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Evolution of the scale and manner of brother competition in pollinating fig wasps

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Contest competition and male dispersal have evolved a number of times in pollinating fig wasps. Given their highly female-biased sex ratios and high relatedness between competing males, this phenomenon is surprising. Using a comparative approach, we found a significant association between high adult sex ratios (male:female), fighting and dispersal. We conclude that a relatively high proportion of males could have led to the evolution of fighting and to excess males that avoid kin conflict through dispersal. These wasps respond to increased competition between relatives by altering the scale at which they compete, but also by competing more intensely. In support of the new generation of kin selection models, we found that relatedness of competing males has no effect on the likelihood of fighting. Even so, selection at a higher hierarchical level has selected for dispersal and hence a larger scale at which competition occurs. We found that although the sex ratio gives a rough indication of the mating system it fails to be accurate at a finer scale.

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The scale at which kin compete is an important factor affecting the evolution of social behaviour (Grafen 1984; West et al. 2002). Conversely, kin selection can alter behaviours that determine the scale of competition (Hamilton & May 1977). Social behaviour and the kin structure of a population will thus tend to coevolve, presumably to maximize inclusive fitness (Hamilton 1964; Grafen 2006). Therefore, in cases where mothers are constrained to have their offspring in spatially discrete patches, various modes of conflict resolution have evolved to minimize competition between kin.

Dispersal is probably the most common evolutionary response to avoid direct conflict with kin (Hamilton & May 1977). In some cases the mother can reduce anticipated conflicts by biasing her offspring sex ratio towards the sex that is more likely to disperse (i.e. less likely to compete; Hamilton 1967; Taylor 1981). Conversely, in cases where kin interact synergistically they may tend to cluster in family groups and mothers can even bias the sex ratio towards the sex that is more likely to collaborate (Packer & Pusey 1987; Schwarz 1988; Komdeur 1996; Greeff 1999). Ironically,

in cases where kin collaborate there is often competition over reproductive division (Keller 1993; Solomon & French 1997).

For species where siblings do not collaborate, if one works from the assumption that inclusive fitness has been maximized, one would not expect much sibling competition. Either maternal or offspring strategies would evolve to negate kin competition. Even so, extremes such as siblicide (O'Connor 1978) and celibacy (Deady et al. 2006) do occur. An example of reduced kin competition is found in pollinating fig wasps where mothers routinely produce female-biased sex ratios to reduce local mate competition (LMC) between their sons (Hamilton 1979). In light of their highly female-biased sex ratios (Herre et al. 1997), it is thus surprising that brother–brother fighting and male dispersal may have evolved as many as six times in pollinating fig wasps (Michaloud, 1988; Greeff et al. 2003). In this study, our aim was to determine why the kin competition–kin structure problem has been resolved differently for pollinating fig wasps whose males fight and disperse.

The relevant details of the life cycle of a typical pollinating fig wasp can be summarized as follows. One or a few mothers (called foundresses) enter a fig through the small hole on the distal end of the fig inflorescence (the ostiole). Most foundresses are trapped inside the fruit and are constrained to lay all their eggs in one fig (see Moore et al. 2003 for examples where females have evolved a mechanism to spread their eggs over several figs). Each egg is laid in an individual flower, each forming a distinct gall inside the

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inflorescence. Males eclose first from their galls into the cavity inside the fig. In a scramble competition style, males search for galls containing receptive females, chew mating and/or release holes into these galls, and mate with females. Once most females are mated, males start to chew an exit tunnel through the wall of the fruit. Females escape through this tunnel in search of receptive figs to start the cycle again. The fighting species studied here differ from this general pattern by males fighting over mating opportunities with females (i.e. contest rather than scramble competition), by males dispersing to other figs with an exit tunnel, and in a few cases, males can even chew their way into a new fig from the outside (Greeff et al. 2003). Note that some of these species differ from the norm in that males chew exit tunnels before all the females are mated (contrast Moore et al. 2006 and Zammit & Schwarz 2000).

The absence of fighting between pollinating males has been explained as a response to: (1) very female-biased sex ratios favouring scramble competition (Hamilton 1979), (2) the large number of females available for mating (West et al. 2001), (3) the high relatedness between competing males who are often brothers (Hamilton 1979), (4) the risk of entrapment in a fig with too few surviving males to chew an exit hole (Hamilton 1979; Godfrey 1988), and (5) a cramped environment between galls that prohibits bulky morphology for fighting (Vincent 1991; Greeff et al. 2003). Fighting may thus evolve when one or more of these conditions is violated and we next consider the potential merits of each.

