
Evolution of social parasitism in ants: size of sexuals, sex ratio and mechanisms of caste determination

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Social parasitism, one of the most intriguing phenomena in ants, has evolved to various levels, the most extreme form being parasites that have lost the worker caste and rely completely on the host's worker force to raise their brood. A remarkable feature of workerless social parasites is the small size of sexuals. It has been suggested that reduced size evolved as a means to take advantage of the host's caste-determination system, so that parasite larvae develop into sexuals with less food than is required to produce host workers. An important consequence of size reduction is that it might restrict the host workers' ability to discriminate between the brood of the social parasite and their own brood and might protect parasite sexuals from elimination. We found that sexuals of the workerless inquiline ant *Plagiolepis xene* were significantly smaller than the sexuals of their host *Plagiolepis pygmaea*, but remarkably similar to the host workers. The size variance of parasite sexuals was much lower than that of their host; this result possibly suggests that there is very stabilizing selection acting on size of the parasite sexuals. Comparison of the primary (egg) and secondary (adult) sex ratios of the parasite and host showed that miniaturization of *P. xene* sexuals has been accompanied by their ability to develop into sexuals even when the host *P. pygmaea* actively prevents production of its own sexuals. These results suggest that the inquiline's size and caste threshold have been reduced such that all individuals in a parasite brood will develop into sexuals. We also found that the adult sex ratio of *P. xene* was heavily female-biased. This bias probably stems from local mate competition that arises from sexuals mating within the nest. There was no significant difference between the proportion of haploid eggs and adult males produced; this observation indicates that a female-biased sex ratio is achieved by queens producing a higher proportion of diploid eggs rather than by a higher mortality of haploid males.

Keywords: social parasitism; sex ratio; local mate competition; size variance; caste threshold; ant

1. INTRODUCTION

Social parasites have long been recognized as providing one of the most intriguing phenomena in ants (Buschinger 1986; Hölldobler & Wilson 1990). Three main types of parasitic life history are known: slave-making, temporary parasitism, and permanent inquilinism. Slave-making species raid colonies of other species for worker brood that they carry back to their own nest. Enslaved workers rear the brood of the slave-maker and perform other colony work. In temporary social parasites, founding queens invade colonies of other species, kill the resident queen, and use the host worker-force to raise her brood until parasite workers have developed and progressively replaced their hosts. The most extreme form of social parasitism is permanent inquilinism, in which parasites have lost the worker caste and completely rely on the host worker force to raise their brood. Inquiline queens infiltrate host colonies,

where they usually coexist with the host queen, and produce no workers but only sexuals, which are reared by the host workers simultaneously with their own larvae.

A remarkable feature of workerless social parasites is the small size of sexuals. As first suggested by Bourke & Franks (1991), reduced size may have evolved as a means to take advantage of the host's caste-determination system, so that parasite larvae develop into sexuals with less food than is required to produce host workers (see also Nonacs & Tobin 1992). Caste determination in ants is based on the amount of food received during larval development (Wheeler 1994), a female larva becoming a reproductive queen rather than a worker when its biomass passes a certain (caste) threshold. To favour the developmental pathway from female larvae to reproductive individuals, the inquiline's caste threshold might have been reduced such that all female parasite brood would develop into queens. This hypothesis has received support from a comparative study showing that, in 18 out of 19 species, queens of workerless inquilines are the same size

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as or smaller than host workers (Nonacs & Tobin 1992). Three additional predictions stem from this hypothesis. First, males of workerless inquilines should also be the same size as or smaller than host workers. Second, a strong stabilizing selection should be observed on the size of both males and females of workerless inquilines, resulting from two antagonistic selective forces. Although greater size probably results in greater reproductive success, perhaps by conferring a greater fertility on females and a greater mating success on males, greater size probably also increases the probability of being recognized as a sexual by the host species and consequently of being eliminated. Finally, miniaturization should protect parasite sexuals from elimination because host workers cannot discriminate between the brood of the social parasite and their own worker brood.

