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Mating system and sex ratios of a pollinating fig wasp with dispersing males

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Recent studies have used sex ratios to quantify the mating systems of organisms, the argument behind it being that more female-biased sex ratios are an indication of higher local mate competition, which goes hand-in-hand with higher levels of inbreeding. Although qualitative tests of the effects of mating systems on sex ratios abound, there is a dearth of studies that quantify both the mating system and the sex ratio. I use a colour dimorphism with a simple Mendelian inheritance to quantify the mating system of an unusual fig-pollinating wasp in which males disperse to obtain matings on non-natal mating patches. In qualitative agreement with initial expectations, the sex ratios of single foundresses are found to be higher than those of regular species. However, by quantifying the mating system, it is shown that the initial expectation is incorrect and this species' sex ratio is a poor predictor of its mating system (it underestimates the frequency of sib-mating). The species has a very high variance in sex ratio suggesting that excess males can simply avoid local mate competition (and hence a lowered fitness to their mother) by dispersing to other patches.

Keywords: Agaonidae; local mate competition; partial local mating; sex allocation; dispersal

1. INTRODUCTION

Hamilton (1967) was the first to notice that a population's mating structure can affect parents' sex allocation. He showed that when one or a few unrelated females oviposit in a patch and mating is restricted to offspring from that patch, a female-biased sex ratio is favoured. This bias reduces local mate competition (LMC) between the mother's sons and increases the number of matings each son has (Hamilton 1967; Taylor 1981). Much supporting evidence has accumulated and the study of sex ratios is considered a landmark in the application of optimality theory to the study of adaptation (Charnov 1982; Werren 1987; West *et al.* 2000*a*; but see Orzack 2002).

In fact, trust in the connection between mating system and sex ratio is now so established that recent studies have inferred the mating system of organisms from their sex ratios (Read *et al.* 1995; Pickering *et al.* 2000; West *et al.* 2000*a*,*b*). Thus, it is important that we understand how mating systems translate into sex ratios, and we need to test models rigorously to unearth factors that may bias sex ratios systematically. This requires that data on sex ratios and the mating system, as well as the model assumptions (Herre *et al.* 2001), be quantified. We also need to quantify the variation in sex ratios, since this gives us some idea of how efficient selection is at attaining optima (Orzack *et al.* 1991; Orzack & Sober 1994; West & Herre 1998*a*), and it may also be used to deduct selective regimes and additional information on the mating system.

Pollinating fig wasps are one of the textbook examples of the effects of LMC; sex ratios become more female biased as the LMC increases (Hamilton 1979; Frank 1985; Herre 1985; Herre *et al.* 1997, 2001; but see Orzack 1995). Furthermore, variation in optimal sex ratios of the wasp is less in more frequently encountered conditions (West & Herre 1998*a*). Their usefulness stems from a life history that is both amenable to modelling and contains key features proposed to bias sex ratios. Most important of these are: (i) one or more females (called 'foundresses') enter a fig almost simultaneously and are trapped inside the fig's lumen; (ii) females lay clutches that are similar in size; and (iii) all matings occur inside the fig before mated females disperse to find another tree with receptive figs where they can lay their eggs (but see Greeff & Compton 1996; Kathuria *et al.* 1999; Moore 2001; and J. C. Moore and J. M. Greeff, unpublished data, for exceptions to all these assumptions in pollinating fig wasps).

Recently, it was discovered that the males of a number of pollinating fig wasp species disperse from their natal fig and enter other figs where they mate with additional females (J. M. Greeff, S. van Noort, J.-Y. Rasplus and F. Kjellberg, unpublished data). Such dispersal would reduce the LMC and one would expect these wasps to produce higher proportions of sons (Hamilton 1979); the sex ratios of single foundresses should be the most dramatically affected (Nunney & Luck 1988). Sex ratios of dispersing species could thus be a good negative control since their sex ratio should not be as female biased, but by how much would their sex ratios (proportion of offspring that are male) be increased?