The importance of the operational sex ratio (OSR = the ratio of sexually active males to receptive females, Emlen & Oring 1977) in determining the strength of sexual selection is well appreciated (Shuster & Wade 2003). Recently, Kokko & Jennions (2008) have argued that the adult sex ratio (ASR) may in fact capture the strength of sexual selection very well. When males have access to multiple females without encountering each other (i.e. a female-biased OSR or ASR), they will be less likely to compete. If, however, males frequently encounter females in the presence of other males, competition may ensue as each male tries to mate with the contested female (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Reinholds 1996). Pollinator wasps with their extremely female-biased ratios (often less than 0.2, especially at low foundress numbers, Hamilton 1979; Herre et al. 1997; Kjellberg et al. 2005) can thus be expected to be peaceful lovers rather than fighters (Hamilton 1979). However, at least three phenomena can select for less female-biased ratios that may favour fighting: (1) species with higher average foundress numbers (Herre 1985) and (2) species with male dispersal will experience less LMC which will result in more even sex ratios (Greeff 2002). The former can easily be tested by counting the foundresses and the latter may be especially relevant, since most, but not all, species that fight also disperse (Greeff et al. 2003). (3) Mothers may produce backup males to guard against the chance that either a binomial sex allocation process or male mortality will result in too few males to prevent entrapment. In fact, siblicide in organisms as diverse as birds (O'Connor 1978; Gonzalez-Voyer et al. 2007) and bees (Harano & Obara 2004) may well be the result of the production of such backup offspring. It is unclear why certain pollinators would produce more backups, and such backup males are not expected in species with male dispersal or higher foundress numbers where the sex ratio is already higher.

In a comparative study, West et al. (2001) showed that the severity of fighting increased as the number of females per fig decreased (note that this study did not consider fighting pollinating species). Waage (1982) found a similar trend in scelionid wasps and these results support the general idea that when there are few females, the relative value of each female is high and males are likely to escalate their conflicts to secure access to females (Murray & Gerrard 1985; Enquist & Leimar 1987). This is certainly possible in

these fighting pollinating fig wasps. However, it is important to disentangle effects of sex ratio and number of females as they covary (West et al. 2001).

Although Hamilton (1979) originally felt that high relatedness will reduce conflict in pollinating fig wasps, he (Hamilton 1996) later agreed with others that this is incorrect, because when close relatives are constrained to compete locally against each other the positive effects of relatedness can be cancelled exactly by competition (Grafen 1984; Murray 1984; Frank 1998; West et al. 2001; Reinholdt 2003). In other words, when a male fights over a mating opportunity in a large panmictic population he is very unlikely to compete with a sibling. However, in a fig the male may very well be fighting with his brother over a mating opportunity. So one may feel that pollinator 'males may be restrained because many of the rival males are brothers, and a male doesn't care so much whether he or a brother does the mating' (Hamilton 1979, page 177). However, the male is also more likely to be challenged and concede matings to said brothers, and this increased competition cancels the inclusive fitness benefits. Recent empirical studies support this theory (Clutton-Brock et al. 1999; West et al. 2001; Spong & Creel 2004). Of specific interest is West et al.'s (2001) study illustrating a lack of a kin effect in fig wasps (note that this study did not consider fighting pollinating species).

A possible weakness of West et al.'s (2001) study is that they used population sex ratio as an indirect measure of relatedness. Nee et al. (2002) argued that sex ratios are in fact an excellent proxy for the mating structure. However, in some cases the sex ratio may not give an accurate measure of relatedness (Greeff 1997, 2002; Antolin 1999; Ferguson 2002, 2003; Kjellberg et al. 2005; Pienaar & Greeff 2006). In pollinating fig wasps, such as those studied here, relatedness of competing males can be determined in an alternative way by counting the foundresses that oviposit in the fig. Several studies have argued that counting foundresses can also be flawed, because in some species foundresses may leave the fig after oviposition (Moore et al. 2003; Zavodna et al. 2007) and in other species not all females found inside the fig contribute to the progeny (Molbo et al. 2004). Of the wasps studied here, Moore et al. (2003) concluded from data published by Ware & Compton (1992) that the females of one species, *Allotriozoon heterandromorphum*, disperse from their figs. In another study where the focus was on sex ratio (Kjellberg et al. 2005), we found no evidence for females leaving figs and we believe that the foundresses were overlooked in the Ware & Compton (1992) study cited by Moore et al. (2003). When not all females contribute to the brood, or do so in unequal proportions, the optimal sex ratio is more female biased than with equal contributions (Frank 1985; Moore et al. 2005). Below, we use data showing higher than expected sex ratios to argue that overcounting is not likely to be a problem, and if it is, it seems unlikely that there will be a systematic difference between fighting and nonfighting species.

