

Alternative mating tactics and extreme male dimorphism in fig wasps

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SUMMARY

The dimorphisms in morphology and behaviour of male fig wasps are among the most extreme in the animal kingdom, and offer excellent opportunities to test the predictions of certain sexual selection models. Winged males resemble their conspecific females closely, but wingless males are so divergent in form that they have repeatedly been classified into different taxa. Wingless males mate within their natal fig fruits, whereas winged males disperse to mate. Individual species may have winged males, wingless males or both morphs. A key hypothesis proposes that sexual selection on male mating opportunities favours winged males in species with small broods and wingless males in species with large broods. Using data from 114 species in 33 genera, we show that both simple and formal comparative analyses support the correlated evolution of large brood size and male winglessness. Theoretical models further predict that, in male dimorphic species, the proportion of winged males should equal (in cases without local mate competition) or exceed (in cases with local mate competition) the proportion of females developing in fig fruits without wingless males. These predictions are met by eight out of nine male dimorphic species studied. Taken together, the patterns across all species, and between different male dimorphic species, strongly support sexual selection on mating opportunities as the major determinant of male morph ratios in fig wasps.

1. INTRODUCTION

Sexual selection is responsible for many of the familiar, and often extreme, differences between the sexes (Darwin 1871; Andersson 1994). However, polymorphism within one sex, usually the male, also occurs and is often associated with alternative mating tactics (Gadgil 1972; Andersson 1994; Gross 1996). Male mating polymorphisms involve alternative behaviours and, in some cases, alternate morphologies. Most male dimorphisms appear to involve a single conditional strategy, in which high quality males adopt one mating tactic and lower quality males another (Gross 1996). The fitness payoff of the tactic used by low quality males is inferior, but they adopt this tactic to make the 'best of a bad job'. Of greater theoretical interest is the possibility that frequency-dependent selection might lead to an evolutionary equilibrium involving two or more mating tactics with equal fitness at the equilibrium (Gadgil 1972; Hamilton 1979; Maynard Smith 1982). Frequency-dependent selection determines the Evolutionarily Stable Strategy (ESS) frequencies of the different tactics, but this can be achieved in two ways: (i) individuals use only one tactic and occur at the ESS frequencies (pure strategies), or (ii) individuals use different tactics with probabilities equal to their ESS frequencies (mixed strategies). No case of a mixed strategy is known (Gross 1996), but pure

strategies are suggested by data from several fish (Gross 1991*a, b*; Ryan *et al.* 1992), a bird (Lank *et al.* 1995), and a marine isopod (Schuster & Wade 1991).

Fig wasps (Hymenoptera: Agaonidae) show some of the most extreme examples of male dimorphism in the animal kingdom (Hamilton 1979). Individual species may have winged males, wingless males, or both types of male (see figure 1). Winged males closely resemble their conspecific females but wingless males are so divergent in form that they have been repeatedly classified into different species, or even genera, from their conspecific females (Frank 1987). Considerable diversity is seen also between different types of wingless males (see §6) but the fundamental dimorphism is between winged and wingless males, which have very different mating behaviours. Winged males leave their natal fig fruits and mate elsewhere with females that have already dispersed from their own natal fig fruits. Wingless males, in contrast, mate with conspecific females within the closed receptacle of their natal fig fruit, which they never leave (Hamilton 1979). Wing loss is best interpreted as an adaptation to mate location within the closed confines of the fig fruit. Wings would hinder movement between the tightly packed fig flowers, and wing loss presumably also permits reallocation of resources to other functions, such as sperm production (Hamilton 1979).