The first aim of this study was to test these predictions. We determined the size of male and female pupae of the workerless inquiline ant *Plagiolepis xene* and its host, *Plagiolepis pygmaea*. We also compared the primary sex ratio (proportion of haploid eggs) and the secondary sex ratio (proportion of males at the adult stage) of both *P. xene* and *P. pygmaea* to test the hypothesis that size reduction allows the parasite to escape worker control of the host species and thus to produce sexuals even when the host actively prevents production of its own sexuals.

The second aim of the study was to investigate the effect of the shift of the *P. xene* mating system on sex-ratio allocation. In *P. xene*, as in many other workerless social parasites, sexuals mate within the host nest and laboratory observations indicate that mating commonly occurs among sibs (Kutter 1952; Passera 1969; this study). Because the fitness return value of males is decreased when local mating competition occurs, queens should produce a female-biased sex ratio (Hamilton 1967; Werren 1980; Bulmer & Taylor 1980; Herre 1985; Frank 1987; Bourke & Franks 1995). We therefore determined the adult sex ratio of *P. xene* and compared these values with the primary sex ratio produced by queens to investigate whether local mate competition leads to female-biased sex ratios. We also determined the proximate mechanism responsible for such a potential bias.

2. MATERIALS AND METHODS

(a) *Ant colonies and laboratory rearings*

Plagiolepis pygmaea forms polygynous colonies (5–30 reproductive queens per colony). Both male and female sexuals develop in early July from overwintering brood; they usually mate during nuptial flights, but intranidal mating also occurs (Passera 1969). Colonies reproduce by budding, a process whereby newly mated queens and workers jointly leave their colony to initiate a new colony nearby.

Plagiolepis xene is an obligate workerless social parasite of *P. pygmaea* (Stumper & Kutter 1952; Le Masne 1956; Passera 1964). As is typical of social parasites, *P. xene* is rare and only a few host colonies are parasitized. Parasitized colonies may contain more than 100 *P. xene* reproductive queens (Passera 1969). The production of *P. xene* sexuals (new queens and males) occurs in August–October from eggs laid in early spring. Males are apterous and mating takes place within the host nest, where queens

remain when fertilized (Kutter 1952; Passera 1969). As in other workerless inquiline ants, dispersal of the mated queens is very limited (Hölldobler & Wilson 1990). Dispersal generally occurs when host colonies reproduce by budding, with *P. xene* queens following the host workers and queens to establish a new colony (Passera 1969).

We found and collected five parasitized and six unparasitized colonies of *P. pygmaea* between 14 and 27 January 1997 (before queens resumed egg-laying) from the Lauragais region (France). Each of the five parasitized *P. pygmaea* colonies was split into two halves consisting of 1–3 *P. pygmaea* queens, 200–350 *P. pygmaea* workers and 21–87 *P. xene* queens. The six unparasitized *P. pygmaea* colonies contained 1–3 queens and 200–300 workers. All colonies were fed on crickets and honey, and maintained under standard laboratory conditions at 26 ± 1 °C (Passera 1969).

(b) *Primary and secondary sex ratios*

Eggs were gathered from the experimental colonies during the first two weeks after collection. Eggs from each species are easy to recognize: the eggs of *P. xene* are more rounded and significantly smaller ($X \pm \text{s.d.} = 0.28 \pm 0.019$ mm, range 0.24–0.33 mm, $n = 78$) than those of *P. pygmaea* ($X \pm \text{s.d.} = 0.47 \pm 0.035$ mm, range 0.41–0.54 mm, $n = 167$) (Passera 1969). In the parasitized colonies, half of the eggs laid by *P. xene* were removed for the determination of the primary sex ratio and the other half kept for subsequently determining the secondary sex ratio. The same procedure was used to determine the primary and secondary sex ratios of the host in unparasitized colonies. The primary sex ratio of *P. pygmaea* cannot reliably be determined in parasitized colonies because a high proportion of the host eggs are eaten by *P. xene* queens (L. Passera and S. Aron, unpublished data). Egg-eating by *P. xene* queens is adaptive because it allows the parasite to obtain more resources, and perhaps also because it makes it less profitable for *P. pygmaea* workers to discriminate and eliminate *P. xene* eggs. Worker reproduction in *P. pygmaea* occurs exclusively in queenless colonies (Passera 1966, 1978). Because all our colonies contained queens our estimates of the primary sex ratio in *P. pygmaea* was not influenced by worker-laid eggs.