If the pollinating males are disabled or exhausted from fighting they may not be able to chew an exit hole. This would trap the females inside the fig where they would die and the group of kin would produce no progeny. In two of the five genera containing fighters, the fighting pollinator males can excavate exit tunnels from the outside (Greeff et al. 2003) and thus rescue potentially trapped females. Although this may be an important factor, we do not consider it here since it is very difficult to determine how the risk of entrapment varies with the number of males.

Males are expected to evolve fighting equipment only if the environment permits its use (Vincent 1991). Support for this is seen in the work done on nonpollinating fig wasp species where mating site plays a role in male morphology and mating behaviour (Vincent 1991; Bean & Cook 2001). The same constraints may be important in pollinating fig wasps, with bulky fighting

morphologies evolving only if males encounter each other in an environment spacious enough for fighting. In work on the same set of species we found that gall density and lumen volume are not correlated with male fighting behaviour (Nelson 2005).

Using the comparative method, we tested whether number of females, sex ratio, relatedness of competing males and their dispersal strategy covary with whether a species fights or not. We also tested whether wasps produce optimal sex ratios and whether these are affected by dispersal.

METHODS

We considered 11 species of pollinating fig wasps that occur in southern Africa (Fig. 1).

Foundress Numbers and Relatedness

Figures where the female wasps laid their eggs but where the next generation has not yet started to eclose are called C-phase figs (Galil & Eisikowitch 1967). We collected C-phase figs for all the species from their indigenous habitats in South Africa and Swaziland, during 1997–2008. The figs were opened and the foundress pollinator wasps were identified and counted using a binocular dissecting microscope. The bodies of the foundress females were usually undamaged and, since the species investigated here do

not re-emerge from the figs (Moore et al. 2003; J. M. Greeff, unpublished data), the numbers of foundress females in a fig could be determined accurately.

The foundress numbers were used to calculate the proportion of sibmating (p) as the inverse of the arithmetic foundress mean (X_a) and the harmonic foundress mean (X_h). For the proportion of sibmating, the inverse of the arithmetic mean estimate assumes that all females produce the same number of daughters (Greeff 2002), whereas the inverse of the harmonic mean estimate assumes that the number of females eclosing per fig are the same, regardless of the number of foundresses per fig (Herre 1985). A true estimate of the proportion of sibmating should be somewhere between the inverse of the arithmetic and harmonic means. Note that these estimates assume that all females in a fig lay equal-sized clutches with the same sex ratio. The proportion of sibmating when a proportion, k , of matings are between a disperser and a female was calculated as: $p = (1 - k)/X$ with the arithmetic and harmonic means, respectively. Genetic studies have estimated that 8% of *Platyscapha awekei* (Jansen van Vuuren et al. 2006) and 6% of *Alfonsiella pipithiensis* (Greeff 2002) matings are between non-native males and native females. We do not have a similar estimate for the remaining dispersing species, *Alfonsiella binghami* sp. 2, but feel it is fairly safe to set $k = 0.07$ in all three dispersing species. We calculated the inbreeding coefficient as $F = p/(4 - 3p)$ (Suzuki & Iwasa 1980) and the relatedness of the competing brothers as