Hamilton (1979) proposed an explanation for male

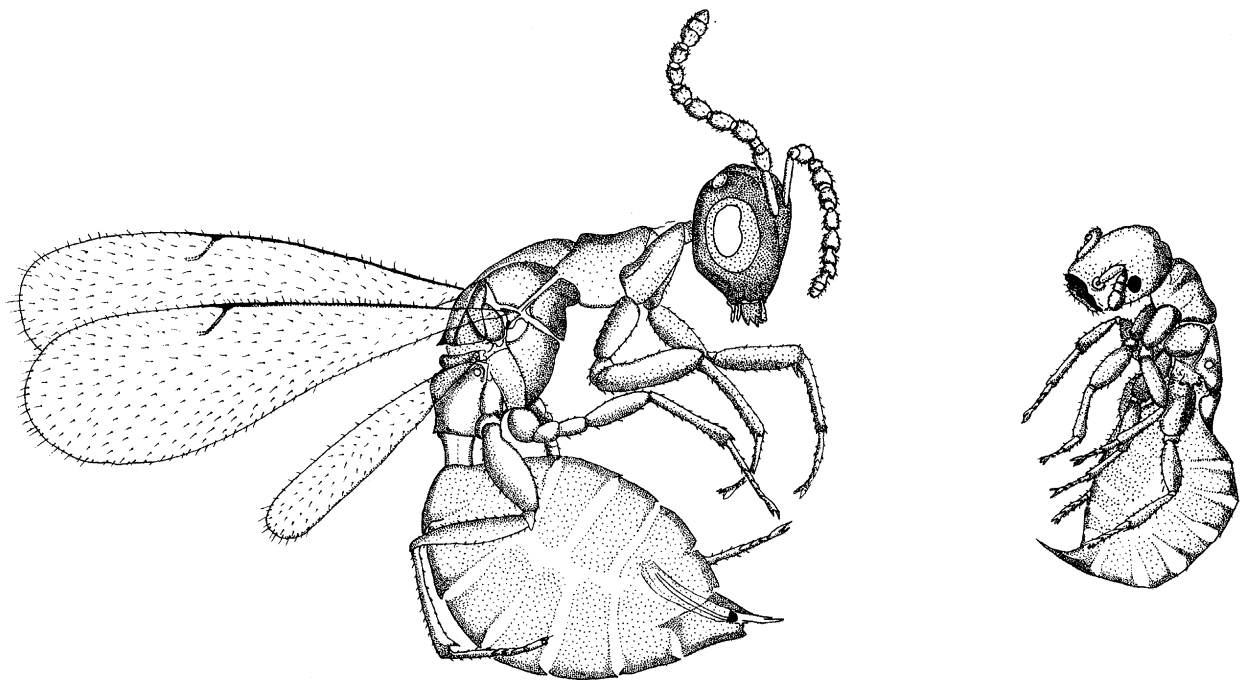


Figure 1. Winged and wingless males of *Pseudidarnes minerva* provide an example of extreme male dimorphism within a single species.

winglessness dependent on the mean number of conspecific wasps developing per fig fruit (hereafter brood size; note this does not imply that all eggs in a given fruit are laid by a single female). He noted that species with large broods tend to have wingless males while those with small broods have winged males. At intermediate brood sizes, both male forms sometimes occurred in the same species. This pattern appears to reflect the distribution of mating opportunities for winged and wingless males. In species with large broods, most females develop in fruits with conspecific males and mate before dispersal. Consequently, most mating opportunities fall to wingless males. In species with small broods, however, most females develop in fig fruits without conspecific males, and winged (dispersive) males enjoy most mating opportunities. Between the extremes there should be a range of brood sizes where sufficient pre- and post-dispersal mating opportunities exist to produce male dimorphism.

Hamilton (1979) constructed a simple model relating male morph proportions to mating opportunities in male dimorphic species. He assumed that females mate with only one type of male, either a wingless male(s) before dispersal or a winged male(s) after dispersal. The model generates a simple quantitative prediction: if the male morphs have equal fitness, the proportion of winged males should equal the proportion of females developing in fruit without wingless males. However, Hamilton's model includes the unlikely assumption that females lay only one egg per fig fruit. Greef (1995) has recently developed models that relax this restrictive assumption and incorporate the ensuing effects of local mate competition (LMC; Hamilton 1967, 1979). LMC occurs when brothers compete for matings in the same patch and is therefore experienced only by wingless males, reducing their

reproductive value relative to winged males. Consequently, Greef's (1995) models predict that, in some species, LMC may cause the proportion of winged males to exceed the proportion of females (defined as j by Greef (1995)) developing in broods without wingless males.

In this paper we test the predictions of Hamilton (1979) and Greef (1995) using data from 114 species in 33 genera from four different continents. First, we compare the brood sizes of species with winged, dimorphic and wingless males to test Hamilton's prediction that winglessness increases with brood size. However, species may not provide independent data points if the characters of interest are evolutionarily conserved and inherited through a shared ancestor, or if one character is highly correlated with an unknown third variable that is phylogenetically inert (Ridley 1988; Harvey & Pagel 1991). Consequently, we also conduct a formal comparative analysis, using paired independent contrasts (Felsenstein 1985; Burt 1989). Finally, we focus on male dimorphic species, and test the predictions of Hamilton (1979) and Greef (1995) that the proportion of winged males should equal or exceed the proportion of females developing in fruit containing no wingless males.