The sex ratio (r^*) that is an evolutionarily stable strategy (ESS; Maynard Smith 1982) can be expressed in terms of the probability of sib-mating (s); for diploid taxa, it is $r^* = (1 - s)/2$ (Hamilton 1967), and for haplodiploids, the equivalent is

$$r^* = (1 - s)(2 - s)/(4 - s) \qquad (1.1)$$

(Taylor 1993). Equation (1.1) gives a slightly more female-biased value than the diploid equivalent because, unlike diploids, haploid males' genetic values do not increase with inbreeding (Hamilton 1979). This gives a straightforward relationship between the mating system and sex ratios, but a number of researchers have pointed out that this relationship may not always hold and depends on the details of sib-competition (Taylor &

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Bulmer 1980; Charnov 1982; Uyenoyama & Bengtsson 1982; Karlin & Lessard 1986).

Whereas sex ratios are relatively easy to quantify, the same cannot be said for the degree of local mating (Hardy & Mayhew 1998*a*; Fellowes *et al.* 1999). Researchers often resort to surrogate measures of breeding structure, such as morphology (King & Skinner 1991; Hardy & Mayhew 1998*b*; West & Herre 1998*b*; Fellowes *et al.* 1999), and observational studies on mating behaviour (Nadel & Luck 1992; Drapeau & Werren 1999; Fauvergue *et al.* 1999; Hardy *et al.* 1999) and oviposition (Waage 1982; Hardy 1994), to infer possible trends in the mating system. As a result, most studies have tested, and also confirmed, the qualitative prediction that partial local mating should lead to less biased sex ratios (Hamilton 1979; Waage 1982; Nadel & Luck 1992; Hardy 1994; Greeff 1995; West & Herre 1998*b*; Fellowes *et al.* 1999). What is now required are studies that accurately quantify both the mating system and sex ratios (Molbo & Parker 1996). To this end, I investigated the sex ratios and mating system of a fig-pollinating wasp with dispersing males.

2. MATERIAL AND METHODS

(a) *Study species*

The *Alfonsiella* wasp that pollinates *Ficus craterostoma* in South Africa is not *Alfonsiella michaloudi*, the wasp described from *F. craterostoma* collections further north in Africa (Wiebes 1988), and its specific status is currently under investigation (S. van Noort, personal communication). *F. craterostoma* are stragglers in Afromontane forests.

The males of this *Alfonsiella* species are perhaps unique among pollinating fig wasps in that they exhibit a colour dimorphism. If such a dimorphism is genetically determined, it can be used as a genetic marker to estimate the mating history of the population. Both of the colour morphs mate inside figs and disperse from fig to fig.

(b) *Foundress numbers*

To estimate the average foundress number in natural populations, I collected interphase figs from natural forests: along the Drankensberg escarpment, I sampled two crops from Peddler's Bush on 19 June 2001 and 22 February 2002, and one from Buffelskloof Nature Reserve on 6 October 2001. In the Soutpansberg, I made nine collections from four forests during March 2002. Interphase figs were dissected under a compound microscope either immediately or after storage in the freezer in order to count the foundresses. Apart from the pollinators, a number of other internal parasites belonging to the Sycoecinae were also encountered in figs.

(c) *Expected sex ratios*

A number of factors can affect the sex ratio of single foundresses and I consider these here. When no dispersal occurs, mothers are expected to produce just enough sons to mate with all their sisters and set them free. To estimate what this number may be, fruits were collected from additional crops on campus that remained closed after the wasps from others figs had already left. In these figs, the number of males was presumably too low both to mate with and to set females free. These 'coffin' figs were dissected immediately to confirm that all the males were dead, and the contents were then quantified. The expected sex ratio for this species should exceed the sex ratio recorded in these coffin figs.

Based on the proportion of sib-mating estimated from the inbreeding coefficient (see below), we can predict the sex ratio for a population where each female has the observed expectation of sib-mating using equation (1.1).