Estimation of the proportion of haploid (male) and diploid (female) eggs laid by queens was based on staining and counting the number of chromosomes in several nuclei of each egg (see Aron *et al.* (1994, 1995) and Keller *et al.* (1996a) for more details of the methods). The number of chromosomes is as follows: $n = 9$ and $2n = 18$ in *P. pygmaea* (Hauschteck-Jungen & Jungen 1983), and $n = 10$ and $2n = 20$ in *P. xene* (this study).

The secondary sex ratio was determined for each colony as the proportion of adult males among all sexuals produced. Because the minimum time for adult sexuals to develop from eggs under laboratory conditions is about eight weeks for both species (Passera 1969) the secondary sex ratio was determined about two months after colonies were established in the laboratory.

(c) *Statistical analysis*

The sizes of *P. pygmaea* workers, males and female sexuals were not normally distributed (Kolmogorov–Smirnov goodness-of-fit test on the original or arcsine-transformed data, all $p < 0.01$). We therefore used Kruskal–Wallis non-parametric ANOVA tests for comparing the size of the different classes of individuals of the two species. Multiple comparisons among pairs of means were performed by using Dunn's test. The coefficients of variation of size between different classes of individuals were compared with two-tailed *t*-tests (Zar 1984).

Table 1. Mean lengths of worker, male, and female pupae of *P. pygmaea*, and of male and female pupae of *P. xene* (Values are means (mm) \pm s.d.; sample size is given in parentheses.)

	workers	males	females
<i>P. xene</i>	—	1.33 \pm 0.023 (13)	1.35 \pm 0.018 (25)
<i>P. pygmaea</i>	1.38 \pm 0.10 (1609)	1.59 \pm 0.098 (682)	2.80 \pm 0.127 (764)

Table 2. Primary and secondary sex ratios in the parasitic ant *P. xene* and its host *P. pygmaea*

(No sexuals were produced in *P. pygmaea*, the colonies producing only workers. Sample sizes shown in parentheses are the number of eggs for which the gender was determined per colony.)

<i>Plagiolepis xene</i>				<i>Plagiolepis pygmaea</i>	
colony	primary sex ratio	no. sexuals produced	secondary sex ratio	colony	primary sex ratio
1	0.14 (50)	84	0.12	1	0.12 (17)
2	0.14 (50)	23	0.13	2	0.18 (22)
3	0.14 (42)	—	—	3	0.12 (26)
4	0.16 (50)	—	—	4	0.10 (40)
5	0.17 (47)	8	0.25	5	0.21 (28)
6	0.07 (30)	—	—	6	0.10 (29)
7	0.20 (30)	—	—		
8	0.13 (38)	12	0.08		
9	0.10 (50)	49	0.12		
10	0.07 (46)	51	0.14		
$\bar{X} \pm$ s.d.	0.13 \pm 0.042		0.14 \pm 0.058		0.14 \pm 0.046

3. RESULTS

(a) Size variation

The size of individuals belonging to each sex and caste differed significantly (KW = 275523; $p < 0.0001$) (table 1). Multiple comparisons among pairs indicate that male and female *P. xene* pupae were significantly smaller than sexual pupae of *P. pygmaea* (Dunn's test, $p < 0.001$). Remarkably, the mean size of male and female *P. xene* pupae was very similar and not significantly different from that of worker pupae of their host (Dunn's test, $p > 0.05$).