2. BACKGROUND BIOLOGY AND TAXONOMY

Fig wasps develop in the fruits of figs (*Ficus* spp.) and can be divided into three ecological groups: (i) the mutualistic pollinating wasps, (ii) non-pollinating wasps, including cleptoparasites of the pollinators, that feed on fig tissue, and (iii) true parasitoids of other fig wasps. Bouček (1988, 1993) proposed recently that all pollinating and non-pollinating wasps whose larvae

feed on fig tissue form a monophyletic family, the Agaonidae. The Agaonidae contains six subfamilies; one of these, the Agaoninae, contains all the pollinating wasp species. The five other subfamilies (Sycophaginae, Sycoryctinae, Epichryso-mallinae, Otitesellinae and Sycococinae) contain a diversity of non-pollinating wasps. A small number of non-agaonid parasitoid wasps also develop in fig fruits and these belong to related chalcidoid families (e.g. Torymidae, Eurytomidae and Pteromalidae), whose more numerous other members are not associated with figs. It is likely that the 'proto-agaonid' arose originally from one of these other chalcidoid families (Bouček 1988).

Each of the several hundred extant fig species typically has a single, host plant-specific pollinating wasp (Ramirez 1970; Wiebes 1979), and recent molecular analyses (Yokoyama 1995; Herre *et al.* 1996; Machado *et al.* 1996) support a long history of coevolution between figs and their pollinating wasps. The pollinating wasps (Agaoninae) all have essentially similar biologies. Receptive fig fruits are entered by one or a few female wasps who both pollinate the fig flowers and lay wasp eggs. The pollinator wasp larvae feed on the flower tissue and develop in synchrony with the fig seeds (Herre 1989; Bronstein 1992). As the fig fruit approaches ripeness, the male pollinator wasps hatch into the fig cavity. All pollinator wasp males are totally wingless, whereas all female pollinator wasps are winged. The wingless males chew their way into flowers containing females and use their telescopic genitalia to mate with the still-enclosed females. The male wasps then chew exit holes in the wall of the fig and the winged females disperse from the ripe fig fruit to search for receptive fig fruits on other trees.

Non-pollinating fig wasps are much more diverse than the pollinators and a single *Ficus* sp. may host as many as 29 non-pollinator species (Compton & Hawkins 1992). The females of most non-pollinating wasps use their very long ovipositors to penetrate the fig wall and lay eggs without entering the fig fruit. Their larvae may feed on fig flowers and compete with the pollinator larvae (e.g. some *Idarnes* spp.; West & Herre 1994), induce large galls (e.g. Epichryso-mallinae; Godfray 1988; Cook & Power 1996; West *et al.* 1996) or behave as true parasitoids of other non-pollinating wasps (Godfray 1988; West *et al.* 1996). The mating behaviour of non-pollinating wasps is also diverse. Males of a given species may be winged, wingless or dimorphic (Hamilton 1979). Whereas winged males mate outside the fig fruits, wingless males mate either in the fig cavity or inside the flowers containing their conspecific females. The wingless males of non-pollinator species include divergent forms showing features such as large jaws for male combat, dwarfism and eye reduction (Hamilton 1979; Frank 1987; Murray 1990).

3. METHODS

Data for 72 fig wasp species were collected by the authors in Australia (J.M.C.), Panama (S.A.W. and E.A.H.) and South Africa (S.G.C.). The collection methods used in the different localities are described in detail elsewhere (Herre

1989; Compton & Nefdt 1990; Cook & Power 1996; West *et al.* 1996). However, all studies essentially involved the collection of near-ripe fig fruits just before the developing wasps were ready to emerge, followed by detailed dissection of fig fruits to reveal all the wasps within each fig fruit. The wasps were counted and identified as far as possible before voucher specimens were sent to taxonomic experts for definitive identification.

Data for a further 43 species were gleaned from the literature. These data, from Brazil (Hamilton 1979), Papua New Guinea (Godfray 1988), and Malaysia (Murray 1989), were collected by the respective authors in much the same way as described above. The full dataset, comprising 114 species, is available on request.