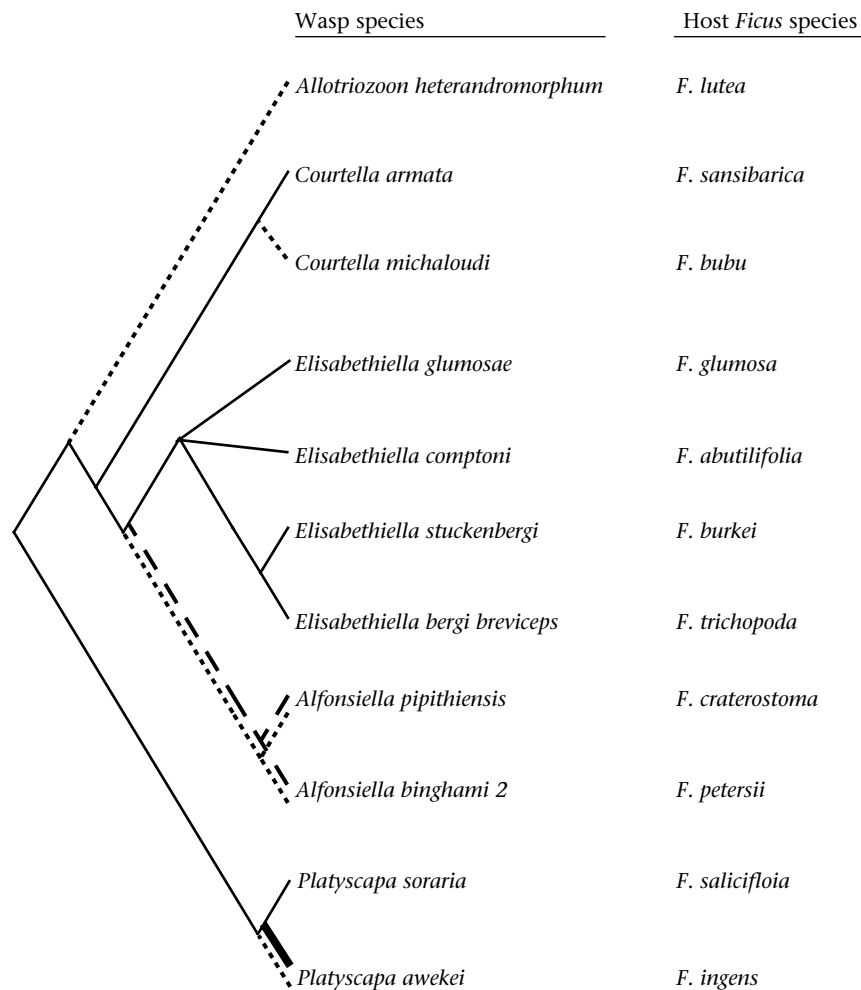


Figure 1. Working phylogeny used for phylogenetic regression, based on the internal transcribed spacer tree from Erasmus et al. (2007). Thinner solid lines represent nonfighting lineages and dotted lines represent fighting lineages. Dashed lines are taxa that disperse to other figs that already contain an exit hole; the heavy solid line is the one taxon that can chew an entrance hole from the outside of the fig.

$r_b = (1 + F)/2$ (Hamilton 1972) and between competing individuals as:

$$r_c = r_b(1 - k)/X. \quad (1)$$

Adult Sex Ratio

Early D-phase figs (Galil & Eisikowitch 1967), that is, figs where males have just started to mate with females but have not eaten an escape hole through the fig wall, were collected for all the species during 1997–2008. Figs were examined to ensure that no exit tunnel existed. The figs were opened and individually placed in vials sealed with fine mesh gauze. The wasps normally started to exit within a few minutes of opening and were completely released within 24 h, before desiccation of the fig could constrict them to their respective galls. The number of male and female pollinator wasps, as well as the clutch size for each fig, was determined after the wasps died. Wasps from within and outside the fig were taken into account but only if completely released from their respective galls (a negligible number of wasps were not released from their galls). The adult sex ratio was determined as the proportion of males in the clutch for each fig. Figs containing male-only broods were removed from analyses as they represent virgin foundress females with no choice in sex allocation and do not contribute to the mating environment, as no females are present.

The data allowed us to test how accurately adult sex ratios reflect the mating system, specifically the degree of sibmating. We used the proportion of sibmating, calculated from the harmonic foundress mean and including 7% dispersal, for dispersing species, to calculate the expected sex ratio (s) as (Taylor 1993):

$$s = (1 - p)(2 - p)/(4 - p) \quad (2)$$

Dispersal should reduce the proportion of matings that are with siblings and will thus result in less female-biased sex ratios.

Statistical Analysis

Although fighting has possibly evolved five times in African pollinating fig wasps, one genus's phylogenetic position has not been resolved (Erasmus et al. 2007). This left us with four evolutionary switches implying limited statistical power. As a result, it is unrealistic to fit models with many terms. However, we tested all independent variables separately and several pairs of independent variables. This approach is in line with the suggestion of Møller & Jennions (2003) to avoid biased reporting.

We used phylogenetic regression (Grafen 1989; version 0.5 implemented in the SAS statistical package, SAS Institute, Cary, NC, U.S.A.) which is well suited to test discrete as well as continuous parameters (Grafen & Ridley 1996). To gauge the robustness of these statistics we also did phylogenetic generalized least squares (Martins & Hansen 1997; as implemented in Compare, Martins 2004), Felsenstein's independent contrasts (Felsenstein 1985, as implemented in Compare, Martins 2004) and finally we ignored dependence of species and analysed the data with generalized linear models with binomial errors considering each species as an independent data point (R version 2.6.1; R Development Core Team 2007).

To test which variables explain the distribution of fighting, we regressed dispersal, the adult sex ratio, number of female offspring and the relatedness between competing males against fighting. Because female number and sex ratio may covary, we controlled and tested for both these variables to obtain their independent effects. Because both dispersal and sex ratio have a significant effect on fighting, we tried to test each of these parameters while

controlling for the other. To test the proposed link between the mating system and the sex ratio, we regressed the adult sex ratio against dispersal and the predicted sex ratio. All variables were tested without transformation. All the data were treated as continuous except the occurrence of fighting and dispersal.