Another striking feature is the difference in the magnitude of the pupal size variation between the host and its parasite. The coefficient of variation of *P. xene* pupal length was $V = 0.018$ (s.e. (across colonies) = 0.004) for males and $V = 0.014$ (s.e. (across colonies) = 0.002) for females, whereas in *P. pygmaea* these coefficients reached values of $V = 0.062$ (s.e. (across colonies) = 0.002), $V = 0.045$ (s.e. (across colonies) = 0.001) and $V = 0.072$ (s.e. (across colonies) = 0.001) for males, females and workers, respectively. Size variation was significantly higher for the male, female and worker pupae of the host (t -test on coefficients of variation with sequential Bonferroni's correction of significance level, all $p < 0.0002$). Size variation was not different between male and female pupae of *P. xene* ($t = 1.11$, $p = 0.274$).

(b) Primary and secondary sex ratios

The proportion of haploid eggs laid by *P. xene* queens ranged between 0.07 and 0.20, the overall mean being 0.13 (table 2). There was no significant difference in the proportion of haploid eggs among colonies ($\chi^2_9 = 5.62$,

$p = 0.78$). Six out of the ten experimental colonies produced sexuals. The proportion of males reared in these colonies (0.14) was very similar to the proportion of male eggs (0.13). A comparison between the primary and secondary sex ratios for the six colonies producing sexuals revealed no significant change over time in the proportion of males and females (Wilcoxon signed-rank test, $p = 0.687$).

The proportion of haploid eggs laid by *P. pygmaea* queens was very similar to that of *P. xene* (0.14, range 0.10–0.21) and also did not vary significantly among colonies ($\chi^2_5 = 2.70$, $p = 0.75$; table 1). However, in stark contrast with *P. xene*, neither adult males nor alate queens were produced, the six colonies producing only workers.

4. DISCUSSION

The comparison between the primary and secondary sex ratios in the workerless social parasite *P. xene* and its host *P. pygmaea* revealed that spring eggs produced by queens of both species follow a completely different developmental pathway. Whereas *P. pygmaea* workers invariably destroyed all the male brood of their own species, there was no selective elimination of males in *P. xene*. Moreover, *P. pygmaea* females gave rise to workers only, whereas *P. xene* females all developed into sexuals. These data demonstrate that the parasite has evolved the ability to produce sexuals even when the host actively prevents production of its own sexuals. The complete lack of production of *P. pygmaea* sexuals in our colonies is consistent with previous studies (Passera 1969) that showed that eggs laid in spring never developed into sexuals in this species. All male and female sexuals invariably

develop from overwintering brood (i.e. eggs laid by queens in late summer and autumn).

Several lines of evidence suggest that the ability of the parasite larvae to develop into sexuals has evolved jointly with miniaturization and a decrease in caste threshold. Male and female *P. xene* pupae were significantly smaller than sexual pupae of their host but remarkably similar to the host's worker pupae. This is the predicted pattern if miniaturization is favoured until the amount of food needed to produce an inquiline queen is equal to or less than that needed for a host worker (Nonacs & Tobin 1992). Moreover, the coefficient of variation of male and female *P. xene* pupal length was nearly four times smaller than the coefficients for *P. pygmaea* workers, male and female sexuals. This supports the view that there is strong stabilizing selection on the size of the parasite brood: greater size probably allows individuals to increase their reproductive success, perhaps by conferring greater fertility on females and greater mating success on males, but greater size probably also increases the probability of being recognized as a sexual by the host species and consequently being eliminated.

The secondary sex ratio in *P. xene* was heavily female-biased, the proportion of males being 0.14, a value very similar to the sex ratio observed in another experimental study (0.12) (Passera 1972) and under natural conditions (0.09–0.17) (Kutter 1952). Because males and females of *P. xene* have the same weight (dry weight = 0.04 ± 0.01 mg for both sexes, this study) the investment sex ratio is also heavily female-biased.