4. ANALYSES

We first treated species as independent data points to test the hypothesis that mean brood size increases from species with wingless males to those with dimorphic males and winged males. Due to extreme heterogeneity of variances between the different groups, neither brood size nor any transformation of brood size was suitable for analysis of variance. Consequently, non-parametric Kruskal–Wallis tests (Zar 1984) were used. When a significant result was obtained, multiple comparisons between groups were assessed for significance using the *Q*-test statistic, which is equal to the difference in mean rank of two test groups, divided by its standard error (Zar 1984).

The hypothesis was first tested for all fig wasp species ($n = 114$) and then for a subset of the data comprising of parasite species only ($n = 88$). The pollinators were excluded from this second analysis because they comprise a large monophyletic subfamily (Agaoninae) fixed for the condition of male winglessness.

We also carried out a formal comparative analysis to test whether winglessness increases with brood size. The hypothesis tested is that, in comparisons between pairs of taxa that fall into different wing categories (wingless, dimorphic, winged males), brood size is larger in the taxon with greater wing reduction. Two comparisons (A vs B and C vs D) are considered to be independent if the phylogenetic path drawn between A and B and that between C and D do not meet or cross (see Burt 1989). In our analysis three types of comparison are possible: (i) between wingless and dimorphic taxa, (ii) between dimorphic and winged taxa, and (iii) between wingless and winged taxa. The third type of comparison might be expected to reveal a greater difference in brood sizes if male dimorphism is an intermediate state.

The number of phylogenetically independent contrasts depends on the number of taxa in the dataset, the degree of resolution of the phylogeny of these taxa and the distribution of character states. In this study, the distribution of character states and rather limited resolution of the phylogeny permitted six independent contrasts. These were used to conduct a sign test.

Finally, we focused on nine male dimorphic species and tested the prediction that the proportion of winged males should equal (Hamilton 1979; Greef 1995) or exceed (Greef 1995) the proportion of females developing in fruits without wingless males. The epichryso-

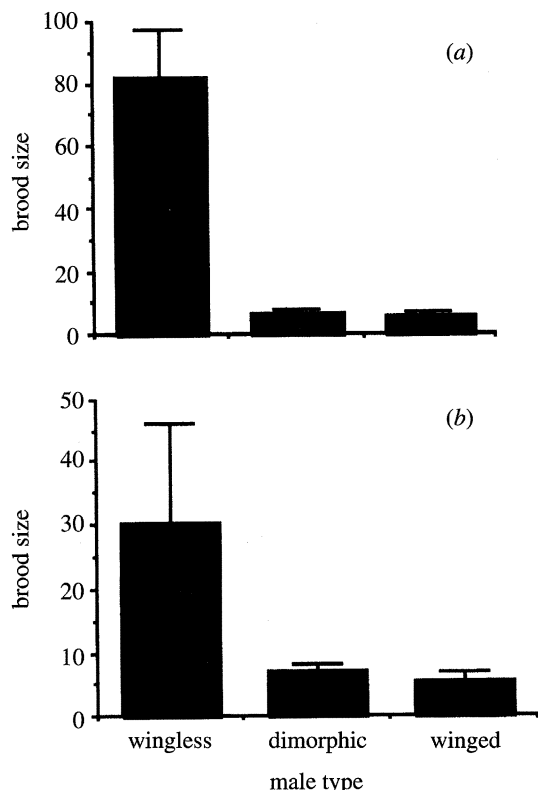


Figure 2. Mean brood sizes (\pm s.e.) for fig wasps with wingless, dimorphic, and winged males. Bar charts show all species (a) and parasite species only (b).

malline species studied by Murray (1989) was excluded as we do not know the number of females developing in fruits with wingless males. A likelihood ratio test was applied to each species and the computed G -statistics

Table 1. *Kruskal–Wallis tests of the brood size hypothesis*

(The Kruskal–Wallis statistic H and its corresponding p value indicate the overall significance of the test. The significance of each pairwise comparison between groups (e.g. wingless vs winged males) is also shown. *** $p < 0.001$, ** $p < 0.005$, * $p < 0.05$.)

data	n	H	wingless vs winged	wingless vs dimorphic	dimorphic vs winged
all species	114	45.22***	6.32***	3.33**	0.84
parasite spp.	88	30.25***	5.33***	2.55*	1.08

