits than species that are more distantly related, as some characters will be present through common descent rather than through independent evolutionary events. Statistical methods have been proposed to overcome this confounding problem (Harvey and Pagel 1991), and such methods require phylogenies. We use the method of independent contrasts (Burt 1989), which is simple but makes very few assumptions about the underlying data. Full exploitation of Burt's (1989) method requires a well-resolved phylogeny. This is not yet available for fig wasps, preventing some of the analyses from being conducted in this manner.

Species as independent data points

Between species with different male morphs

First, we compared the mean sex ratio (proportion male) of species with winged, wing-dimorphic and wingless males. Initial inspection of the data showed that there was considerable overdispersion, which precluded analysis by parametric ANOVA. Instead, we analysed the data using non-parametric Kruskal-Wallis ANOVA (Sokal and Rohlf 1995) and made pair-wise comparisons between groups using the Q-test statistic (Zar 1984, p. 200).

Between species with the same male morph

Again, levels of overdispersion in the data set precluded analyses using parametric approaches. Instead, Spearman rank correlations were calculated between the sex ratio and the proportion of figs attacked in a crop for different species with the same male wing morphology. Analyses were performed for winged species ($n = 8$) and wingless species ($n = 19$), but not for the limited number of wing-dimorphic species ($n = 3$).

Within species

There were also enough data to enable us to perform Spearman rank correlations between the sex ratio and the proportion of fig fruits attacked in a crop for one of the better sampled species from each of the wing categories. The three species tested were *Sycoscapter* sp.g (wingless), *Pseudidarnes minerva* (wing-dimorphic) and *Camarothorax* sp.1 (winged).

The comparative analysis

We used the conservative phylogeny shown in Fig. 1 (see Cook et al. 1997 for details). The method of independent paired contrasts (Felsenstein 1985; Burt 1989) was used to investigate the relationship between male morphology and sex ratio. Independent contrasts are derived by calculating the difference in sex ratio between pairs of taxa with different male morphs. We tested the hypothesis that, in comparisons between pairs of taxa that fall into different morph categories (winged, wing-dimorphic, wingless males), sex ratio is more female biased in taxa with the greatest wing reduction. Two comparisons (W vs X and Y vs Z) are considered to be independent if the phylogenetic path drawn between W and X and that between Y and Z do not meet or cross (Burt 1989). In our analysis, three types of comparison are possible: (1) between wingless and wing-dimorphic taxa, (2) between wing-dimorphic and winged taxa, and (3) between wingless and winged taxa. As shown in Fig. 1, comparisons were made among taxa with the same identifying letter (i.e. A–E).

Results

The phylogeny-free analyses

Across species there was a significant difference in the median proportion of males of the groups [Kruskal-

Table 1 Data used in comparative analysis (*PNG* Papua New Guinea)