The phylogeny used (Fig. 1) is based on a tree drawn from phylogenies based on ITS2 sequence data from the nuclear DNA (Erasmus et al. 2007), while the placement of the *Platyscapha* genus as an outgroup is well supported in other studies (Machado et al. 2001). Although the exact topology for the species in the *Elisabethiella* genus is unresolved, this made no difference as the whole branch collapsed into one contrast. Even so, we confirmed this by repeating the phylogenetic regression with the alternative topologies for the *Elisabethiella* genus, but as the results were quantitatively the same we report only those from the phylogeny represented in Fig. 1. Apart from said uncertainty in *Elisabethiella* the remainder of the phylogeny used here is robust with well-supported nodes. For the phylogenetic regression, path segment lengths were derived from the default 'Figure 2' method as described by Grafen (1989). For analysis in Compare, path lengths were obtained from trees in Erasmus et al. (2007) and Machado et al. (2001).

RESULTS

The mean number of foundresses was low for all species, with the highest harmonic mean foundress number equal to 2.08 (Table 1). As a result, the relatedness between competing males was fairly high with a range of 0.29–0.94 (Table 1).

The observed sex ratio varied between 0.14 and 0.32 with dispersing species producing higher sex ratios (Fig. 2). The expected sex ratio, calculated from the degree of sibmating, did not explain observed sex ratios (Table 2). Bar one species, *Elisabethiella bergi breviceps*, the observed sex ratio was consistently higher than the expected sex ratios (paired Wilcoxon signed-ranks test: $V = 62$, $P = 0.007$; Fig. 2). Nondispersing species produced significantly more female-biased sex ratios than dispersing species (Table 2, Fig. 3). The number of females released in figs varied from 18.72 to 209.59 (Table 1).

Dispersing species were marginally significantly more likely to fight (Table 2). A less female-biased adult sex ratio was significantly associated with fighting, even when the number of females was controlled for (Table 2). On the other hand, fighting was not significantly associated with the number of females, and controlling for sex ratio did not change the conclusion (Table 2). Relatedness did not affect the likelihood of fighting (Table 2). Phylogenetic regression using arithmetic means to calculate relatedness between competing males gave quantitatively similar results.

These conclusions are unaffected by the method of analysis (Table 2; Felsenstein's independent contrasts are not reported in the table, but gave similar results). From this we can conclude that, despite our small sample size, our conclusions are robust.

DISCUSSION

Our results show an association between dispersal, the presence of fighting and increased proportions of males. However, our results are moot about the causal links between these three traits. Below, we consider additional evidence and come to the conclusion that more male-biased sex ratios may have triggered the evolution of dispersal and fighting.

Theoretically, the mating system and sex ratio are closely linked and have led to the use of sex ratios to infer the degree of sibmating (West et al. 2000, 2001). Since there was no correlation between predicted (based on the frequency of sibmating) and observed sex

Table 1
Summary of foundress and offspring numbers and parameters calculated from these data

Pollinator wasp	Foundress means				Offspring means			
	N (crop)	X_a	X_h	r_c	N (crop)	Sex ratio \pm SD*	Expected sex ratio	Females \pm SD*
A. heterandromorphum	2	2.35	1.58	0.41	3	0.22\pm0.15	0.15	20.37\pm19.07
<i>C. armata</i>	3	2.23	1.61	0.40	1	0.218	0.15	83
C. michaloudi	1	2.03	1.64	0.39	1	0.222	0.16	209.59
<i>E. glumosae</i>	3	1.26	1.13	0.73	5	0.24 \pm 0.12	0.04	21.45 \pm 16.81
<i>E. comptoni</i>	2	1.88	1.35	0.52	6	0.15 \pm 0.11	0.1	67.78 \pm 38.86
<i>E. stuckenbergi</i>	2	1.04	1.02	0.94	8	0.19 \pm 0.09	0.01	27.11 \pm 18.81
<i>E. bergi breviceps</i>	2	2.96	2.08	0.29	2	0.15 \pm 0.04	0.22	29.17 \pm 31.64
Alfonsiella pipithiensis	3	1.09	1.04	0.75	2	0.32\pm0.16	0.04	10.81\pm0.97
Alfonsiella binghami 2	2	1.3	1.14	0.62	7	0.31\pm0.19	0.07	11.52\pm11.12
<i>P. soraria</i>	4	1.16	1.07	0.83	6	0.14 \pm 0.07	0.02	38.95 \pm 19.9
P. awekei	6	1.69	1.44	0.42	16	0.27\pm0.11	0.14	18.72\pm10.83

X_a : arithmetic mean of foundress number; X_h : harmonic mean of foundress number; r_c : relatedness between competing males (using X_h and 7% dispersal); sex ratio: observed adult sex ratios; females: number of female offspring per fig. Bold type indicates fighting species.