If there is a chance that a second foundress may enter the fig after the first has finished oviposition, this can significantly increase the expected sex ratio of the first female (Greeff & Compton 1996; Kathuria *et al.* 1999, see Appendix A). By inserting the observed values of s and p (the probability of a single foundress) into equation (A 3), the predicted sex ratio for a single foundress can be obtained.

(d) *Single-foundress sex ratios*

To investigate single-foundress sex ratios, figs were collected from a *F. craterostoma* tree growing on the University of Pretoria campus. The tree is beyond the normal range of the species, which is found to the north and east of Pretoria. There are a number of *F. craterostoma* trees on campus, but due to their within-tree fruiting synchrony and low number they do not maintain a local wasp population. This is advantageous because the pollinating wasps are not parasitized by any of the parasitoids that normally attack them, and secondary sex ratios are likely to reflect primary sex ratios. Figs were picked from the campus tree a few hours before males had eclosed from their galls. Figs were cut into four pieces, foundresses counted and removed, and the fig pieces placed in a vial, covered with fine mesh. When most wasps had eclosed from their galls (24–48 h later), the figs and their contents were frozen so that the wasps of each fig could be scored at a later stage. To compare these sex ratios with those of other species that have non-dispersing males, I obtained the 95% confidence interval (CI) for a regression (using SPSS 11.0) of the mean single-foundress sex ratio on the proportion of single foundresses' figs from data drawn from the literature (Nefdt 1989; Herre *et al.* 2001).

(e) *Variation in the sex ratio*

If the observed distribution is under-dispersed relative to the binomial expectation, it suggests that there has been selection for precise sex allocation (Green *et al.* 1982). Conversely, over-dispersion would suggest that the trait is either poorly adapted, not under selection or that there is a polymorphism in the population. I tested whether the data conformed to a binomial distribution using the method of Green *et al.* (1982) to determine the Green variance (GV, West & Herre 1998*a*). Despite the possible biases of this technique (Krackow *et al.* 2002), it was used because it gave very similar results to GLIM analyses and was comparable with a large study on fig wasps (West & Herre 1998*a*). GV is equal to the observed variance divided by the expected variance. The observed variance is calculated as the mean squared error (MSE), which is calculated as: $\mathrm{MSE} = s(u)^2(1 - r(u,w)^2)$, where $s(u)^2$ is the variance in the number of sons (u) and $r(u,w)$ is the correlation coefficient of the number of sons and the total brood (w). The expected variance is calculated as the average of $wp(1 - p)$ over all the figs, where $p = (c + b(u,w)w)/w$, and c and b are the constant and the regression coefficient, respectively, when number of sons is regressed on total brood. When $\mathrm{GV} > 1$, the data are over-dispersed and vice versa. Green *et al.* (1982) suggested that the significance of a deviation can be tested by doing a χ^2-test where $\chi^2 = \mathrm{df} \times \mathrm{GV}$, and df is equal to the number of samples minus two.

(f) *Inheritance of colour dimorphism*

If the colour dimorphism in males is the result of two alleles at a single locus, I would expect three types of clutches: homozygous mothers who will either have yellow or brown sons, and heterozygous mothers who will have clutches with an expected 50 : 50 ratio of yellow to brown sons. This expectation was tested using a χ^2-test. The numbers of brown and yellow sons of each fig were also tested against the binomial expectation to see if any ratios were significantly different from the expected 50 : 50 ratio.

(g) *Mating system*

There are three methods with which to quantify the mating structure of the population and I compare these three methods.

(i) *Method 1*

The number of foundress females in natural populations will give an estimate of the degree of sib-mating expected if dispersal did not result in matings outside the natal fig. If it is assumed that each fig contributes the same number of females regardless of the number of foundresses and that foundresses sharing a fig produce identical clutches, then s is equal to the inverse of the harmonic mean number of foundresses (Herre 1985). At the other extreme, s is equal to the inverse of the arithmetic mean when one assumes that all females, regardless of the number of foundresses, produce the same number of daughters. The truth is somewhere between these two extremes, but due to sex ratio adjustments and brood limitations it is closer to the former.