Species	(Sub)family	Origin	Wasp number	Sex ratio
Species with winged males				
Megastigmus sp.	Torymidae	Australia: *Ficus rubiginosa*	12	0.5
Watshamiella sp.	Sycoryctinae	Australia: *F. rubiginosa*	268	0.45
Sycophila sp.1	Eurytomidae	South Africa: *F. thoningii*	27	0.44
Sycophila sp.2	Eurytomidae	South Africa: *F. thoningii*	17	0.47
Sycophila sp.3	Eurytomidae	South Africa: *F. thoningii*	11	0.64
Sycophila dark	Eurytomidae	South Africa: *F. thoningii*	25	0.28
Herodotia subatriventris	Epichrysomallinae	Australia: *F. rubiginosa*	116	0.47
Camarothorax sp.1	Epichrysomallinae	South Africa: *F. thoningii*	139	0.58
Species with dimorphic males				
Epichrysomalline sp.a	Epichrysomallinae	Malaysia: *F. benjamina*	298	0.33
Philotrypesis sp.e	Sycoryctinae	South Africa: *F. burtt-davyi*	639	0.48
Philotrypesis sp.f	Sycoryctinae	South Africa: *F. thoningii*	110	0.42
Pseudidarnes minerva	Sycophaginae	Australia: *F. rubiginosa*	621	0.42
Species with wingless males				
Comptoniella vannoorti	Otitesellinae	South Africa: *F. c. cordata*	104	0.41
Eujacobsonia genalis	Otitesellinae	Malaysia: *F. annulata*	2997	0.21
Eupristina adempta	Otitesellinae	Malaysia: *F. benjamina*	2426	0.14
Lipothymus sundaicus	Otitesellinae	Malaysia: *F. sundaica*	4074	0.14
Otitesella sp.a	Otitesellinae	South Africa: *F. verruculosa*	120	0.38
Otitesella sp.b	Otitesellinae	South Africa: *F. c. salicifolia*	270	0.34
Otitesella sesquianellata	Otitesellinae	South Africa: *F. burtt-davyi*	456	0.42
Otitesella tsamvi	Otitesellinae	South Africa: *F. thoningii*	660	0.44
Otitesella uluzi	Otitesellinae	South Africa: *F. burtt-davyi*	550	0.45
Otitesellinae sp.	Otitesellinae	Malaysia: *F. annulata*	461	0.38
Apocryptophagus sp.a	Sycophaginae	PNG: *F. hispidiodes*	1637	0.26
Eukobelea hallami	Sycophaginae	Australia: *F. rubiginosa*	60	0.23
Eukobelea sp.1	Sycophaginae	Malaysia: *F. beccarri*	359	0.2
Sycophaga cyclostigma	Sycophaginae	South Africa: *F. sur*	1854	0.22
Apocrypta mega	Sycoryctinae	PNG: *F. hispidiodes*	226	0.32
Apocrypta guineensis	Sycoryctinae	South Africa: *F. sur*	4258	0.56
Apocrypta bakeri	Sycoryctinae	Malaysia: *F. hispida*	1121	0.34
Arachonia sp.	Sycoryctinae	Malaysia: *F. annulata*	378	0.27
Philotrypesis sp.a	Sycoryctinae	Australia: *F. rubiginosa*	104	0.38
Philotrypesis sp.d	Sycoryctinae	South Africa: *F. verruculosa*	427	0.39
Philotrypesis sp.1	Sycoryctinae	Malaysia: *F. hispida*	288	0.24
Philotrypesis sp.3	Sycoryctinae	Malaysia: *F. grossularioides*	1432	0.41
Philotrypesis pilosa	Sycoryctinae	Malaysia: *F. hispida*	1127	0.38
Philotrypesis spinipes	Sycoryctinae	Malaysia: *F. fistulosa*	480	0.42
Sycorytes sp.1	Sycoryctinae	Malaysia: *F. annulata*	126	0.12
Sycorytes sp.2	Sycoryctinae	Malaysia: *F. grossularioides*	1596	0.38
Sycoscapter sp.c	Sycoryctinae	Australia: *F. rubiginosa*	1458	0.51
Sycoscapter sp.e	Sycoryctinae	South Africa: *F. c. salicifolia*	173	0.23
Sycoscapter sp.g	Sycoryctinae	South Africa: *F. burtt-davyi*	3430	0.42
Sycoscapter sp.h	Sycoryctinae	South Africa: *F. thoningii*	285	0.36
Sycoscapter sp.3	Sycoryctinae	Malaysia: *F. grossularioides*	1563	0.39
Sycoscapter sp.d	Sycoryctinae	Australia: *F. rubiginosa*	1145	0.45

Wallis ANOVA $H = 11.16$ ($df = 2$, $n = 44$), $P < 0.005$; Fig. 2]. Median sex ratios followed predicted patterns (wingless males: 0.38 < wing-dimorphic males: 0.42 < winged males: 0.47). There was a significant difference in the median proportion of males between those taxa with winged and wingless males ($Q = 3.23$, $P < 0.005$). However, no significant differences were found between the proportion of males of taxa with winged and wing-dimorphic males ($Q = 0.93$, NS) or between those with wingless and wing-dimorphic males ($Q = 1.33$, NS).

Across species with wingless males there was a significant correlation between the proportion of males and the proportion of figs attacked in a crop ($r_s = 0.51$, $n = 19$, $P < 0.05$; Fig. 3). However, this relationship was not found across species with winged males ($r_s = -0.07$, $n = 8$, NS). Within species there were no significant correlations found for wingless *Sycoscapter* sp.g ($r_s = 0.14$, $n = 9$, NS), wing-dimorphic *P. minerva* ($r_s = 0.41$, $n = 6$, NS), nor the winged *Camarothorax* sp.1 ($r_s = 0.2$, $n = 4$, NS).