* These means were calculated using the mean of each crop. Average crop size was 17 figs per crop, with a crop being defined as a sample from one tree at a given time. The standard deviation represents the variation between crops.

ratio, our results suggest that sex ratio is not a very sensitive gauge of the mating system. In these species, sex ratios were consistently less female biased than the optimal prediction (Fig. 2), suggesting that we did not undercount the foundresses. In line with other studies, we found that species with dispersing males produced higher sex ratios than those without (Hamilton 1979; Greeff 1995; West & Herre 1998; Fellowes et al. 1999). Sex ratios should thus only serve as a gross estimate of the mating system and should be used with caution.

It is well known that dispersal and female-biased sex ratios are alternative responses to LMC between brothers and one may thus expect them to coevolve (Perrin & Mazalov 2000). However, Wild & Taylor (2004) concluded that whereas dispersal affects the evolution of sex ratios, sex ratios do not affect the evolution of dispersal. Thus these traits cannot really coevolve in response to one another. Simplifying Wild & Taylor's (2004) model for these fig wasps gives optimal male dispersal as $d_m^* = (C_m - 1/N)/(C_m^2 - 1/N)$, with C_m equal to the cost of dispersal for males and N equal to the number of foundresses. Since most figs have either one or two foundresses we can expect males to disperse often, even if costs are high (Fig. 4). Theory and our results suggest that the question that begs explanation is not why these few species disperse, but why so many do not. This may be tied in with mothers producing just enough sons

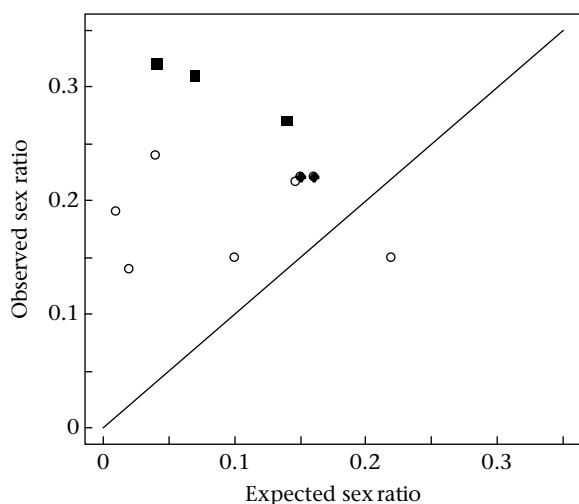


Figure 2. The observed and expected sex ratio of dispersing (squares) and non-dispersing (circles) species. Filled symbols indicate fighting species and open symbols nonfighting ones. The line indicates the diagonal.

to mate with their sisters and chew the exit tunnel. If males were to disperse under these high skews, they would jeopardize their sisters' mating status and hence future fitness. Extrapolating this argument, we suggest that only species with sufficient excess males can afford the costs associated with male dispersal. Alternatively, the standard explanation would be that dispersal led to the increase in sex ratios. However, observed sex ratios were in fact higher than predicted (Fig. 2) and if we accept this alternative explanation we have to admit that we do not understand the complete picture.

Our results agree with those of West et al. (2001) over the lack of a role for relatedness in ameliorating conflict between kin in closed scenarios. This congruence with West et al. (2001) is despite the different ways in which we calculated relatedness. West et al. (2001) inferred relatedness from sex ratios, whereas we derived relatedness in a more direct fashion, by counting mothers. This confirmation adds to the growing number of empirical studies that have concluded that limited dispersal will not lead to more cooperation because increased relatedness with competitors is cancelled by increased competition with relatives.

Our results differ from those of West et al. (2001) in that the number of females had no effect on the probability of fighting in our study whereas it was the most important predictor of fighting severity in their's. This difference may stem from the fact that our dependent variable is different, as they estimated the severity of fighting from the injuries obtained during the wasps' lifetime, whereas we looked at whether males fought or not. Injuries are influenced by the fact that armoury differs markedly between taxa (Murray 1990) potentially confounding the signal. By looking at a more homogeneous group and scoring fighting behaviour as either present or absent, we tried to avoid this problem. Finally, it may also be that the value of the contested resource (inverse of number of females) may be important in determining the severity of fighting, but not the presence or absence of fighting per se.

Another difference in our conclusions is that West et al. (2001) found that sex ratios did not correlate with severity of fighting whereas in our analysis more female-biased sex ratios were significantly associated with a lower probability of fighting. West et al. (2001) fitted relatedness (a decreasing function of sex ratios), number of females (correlated with sex ratios) and sex ratios to their data. Fitting these dependent variables may explain the lack of a sex ratio effect. In contrast, we calculated relatedness with data independent of the sex ratios, namely the number of foundresses.