(ii) *Method 2*

If it is assumed that equation (1.1) applies, it can be rearranged so that the proportion of sib-mating is given in terms of the observed sex ratio. For haplodiploids this is given by

$$s = [3 - r - (1 + 10r + r^2)^{0.5}]/2 . \tag{2.1}$$

(iii) *Method 3*

The genetic marker can be used to estimate the inbreeding coefficient and hence the degree of sib-mating. The inbreeding coefficient, F, can be calculated from the frequency of sib-mating as

$$F = s/(4 - 3s) \tag{2.2}$$

(Suzuki & Iwasa 1980) and, conversely, s can also be estimated from the inbreeding coefficient as

$$s = 4F/(1 + 3F) \tag{2.3}$$

(Werren 1987). If the male colour dimorphism is determined by two alleles at a single locus, the number of mothers of each genotype can be used to calculate the proportion of the two alleles and the inbreeding coefficient as

$$F = 1 - (H_o/H_e), \tag{2.4}$$

where H_o and H_e are the observed and expected heterozygosity, respectively (Hartl & Clark 1989). The variance in F can be calculated using the maximum-likelihood estimate given by Weir (1996, p. 66), and the 95% CI is approximately equal to the square root of this variance.

By comparing the estimates of the mating system using methods 1 and 2 with method 3, their efficacy as surrogate measures for the mating system of this species can be tested.

3. RESULTS

(a) *Foundress numbers*

The arithmetic and harmonic means of the number of foundresses are given in table 1. These values are very close to 1 and the average proportion of figs that contain single females is 0.927. The collections from Soutpansberg tended to have slightly more foundresses.

(b) *Expected sex ratios*

The seven coffin figs contained 2, 4, 4, 6, 7, 7 and 9 males, respectively. This limited sample suggests that more than nine males may be required to mate successfully with and to set females free. Therefore, if this wasp did not disperse, the expected sex ratio would have been 0.112.

The expected sex ratio given by equation (1.1) as a function of the frequency of sib-mating (see table 2) is 0.037.

Substituting the observed values of $s = 0.896$ and $p = 0.927$ into equation (A 3), and setting $u = 1$, gives the highest ESS sex ratio under this model as $r_1 = 0.003$.

The threshold proportion of males required to mate with and to set their sisters free is substantially higher than the other two estimates, and dispersal is not expected to affect the sex ratio. The sex ratio of 0.112 is significantly below the single-foundress sex ratios observed (see below, table 2).

(c) *Single-foundress sex ratios*

There are seven broods in which the number of sons and sex ratios produced are statistical outliers (figure 1). This might be the result of constrained sex allocation (Godfray 1990); when females run out of sperm they are constrained to produce sons only and, as a result, the following data are given with and without these seven cases. Summary statistics are given in table 3. A cubic regression explained most of the variation in the data ($R^2 = 0.681$), and the 95% CIs for individual points are shown in figure 2. The *Alfonsiella* species with dispersing males considered here clearly produce significantly higher sex ratios than non-dispersing species.

(d) *Variation in the sex ratio*

The GV for all 84 figs was calculated as 8.93, confirming a highly significant over-dispersion (MSE = 122.10; expected variance = 13.67; χ^2-test: $\chi^2_{82} = 82(8.92) = 732.2$, $p < 0.001$, figure 2). If the analysis is redone, considering only the sex ratios less than 0.35 ($n = 77$ figs), GV = 1.71, which is significantly over-dispersed (χ^2-test: $\chi^2_{75} = 75(1.71) = 128.27$, $p < 0.001$). The only estimates of GV higher than 1.71 obtained by West & Herre (1998*a*) were 2.18 and 2.03, and this was for species that only had 31% and 27% single-foundress broods.

(e) *Inheritance of colour dimorphism*

Of the 84 single-foundress broods sampled, 58 had brown males only, 16 had yellow males only, and the remaining 10 broods contained both yellow and brown males. Considering the mixed broods only, the total number of brown and yellow sons did not differ significantly from a 50 : 50 expectation (χ^2-test: $\chi^2_1 = 0.1176$, n.s.). Not one of the 10 broods differed significantly from the binomial expectation of 50 : 50.