The comparative analysis

The comparative analysis allowed us to make only five independent contrasts (see Fig. 1), but all of these supported the hypothesis that sex ratio decreases as wing reduction increases (one-tailed sign test: $P = 0.031$), as suggested by the phylogeny-free analysis. Ideally we

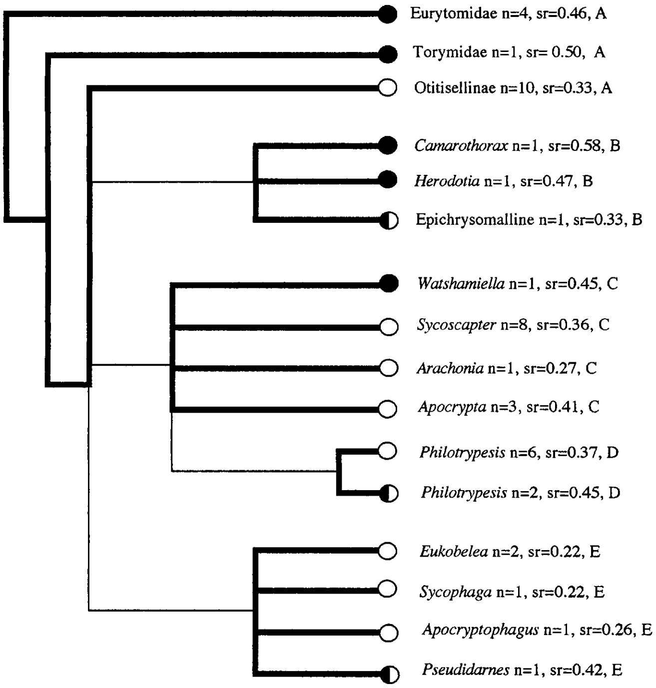

Fig. 1 The phylogeny used for independent contrasts. Taxa displayed have winged males (*filled circles*), dimorphic males (*half-filled circles*) or wingless males (*open circles*). For the sake of clarity, groups of related species with the same type of male morph are collapsed to a single point. The number of species combined is given by *n*, while *sr* denotes the mean sex ratio (proportion of males) of these species. Contrasts were made between taxa of different wing status marked by the same letter (*A*–*E*) and joined by *bold lines*. As an example, contrast *D* is between six *Philotrypesis* species with winged males (mean sr = 0.37) and two *Philotrypesis* species with dimorphic males (mean sr = 0.45)

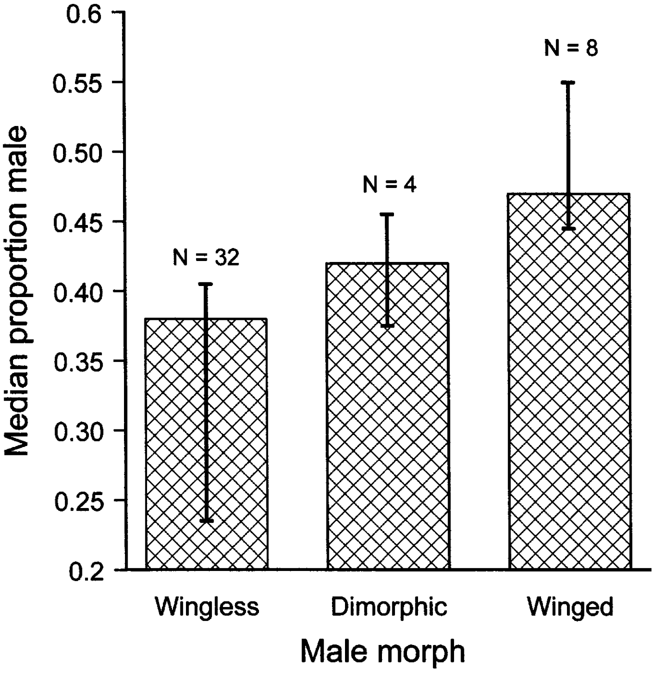

Fig. 2 Median sex ratio (± interquartiles) for fig wasp species with different male morphs

would have used this method to test the other predictions (2 and 3) but lack of phylogenetic resolution at the genus and species level precluded this.

Discussion

Two factors – the amount of non-local (post-dispersal) mating, and foundress number in the local patch (fig fruit) – are predicted to influence LMC and sex ratio variation in non-pollinating fig wasps. Variation in male morphology and mating behaviour provides groups of species to test the first factor. Across species we found that median sex ratio followed the predicted trend: wingless males < wing-dimorphic males < winged males. This result was supported by both phylogeny-free and formal comparative analyses. The second factor, foundress number per patch, is predicted to increase with the proportion of fig fruits parasitised (West and Herre 1998). This, in turn, leads to the prediction that sex ratio should increase with the proportion of figs attacked in a crop. This prediction was met across wingless male species but not across winged male species. The same prediction should hold across crops of fruit within a species if females adjust their offspring sex ratios facultatively in accordance with the degree of LMC. However, we found no evidence for such facultative adjustment within a given species.