Abe et al. (2003a) have suggested that fatal fighting can result in the production of very female-biased sex ratios. Their model critically depends on the fatality of fights and on the asymmetric fighting ability of sons resulting from eclosion order (Abe et al.

Table 2
Results of the phylogenetic regression, phylogenetic generalized least squares (PGLS) and generalized linear models (GLM)

Dependent variable	Parameters	Control	Phylogenetic regression (Grafen 1989)					PGLS (Martins & Hansen 1997)				GLM			
			df	β_1	β_0	F	P	α	$\beta_1 \pm SE$	$\beta_0 \pm SE$	P	r	β_1	β_0	P
Fighting	Dispersal		1,7	1.000	0.250	5.727	0.048	1.89	0.72±0.29	0.34±0.23	0.028	0.64	19.66	-1.10	0.035
	Adult sex ratio		1,7	8.261	-1.310	9.032	0.020	4.23	5.54±2.00	-0.72±0.47	0.017	0.68	64.14	-14.46	0.008
	Female number		1,7	0.001	0.416	0.056	0.820	2.67	0.00±0.00	0.50±0.27	0.08	0.003	-0.337	0.829	
	Relatedness		1,7	-0.594	0.796	0.487	0.508	2.95	-0.36±0.55	0.74±0.38	0.309	-0.22	-2.508	1.243	0.535
	Dispersal	Adult sex ratio	1,6	-1.069	-1.158	0.024	0.880	3.20	0.31±0.44	-0.37±0.64	0.297	0.69	4.06	-12.12	0.667
	Adult sex ratio	Dispersal	1,6	7.427	-1.158	1.708	0.230		3.64±3.19		0.197		53.25		0.116
	Adult sex ratio	Female number	1,7	12.403	-2.333	11.407	0.012	4.61	6.04±2.04	-0.95±0.51	0.013	0.73	77.58	-18.62	0.006
	Female number	Adult sex ratio	1,7	0.003	-2.333	2.488	0.159		0.00±0.00				0.015		0.245
Adult sex ratio	Expected sex ratio		1,8	0.082	0.211	0.041	0.844	3.27	-0.15±0.21	0.24±0.03	0.296	-0.23	-0.143	0.234	0.645
	Dispersal		1,8	0.290	0.191	13.224	0.007	13.76	0.11±0.03	0.19±0.01	0.004	0.81	0.300	0.190	0.002

β_1 is the slope of the regression; β_0 is the constant of the regression. For 'dispersal', β_0 is the estimate of fighting for nondispersing species and β_1 is the estimate of fighting for a dispersing species. For the PGLS, P is the significance of the slope term, β_1 , calculated for estimate/SE compared to a *t* distribution with $df = (N - \text{number of parameters})$ (Gonzalez-Voyer et al. 2007). Bold type indicates significant results.

2003b). As a result, these findings are unlikely to apply to pollinators which, although they engage in contest competition, have never been seen to kill one another. The relative synchronicity of the females' egg laying in each fig and enclosure of offspring also invalidates the appropriateness of these theories. In any case, these models predict lower sex ratios when fighting occurs, not higher (Abe et al. 2003a). On the other hand, the effects of sex ratios on male mating strategies are well appreciated (Shuster & Wade 2003; Kokko & Jennions 2008). When the ratio of males to females increases, males are more likely to encounter females in the presence of other males and contest competition is more likely to ensue.

The operational sex ratio further may be affected by additional factors. In the analysis above, we assumed that the OSR and the adult sex ratio are correlated. This assumption is conservative because most fighting species possess behavioural characteristics that actually increase the OSR. In *Allotriozoon* and *Alfonsiella* species, males remove females from their galls immediately after mating by pulling them out by their antennae, to prevent other males mating with them (Greeff et al. 2003). This leads to a rapid change in the operational sex ratio. A similar effect is seen in *P. awekei* where exit holes are chewed early on and females leave

the fig immediately after mating (Nelson 2005). Thus, in fighting species the behavioural patterns can rapidly make the OSR even more male biased.

It is not clear how the presence of fighting per se would select for dispersal in a pollinating fig wasp. It is possible that zero relatedness with males encountered after dispersal may have triggered the onset of fighting directed towards unrelated males. However, observations suggest that males do not reserve fighting for unrelated males (Greeff et al. 2003). Additionally, at least two origins of fighting were not preceded by dispersal: *A. heterandromorphum* males lack eyes and *C. michaloudi* males have diminutive eyes suggesting that they may be precluded from evolving dispersal, yet they evolved fighting (Greeff et al. 2003). It is also important to note that the significance of the relationship between dispersal and fighting was much less than those between dispersal and the sex ratio and sex ratio and fighting. This suggests that the relationship between fighting and dispersal is not causal but simply a result of each being correlated with sex ratio.