Table 2. *Independent contrasts of brood size and male wing status*

(Contrasts are computed as the brood value for the taxon with less wings minus the brood value for the taxon with more wings, i.e. a positive value favours the brood size hypothesis. The six contrasts are: (A) two winged *Idarnes incerta* species versus nine wingless *Idarnes idarnes* species, (B) one dimorphic *Pseudidarnes* versus five wingless Sycophaginae, (C) two dimorphic versus nine wingless *Philotrypesis*, (D) five winged *Aepocerus* and *Watshamiella* versus 18 wingless *Sycoscapter*, *Apocrypta* and *Arachonia*, (E) four winged versus one dimorphic Epichrysomallinae, (F) two winged Sycococinae versus 26 wingless Agaoninae. Brood values and contrasts with the superscript a, were calculated as simple means of all species in a group. Those with the superscript b, were calculated by taking means at successive nodes. All contrasts by both methods are positive.)

	A	B	C	D	E	F
less wings ^a	44.44	48.14	14.09	17.42	11.04	184.92
less wings ^b	44.44	50.68	14.09	22.24	11.04	159.70
more wings ^a	7.16	5.80	9.37	6.65	3.78	19.46
more wings ^b	7.16	5.80	9.37	5.89	3.63	19.46
contrast ^a	+37.28	+42.30	+4.72	+10.77	+7.26	+165.46
contrast ^b	+37.28	+44.88	+4.72	+16.35	+7.41	+140.24

were compared to the critical value of χ^2 with 1 d.f. Ideally, we would also like to use all these species in independent paired comparisons. However, because we do not know the identities of the dimorphic species studied by Hamilton (1979), only two independent comparisons are possible.

5. RESULTS

Inspection of the mean brood values for all species (figure 2a) and parasite species only (figure 2b) shows that the rank order is wingless male taxa > male dimorphic taxa > winged male taxa. Both analyses (all species and parasite species only) using species as independent data points yielded significant results that were essentially the same (table 1). Wingless male species had significantly larger broods (mean for all species = 82.08, mean for parasites only = 30.66) than both male dimorphic (all are parasites, mean = 7.08) and winged male (all are parasites, mean = 5.57) species. However, although the brood sizes of male dimorphic species were larger than those of winged male species, the difference was not significant.

In each of the six phylogenetically independent comparisons (figure 3, table 2), the taxon with greater wing reduction had a larger brood size. Under the null hypothesis, the probability of six out of six comparisons in the same direction is $p = 0.0156$ (one-tailed sign test). Consequently, the analysis reveals a significant positive association between large broods and wing reduction. There is no clear indication that differences between winged and wingless taxa are larger than those between either group and a dimorphic group.

Figure 4 illustrates the general correspondence between the proportion of winged males and the