The degree of LMC (and hence the female bias of the sex ratio) is predicted to decrease if some matings occur outside the natal patch following dispersal, and the mixture of on- and off-patch mating has been termed partial local mate competition (reviewed by Godfray 1994; Hardy 1994). Unfortunately, direct tests of the consequences of off-patch matings for the sex ratio are rare because of the difficulty of assessing the genetic relationships between individuals on and off patches. However, wing polymorphisms (West and Herre 1998, this study) can provide natural groups for indirect qualitative tests of partial LMC predictions, and other indices such as thoracic sexual size dimorphism may also be appropriate indirect indices of dispersal (Hardy and Mayhew 1998a). In this study, both our phylogeny-free and independent contrast analyses support our prediction (1) that across fig wasp species, the sex ratio decreases as male wing reduction increases (Figure 2). While other studies have found the predicted result with informal comparisons (Hamilton 1979) and phylogeny-free analyses of New World fig wasps (West and Herre 1998) and bethylid wasps (Hardy and Mayhew 1998b), this is the first time that a formal comparative analysis has provided significant support for the predicted correlation between a morphological surrogate of the mating system and the sex ratio. Our data set differs from that of West and Herre (1998) in several ways. Notably, we were able to include data from wing-dimorphic, as well as wingless and winged male species. We also analysed data from a much larger number of

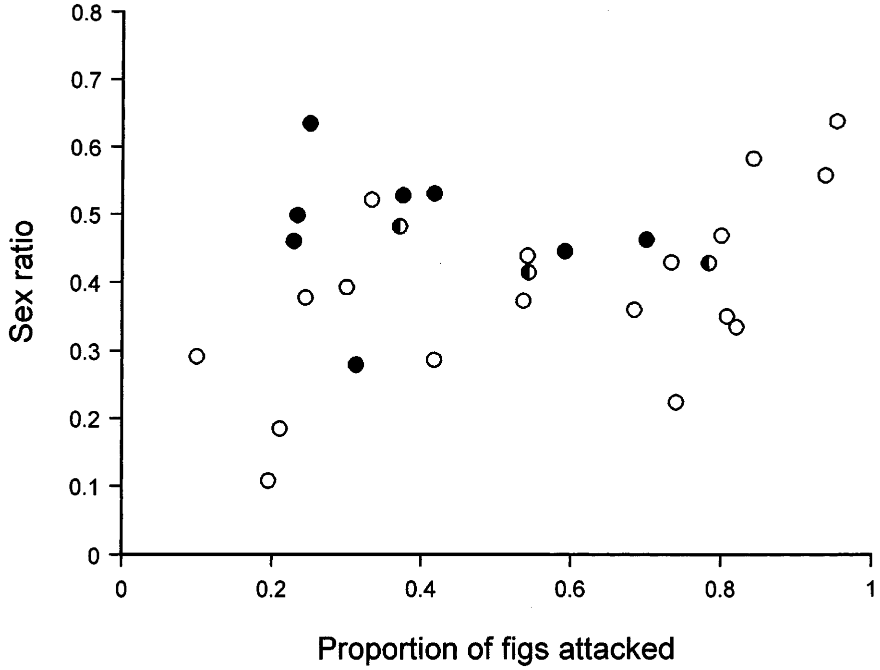

Fig. 3 Relationship between the sex ratio of species with wingless (*open circles*), dimorphic (*half-filled circles*) and winged (*filled circles*) males and the proportion of fig fruit attacked in a crop

species (44) and, although the poorly resolved phylogeny allowed only five independent contrasts, these all supported the prediction. Indeed, if we include the West and Herre (1998) data set in our comparative analyses, we acquire only one extra contrast [between wingless (0.237 male, n = 10) and winged (0.29 male, n = 2) *Idarnes* spp.]. This contrast supports the hypothesis (new $P=0.015$, one-tailed sign test), and none of the other data alter the outcome of our comparative analysis.