Three factors have been proposed to account for a female bias in eusocial Hymenoptera. First, the genetic relatedness asymmetry hypothesis predicts that workers should favour a female-biased population sex ratio because they are more related to their sisters than to their brothers (Trivers & Hare 1976). Second, it has been suggested that a female-biased sex ratio in social Hymenoptera may stem from males suffering higher mortality than females because recessive lethal alleles are more frequently expressed in haploid males than in diploid females (Smith & Shaw 1980). Third, a female-biased sex ratio may stem from local mate competition, when brothers compete with each other for access to females (Hamilton 1967; Alexander & Sherman 1977). The relatedness asymmetry hypothesis is unlikely to play a role in *P. xene* because there are no workers and thus there is no queen–worker conflict over sex ratio. Moreover, the same proportion of males at the egg and pupal stages indicates that the host workers do not significantly alter the parasite sex ratio. The second hypothesis is not supported by our data either: one would predict a significant decrease in the proportion of males between the egg and pupal stages if greater male mortality were the cause of the female-biased sex ratio. This was not the case. Finally, local mate competition is likely to play an important role in *P. xene*. Sexuals mate within the host nest and laboratory observations indicate that mating commonly occurs among sibs (Kutter 1952; Passera 1969; this study). Because the fitness returns of males decrease when local mating competition occurs, queens should therefore produce a female-biased sex ratio (Hamilton 1967; Werren 1980; Bulmer & Taylor 1980; Herre 1985; Frank 1987; Bourke & Franks 1995). The female-biased

primary sex ratio laid by queens thus supports the idea that local mate competition is the cause of the female-biased secondary ratio. Local mate competition leading to female-biased investment is considered to be unusual in ants; it has been reported in three other ant species, a parasitic ant, *Epimyrma krausseii* (Winter & Buschinger 1983), two monogynous species (*Technomyrmex albipes* (Tsuji & Yamauchi 1994) and *Messor aciculatus* (Hasegawa & Yamaguchi 1995)) and a polygynous species, *Myrmica sulcinodis* (Pedersen & Boomsma 1999). However, our study provides the first empirical evidence that a female-biased sex ratio associated with local mating competition is achieved by queens biasing the primary ratio.

The finding that *P. xene* males apparently do not suffer higher mortality than females has important implications for studies on sex allocation in ants. The most likely mechanism by which workers may manipulate sex ratios in their own interest is by selective elimination of males in their colonies. A decrease in the proportion of males between the egg and pupal stages has been reported in four other ant species (*Linepithema humile* (Aron *et al.* 1994; Passera & Aron 1996), *Solenopsis invicta* (Aron *et al.* 1995), *Pheidole pallidula* (Keller *et al.* 1996b) and *Formica exsecta* (Sundström *et al.* 1996)). In contrast to *P. xene*, these species all have workers and a queen–worker conflict has been shown to occur over sex ratio. The reduction in the proportion of males in these ants but not in *P. xene* indeed supports the view that major changes in colony sex ratios stem from workers manipulating sex ratio rather than from differential mortality of males.

In conclusion, this study shows that the decreased size of sexuals in *P. xene* is connected to the parasite's ability to produce sexuals even when the host actively prevents production of its own sexuals. The extremely small variation in size of sexuals possibly suggests strong stabilizing selection, the optimal size being that just below the caste threshold where larvae are recognized as sexuals. The cost associated with larger size (i.e. elimination by the host workers) is quite unusual in animals. The association between size and the worker's ability to identify sexuals may also have unrecognized implications for the evolution of optimal size in eusocial insects where workers control which larvae develop into sexuals. Under some conditions larvae may benefit by developing into small sexuals if this increases, for example, their probability of becoming sexuals rather than workers.

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