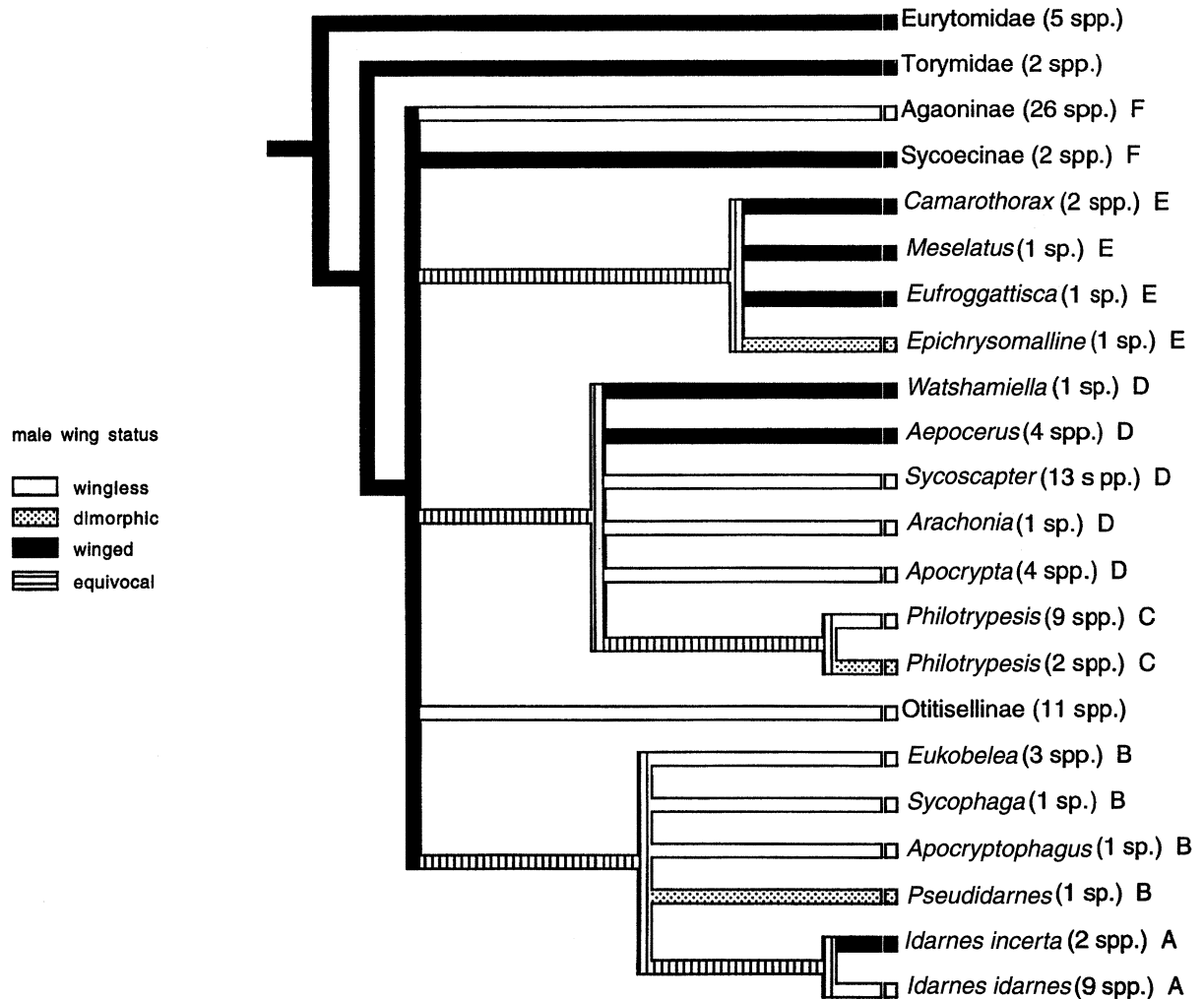


Figure 3. The phylogeny used for independent paired contrasts. The tree is based on morphological (Bouček 1988, 1993) and molecular data (Machado *et al.* 1996). Unresolved nodes are left as soft polytomies to impose more conservative testing. To improve clarity, terminal nodes containing several taxa with the same male wing status are collapsed to a single point and denoted as, for example, 13 *Sycoscapter* spp. Contrasts were made between taxa of different wing status marked with the same letter (A-F), as detailed in table 2. Members of Otitisellinae were not used in contrasts as recent molecular data (C. Machado, personal communication) confirm an earlier suspicion (Bouček 1988) that two genera have been placed incorrectly in this subfamily. However, those genera are not represented in our dataset and inclusion of the Otitisellinae (together with Agaoninae) in the contrast with Sycoecinae does not alter the result.

Table 3. *Morph proportions in male dimorphic species*

(Hamilton's model predicts that the proportion of winged males will equal the proportion of females developing in fruits without wingless males. *G*-tests were carried out for each species; those that departed significantly (in these cases $p < 0.001$) from the predicted values are marked ***)

species	females with wingless males	females without wingless males	winged males	winged males	G_1	excess males
<i>Philotrypesis</i> 1	221	9	29	280	31.91***	winged
<i>Philotrypesis</i> 2	63	1	15	31	67.61***	winged
<i>Pseudidarnes minerva</i>	183	175	202	61	86.17***	winged
E	3	2	1	2	0.06	—
e	44	37	36	27	3.32	—
ε	4	17	7	3	0.58	—
F	34	1	1	7	1.48	—
f	16	29	40	14	2.3	—
φ	18	6	11	102	17.05***	wingless