Table 1. The site of collection, given as forest in province, and the arithmetic mean ($\overline{X}$) and harmonic mean ($\overline{X}_h$) number of foundresses per fig for each crop. (n is the number of figs inspected per crop.)

province	forest	crop	N	$\overline{X}$	$\overline{X}_h$
Mpumalanga	Peddler's bush	1	62	1.048	1.019
		2	72	1.014	1.007
	Buffelskloof	1	100	1.040	1.014
Limpopo	Hanglip	1	70	1.014	1.007
		2	50	1	1
		3	8	1	1
		4	29	1.034	1.018
	Piesanghoek/Molozi	1	60	1.167	1.084
		2	66	1.106	1.050
	Entambeni	1	16	1.063	1.032
		2	80	1.313	1.131
	Thathe Vondo	1	50	1.340	1.167
average				1.095	1.044

Table 2. Expected theoretical relations between the sex ratio (r), proportion of sib-mating (s) and the inbreeding coefficient (F). (Values in bold are data and the remaining values are extrapolations.)

	based on F		based on sex ratio[a]		based on sex ratio[b]	
	$\overline{X}$	95% CI	$\overline{X}$	95% CI	$\overline{X}$	95% CI
r	0.037	0.024–0.054	**0.196**	**0.169–0.222**	**0.165**	**0.152–0.178**
s	0.896	0.852–0.933	0.537	0.484–0.591	0.600	0.572–0.627
F	**0.683**	**0.590–0.775**	0.225	0.190–0.266	0.272	0.251–0.296

[a] n = 84, with outliers.
[b] n = 77, without outliers.

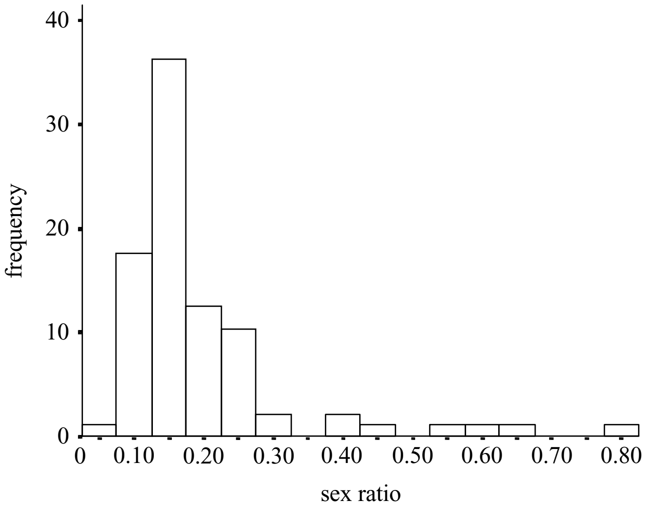

Figure 1. Frequency distribution of sex ratios.

(f) *Mating system*

(i) *Method 1*

Based on the average harmonic and arithmetic mean number of foundresses, the expected proportion of sib-mating if no male dispersal occurred is equal to 0.958, but can be as low as 0.913. This leads to an expected F between 0.723 and 0.850, using equation (2.2).

Table 3. Summary statistics of single-foundress clutch compositions.

	$\overline{X} \pm$ s.d.	
	$n = 84$[a]	$n = 77$[b]
sex ratio	0.196 ± 0.125	0.165 ± 0.059
number of sons	16.98 ± 11.14	14.13 ± 4.40
number of daughters	72.04 ± 19.45	74.65 ± 17.37
total brood size	89.01 ± 17.41	88.78 ± 17.73

[a] Including and [b] excluding seven outliers.

(ii) *Method 2*

The proportion of sib-mating that would result in the observed sex ratio can be calculated using equation (2.1). In turn, such a mating pattern will result in a value of F that can be calculated with equation (2.2) as 0.225 or 0.272, depending on whether the figs with high numbers of males are considered or not (table 2).