Foundress number within a patch is easy to estimate directly in some pollinating fig wasps because the foundresses do not leave the patch and their dead bodies can be counted at the time of offspring emergence (Herre 1985, 1987; Herre et al. 1997). However, this method cannot be used for non-pollinating fig wasps, or indeed most other Hymenoptera, so other techniques must be employed. Molbo and Parker (1996) used allozyme polymorphisms in a population of *Nasonia vitripennis* to show that the sex ratio in a patch increased with the number of female foundresses per patch. Nevertheless, while genetic markers can provide valuable tools for single species studies, data are available for few species and this limits the capacity to perform worthwhile comparative analyses. Indirect measures are again attractive, even though they may only be applicable to certain taxa. West and Herre (1998) developed such a measure for non-pollinating fig wasps, and showed that the proportion of figs attacked in a crop is a good measure of the average number of foundresses present in a patch. Consequently, our prediction (2) was that sex ratio should increase across species as the proportion of fig fruits attacked in a crop increases.

While it is unfortunate that the phylogeny is insufficiently resolved for comparative tests of prediction (2), the results of phylogeny-free analyses may still prove instructive. We found a positive correlation between offspring sex ratio and the proportion of figs attacked across wingless male species but not across winged male species (Fig. 3). In comparison, West and Herre (1998), using independent contrasts, found such a positive correlation in both wingless male and winged male species in Panama. The discrepancy between the two studies could be due either to limitations of the data or because of real biological differences. Due to the lack of phylogenetic resolution, our analysis was not supported by a comparative test. It is possible that a formal comparative test would show a significant correlation but we must await a better estimate of phylogeny. An important biological difference is that, in the species studied by West and Herre (1998; and also probably by Hamilton 1979), the winged males searched actively for females within the natal fig before dispersing. We have not noted this behaviour, which may result in some local mating, in the winged species that we have studied (see also Hamilton 1979). Consequently, the species with winged males that we studied are likely to experience little or no local mating. The data appear to support this view, since of the species with winged males, only the mean sex ratio of *Sycophila* dark was significantly different from equality ($G=5.01$, $P<0.05$; Table 1). Indeed the mean of means for sex ratios of winged male species is 0.48 in our study and only one species has a mean sex ratio of less than 0.44. In contrast, six out of seven winged male species in West and Herre's study have sex ratios between 0.2 and 0.38, with just one species effectively unbiased at 0.48. If selection for biased sex ratios is only weak in the species we have studied, any correlation across species will be difficult to detect.

Our prediction (3) was that, within a given wasp species, sex ratio should increase across fig crops as the proportion of fig fruits in a crop attacked increases. The absence of any such correlation in the three species studied is perhaps surprising. While it could be argued that there may be only weak selection to bias sex ratios facultatively in winged male and wing-dimorphic male species (see above), this argument does not hold for the wingless-male *Sycoscapter* species that we studied. Facultative sex ratio biasing within a species is shown by fig-pollinating wasps (Herre et al. 1997), as well as several parasitoid wasps (Godfray 1994), and other Hymenoptera. However, females can only respond facultatively if they have some means of assessing foundress number or patch contents, and it is possible that sequential oviposition by externally ovipositing wasps may prevent this assessment (Greeff 1997). This is clearly an area for further work, but we have observed that, in at least some *Sycoscapter* species, several females may probe (and presumably lay eggs) simultaneously into the same fig fruit. If individual females do not show conditional sex ratio responses, it is still possible that adaptive sex allocation can occur via strategies that are moulded by the average level of LMC in the population (see Charnov et al. 1981 for an analogous discussion). Another possibility is that our data are too limited to detect existing correlations, as only nine data points were available for *Sycoscapter* sp.g. There may also be considerable error in estimates of the proportion of fig fruits attacked, since a single crop may contain hundreds of fig fruits.

LMC theory has established itself as one of the most satisfying areas of investigation for evolutionary ecologists. Not only is theory well-developed, it has also proved to be robust in the face of empirical enquiry. While recent work (Greeff 1995, 1996, 1997; West and Herre, 1998; this study) has built considerably on Hamilton's (1979) early studies on sex ratios of externally ovipositing fig wasps, there is considerable scope for further research. Current comparative studies are still hindered by poor phylogenies but recent (Machado et al. 1996) and ongoing molecular studies may soon improve this situation. There is, however, an urgent need for detailed field studies of individual species, using genetic markers where appropriate. For example, we need to know whether foundresses in species of externally ovipositing fig wasps show even, clumped, or aggregated distributions (West and Herre 1998), whether foundresses assess and respond to cofoundress number (Greeff 1997), and how closely the offspring maturing within a single fig are related (Greeff 1995, 1996). These important assumptions and predictions of sex ratio models are eminently testable.

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