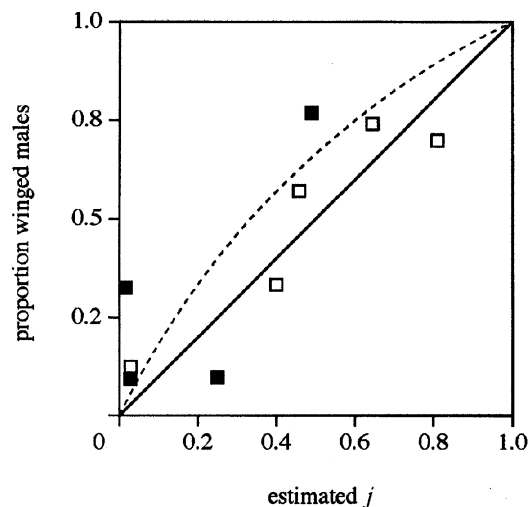


Figure 4. The relationship between the proportion of winged males and j (the proportion of females developing in fruits without wingless males) in male dimorphic species. The two lines display model predictions; the solid line predicts the proportion of winged males when there is no LMC (Hamilton 1979; Greef 1995), the broken line applies when 50% of matings are between siblings (Greef 1995). Each square is the mean value for a single species. Open squares show species that conform to, and solid squares show species that differ significantly (table 3) from Hamilton's prediction.

proportion of females (j) developing in fig fruits without wingless males. For five of the nine species tested, these proportions are not significantly different, as predicted by Hamilton's model. However, the results for three of these species (E, ϵ , F) should be regarded as preliminary because the sample sizes are so small. Significant excesses of winged males were found in three of the remaining species, with only one species (ϕ) manifesting an excess of wingless males. Thus eight out of nine species are consistent with Greef's prediction that the proportion of winged males should equal or exceed the proportion of females developing in fruits without wingless males (table 3).

6. DISCUSSION

The results of both simple and formal, comparative analyses show that winglessness increases with brood size across fig wasp species. In all analyses the rank order of brood size is wingless male species > male dimorphic species > winged male species, and the different analyses consistently show that taxa with wingless males have significantly larger broods than those with dimorphic or winged males. These results support Hamilton's (1979) suggestion that brood size influences strongly the balance of mating opportunities for the two male morphs, such that winged males are favoured at low brood sizes and wingless males at high brood sizes.

Hamilton (1979) and Greef's (1995) models for male dimorphic species predict that the proportion of winged males should either equal (no LMC) or exceed (with LMC) the proportion of females that develop in fruits without wingless males. Eight of the nine dimorphic species tested are in agreement with these predictions

and only one has an excess of wingless males. These results, and the wide range of male morph proportions observed (9–77% winged), further support the suggestion that male morph ratios have evolved in response to selection on the relative mating opportunities for winged and wingless males.

The excess of winged males observed in three species may be a result of LMC reducing the reproductive value of wingless males in these species (Greef 1995). However, there are at least two alternative explanations. First, not all females that develop in fruits with wingless males may be mated by those wingless males. This factor seems likely to apply to at least some male dimorphic species, as it has already been demonstrated in some species with only wingless males (West *et al.* 1997b), but it may well have very minor effects. Second, winged males may sometimes mate within the fig, obtaining some of the matings that existing models assume are reserved for wingless males. While Hamilton (1979) noted that winged males of several species showed no interest in mating before dispersal, winged males of several other species have recently been observed to enter galls containing females and mate with them (West & Herre 1997). However, it is important to realize that pre-dispersal matings by winged males only alter predictions if they occur in fig fruits that also contain conspecific wingless males.

Wing dimorphism is known in many insects but tends to involve either both sexes or, more commonly, to be limited to the female sex (Hamilton 1979; Roff 1986). In contrast, male dimorphism is more often a body size phenomenon associated with fighter/sneaker mating behaviours. The six male dimorphic fig wasps studied by Hamilton (1979) all have fighting wingless males, leading to the common description of the system as a fighter–flier dimorphism (e.g. Hamilton 1979; Krebs & Davies 1993; Andersson 1994). However, at least two male dimorphic fig wasps (*Pseudidarnes minerva* (figure 1) and *Camarothorax* sp.; Vincent & Compton 1992) have small, non-fighting, wingless males that enter intact galls to mate with unemerged females. While the divergent morphologies and behaviours of wingless males still require adequate explanations (Frank 1987), these will probably depend on differences in mating site (e.g. in galls or fig cavity) and mate competition economics (Murray 1987, 1989, 1990) within the fig fruit, and it is clear that male dimorphism need not imply a fighting wingless male.