(iii) *Method 3*

Using equation (2.4), the inbreeding coefficient was calculated as 0.683. The proportion of matings that had to be sib-matings to give $F = 0.683$ can be calculated using equation (2.3) as 0.896 (table 2).

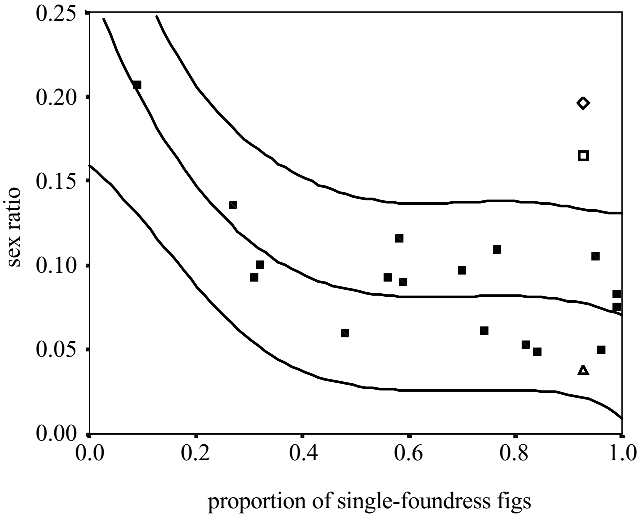

Figure 2. The average sex ratio of single foundresses against the proportion of single-foundress figs. Data are from the literature of species without male dispersal (filled squares), and the *Alfonsiella* species studied here—observed sex ratios including (open square) and excluding (open diamond) the seven outliers and the expected ratio based on equation (1.1) (open triangle). The central line is the fitted regression and the top and bottom lines are the 95% CI for individual species averages.

By comparing methods 1 and 3, it is possible to see that males that disperse significantly reduce the proportion of sib-mating from 0.958 to 0.896. However, if multi-foundress figs produce substantially more females than single-foundress figs and the estimate of sib-mating is closer to 0.913, this reduction is not significant. Comparing method 2 with method 3 shows that the sex ratio is a poor estimator of the breeding structure, consistently underestimating the amount of sib-mating by between 33 and 40%.

4. DISCUSSION

The colour polymorphism is indeed inherited in a simple Mendelian fashion, and hence it can be used to calculate the inbreeding coefficient, giving an estimate of 0.683. Most figs contained a single foundress and, if no dispersal occurred, an inbreeding coefficient of 0.850 would have been expected (table 2). By comparing these genetic and ecological data, it is clear that the males that disperse do succeed in obtaining matings in the figs to which they disperse; these matings lead to a 6.5% reduction in the frequency of sib-matings. Consequently, the first expectation is that the sex ratio should be less female biased than other non-dispersing species, and this is indeed the case (figure 2). However, the minimum proportion of sons required to fertilize and set their sisters free (0.112) exceeds the estimate based on the frequency of sib-mating (0.037) and the estimate based on sequential oviposition (0.003). Dispersal therefore does not account for the observed increase in the sex ratio, at least not in the model resulting in equation (1.1). Note also that the minimum proportion of sons correlates well with that inferred for other species (figure 2).

The sex ratios could be inflated if an unusual number of sperm-limited females oviposited. However, if all broods with sex ratios over 0.35 are ignored, the average sex ratio is still very high (figure 2). Alternatively, some foundresses may have been overlooked so that figs with two foundresses were also counted. This is unlikely as the females were normally retrieved in a fairly good condition.