These considerations suggest that less female-biased sex ratios triggered the evolution of contest competition between males in order for females to be successful at procuring matings and resulted

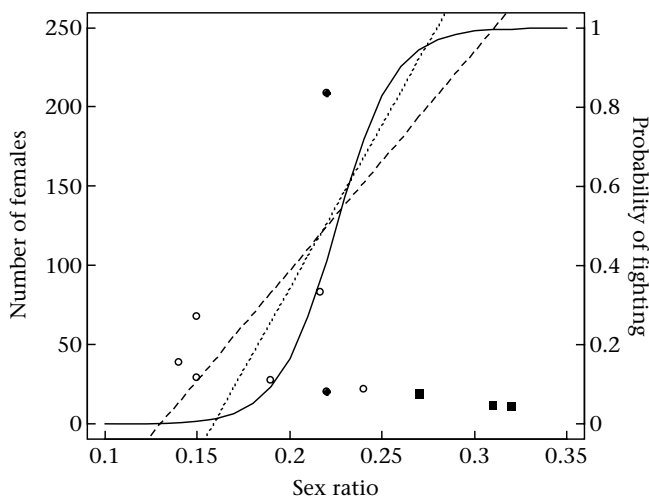


Figure 3. A scatterplot of observed adult sex ratio and number of females to show the values for fighting (filled symbols) and nonfighting (open symbols) in dispersing (squares) and nondispersing (circles) species. The lines give the probability that a species will fight given its sex ratio for the three models in Table 2: solid: GLM; dashed: PGLS; dotted: phylogenetic regression.

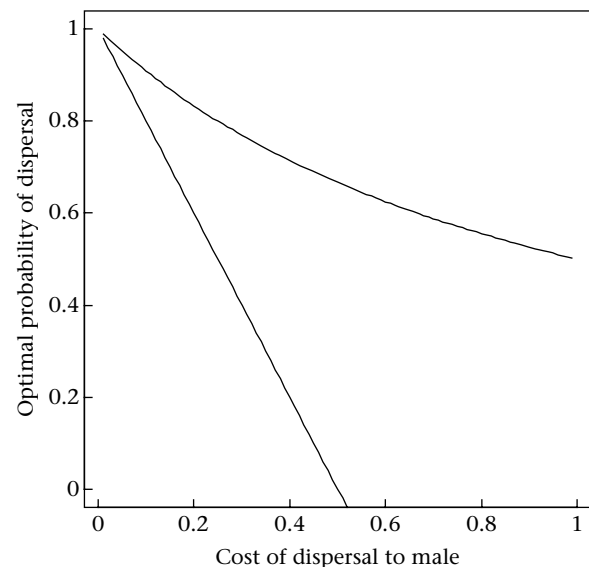


Figure 4. The optimal dispersal as a function of cost to male migration, for figs with single (top line) and two (bottom line) foundresses.

in excess males that disperse to avoid LMC with close relatives. Our suggestion that an increased sex ratio triggered the evolution of dispersal and fighting begs the question of why the sex ratios would have become less female biased in the first place. There are a number of possibilities but we have no data to support any of them. Small clutch sizes are less female biased (Kjellberg et al. 2005), but fighting species such as *A. heterandromorphum* and *C. michaloudi* have large clutches. Parasitic species may kill more females, but we have no support for this nor that fighting species are attacked more.

Despite this lack of clarity, the sex ratio, the mating system, dispersal and kin competition have clearly often coevolved. A number of systems have found similar, but also different solutions to the same type of problem because of small differences in the organism's biology. For parasitoid wasps, Pexton et al. (2003) argued that the trigger for the evolution from siblicidal to non-siblicidal behaviour is a lack of dispersal. Here, a lack of dispersal results in siblings being less likely to interact. In *Cardiocondyla* ants, a lack of dispersal is associated with fighting between siblings (Heinze et al. 1998), although the fighting is not directed to dispersing males which have a different scale of competition for matings (Anderson et al. 2003). Also, queens adjust their sex ratio to LMC (Cremer & Heinze 2002; de Menten et al. 2005) and when there is a single queen, the sex ratio is so female biased that fighting has been lost again (Heinze et al. 2005; Schrempf et al. 2005). This last observation is reminiscent of what may have happened with nonfighting pollinators. From these examples and the present study, it seems that no clear pattern may exist and the devil is in the details.

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