The proximate control of male morph determination in animals is often environmental (e.g. Eberhard 1982; Radwan 1993; Emlen 1994), or subject to both genetic and environmental influences (Crespi 1988; Radwan 1995). However, if male morphs represent alternative mating strategies with equal fitness, alternative genotypes are expected. The simplest possibility is a single locus with two or more alleles, as suggested by data from studies of male polymorphism in a marine isopod (Schuster & Wade 1991), a freshwater fish (Zimmerer & Kallman 1989) and a bird (Lank *et al.* 1995). Another possibility is adaptive morph determination by the mother. Female fig wasps are already known to exert adaptive control over the sex ratios of their offspring (Frank 1985; Herre 1985, 1987; Herre *et al.*

1997), and control of the morph of male eggs might allow them to place winged sons in broods containing few females and wingless sons in broods containing many females. A similar pattern could result if chemical cues from developing conspecifics influenced morph determination, as is the case in a mite (Radwan 1993, 1995). Both the maternal control and chemical cue hypotheses predict a within-species decrease in the proportion of winged males as brood size increases. However, a large dataset (> 100 broods) from *P. minerva* showed no change in proportion of winged males with brood size (J. Cook, unpublished data). The observed pattern is consistent with a simple one locus, two allele model. Although this is known to be the basis of male wing dimorphism in a bethylid wasp (Kearns 1934), bethylids are only very distantly related to fig wasps and experimental investigations of morph control in dimorphic fig wasps are required.

Outgroup comparison suggests that the proto-agaonid wasp had fully winged males. However, estimating the number of subsequent transitions to dimorphic and wingless males is hindered by the limited resolution (both within and between subfamilies) of the current phylogeny (figure 3). Nevertheless, it is still interesting to estimate a minimum number of male character changes. Estimates for four subfamilies are straightforward; no wing loss event is required in the Sycoecinae, and one is required for each of the Otitesellinae, Agaoninae and Epichryso-mallinae. The two remaining subfamilies (Sycoryctinae and Sycophaginae) show greater male diversity and are more problematic. However, assuming an ancestral state of fully winged males in each clade, a minimum of one origin of dimorphism, followed by two independent fixations of winglessness, is inferred in each subfamily. This yields a minimum of five different origins of dimorphism, followed by seven independent fixations of winglessness. These calculations also make the second assumption that male wing status changes from winged to dimorphic to wingless. Although we believe that reversals from winglessness are rare or absent (see next paragraph), reversals from dimorphic to fully winged males may be more common. However, allowing the latter reversals would not reduce the current estimate of the minimum number of character transitions. This estimate will be revised, probably upwards, when the phylogeny is better resolved, and more species are studied. However, one extra independent origin of dimorphism is already known; wingless males occur in some fig-associated *Physothorax* species (Burks 1969). These are not agaonids but represent a secondary radiation of the family Torymidae (figure 3) to exploit figs.

In our dataset, brood size varies from one to 802 across all fig wasps and from six to 120 within one genus (*Eukobelea*). It is therefore likely that wing loss has occurred in some lineages only for subsequent brood size decreases to select for winged males. In general, the evolution of winglessness is probably an example of irreversible evolution (Bull & Charnov 1985) but it is possible that sex-limited wing loss may be more amenable to evolutionary reversal. However, West *et al.* (1997a) have shown that several wingless

male fig wasp species have relatively small brood sizes (< 10), coupled with high percentages (10–40%) of females that do not occur in fruits with conspecific males and thus appear doomed to remain unmated. Winged males do not occur in the genera *Sycoscapter* and *Otitesella*, which probably include species in which selection favours winged males, but the appropriate genetic variation is not available. Interestingly, the wingless males of two *Otitesella* species react positively to light and crawl out on to the outer surface of their natal fig fruits where they subsequently mate with females (S. G. Compton, personal observation). This contrasts markedly with wingless males of almost all other fig wasp genera studied (*Walkerella yoshiroi* is an exception; males sometimes leave their natal syconium and enter another; M. Hossaert-McKey, personal communication), which are morphologically, behaviourally and physiologically adapted to the unusual closed environment of the fig fruit, which they do not leave. The secondary modification of behaviour, and presumably physiology, in some *Otitesella* species may be an example of an evolutionary alternative to irreversible male wing loss.

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