Dispersal can change the adaptive landscape of sex ratios. Excess males need not compete locally but can disperse and compete for matings against unrelated males. Hence, females who produce slightly too many sons need not suffer severe fitness losses as their sons can disperse. This has two consequences: first, variation around the ESS will either be selectively neutral or lead to a small decline in fitness; second, the proportion of sib-matings will be a function of the sex ratio. This last prediction means that, as sex ratios become less female biased, the degree of sib-mating decreases and, in turn, it results in less-female-biased optimal sex ratios (J. M. Greeff, unpublished model). In support of these ideas, this *Alfonsiella* species produced both more males than expected and significantly over-dispersed sex ratios. This suggests that there is not a set proportion of females 'reserved' for sib-mating but, rather, the extent of male dispersal determines the frequency of sib-mating. Under these conditions, the relationship described by equation (1.1) breaks down and the ESS sex ratios will be less female biased (J. M. Greeff, unpublished model).

The dependence of dispersal on the sex ratio is not the only scenario that will lead to less-female-biased sex ratios. It can also result from fitness-enhancing interactions between the sexes. Zammit & Schwarz (2000) have argued that this may be the case for another pollinating species in which males help females out of their galls.

When the sex ratio is used to calculate the incidence of sib-mating, a significantly lower estimate of sib-mating is obtained than actually occurred. This may result from the fact that equation (1.1) does not take into account that the incidence of sib-mating may depend on the sex ratio (J. M. Greeff, unpublished model). The incongruence suggests that some caution should be taken when sex ratios are used for establishing trends in the mating system as they may predict less inbreeding than that which actually occurs.

As it is not known from how many populations wasps were drawn, it is possible that the estimate of the inbreeding coefficient is somewhat inflated due to Wahlund's principle. This means that the mating success of dispersing males is higher and the sex ratio estimate of inbreeding is closer to the mark. However, these two estimates are so far apart from each other that a slight inflation of F will not reconcile the datasets. Different loci in one population often give different estimates of the degree of inbreeding, so the one locus studied here may be giving an unrepresentative answer. This is impossible to check without additional loci.

Two other studies on wasps also recorded higher sex ratios than were predicted from the estimate of sib-mating: Antolin (1999) observed a sex ratio of 0.24, while his estimate of $s = 0.566$ predicts a sex ratio of $r = 0.184$; and Nadel & Luck (1992) observed a sex ratio of 0.18, whereas their estimate of $0.63 < s < 0.74$ predicts a sex ratio of $0.1 < r < 0.15$. This consistent failure of equations (1.1) and (2.1) to reconcile the sex ratio and mating patterns suggests that, at least as far as wasps are concerned, care should be taken in making the inference. Detailed information on the mating behaviour is required to obtain an accurate estimate of the frequency of sibmating from the sex ratios. As facultative dispersal by males will reduce or nullify the fitness impact of inaccurate sex ratios, the variance in sex ratios may, in addition to the sex ratios themselves, give us some information on the mating system.

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APPENDIX A

If p is the probability of the first female remaining the only female, we ignore foundress numbers above two and ignore male dispersal, and assume that the second females produce a clutch u times the size of the former, we can write the following two fitness equations:

$$w_1 = (1 - r_1)Gf + \left(p(1 - r_1) + (1 - p)\frac{1 - r_1 + u(1 - r_2)}{r_1 + ur_2}r_1\right)G_m , \qquad \text{(A 1)}$$

$$w_2 = (1 - r_2)Gf + \left(\frac{(1 - r_1)/u + (1 - r_2)}{r_1/u + r_2}r_2\right)G_m , \qquad \text{(A 2)}$$

where G_i is equal to the reproductive value of that sex (m, male; f, female) multiplied by the relatedness of offspring of that sex to the mother (for haplodiploids, this gives us the values of $G_f = 1/(2 - s)$ and $G_m = 1/2$; Taylor 1993), and r_1 and r_2 are the sex ratios of the first and second foundresses, respectively. Simultaneously solving $\partial w_1/\partial r_1 = 0$ and $\partial w_2/\partial r_2 = 0$ for r_1 and r_2 gives the ESS sex ratios for the first ($i = 1$) and second ($i = 2$) females as

$$r_i = \frac{G_m(1 - p)^{3-i}(1 + u)}{(G_m + G_f)(2 - p)^2} . \qquad \text{(A 3)}$$

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