

Research article

Social parasitism in ants: effects of the inquiline parasite *Plagiolepis xene* St. on queen distribution and worker production of its host *Plagiolepis pygmaea* Latr.

L. Passera¹, M. Gilbert² and S. Aron^{2,*}

¹ Laboratoire d'Ethologie et Psychologie Animale, CNRS UMR 5550, Université Paul-Sabatier, F-31062 Toulouse, France, e-mail: passera@cict.fr

² Unit of Animal Communities, CP 160/12, Université Libre de Bruxelles, B-1050 Brussels, Belgium, e-mail: mgilbert@ulb.ac.be; saron@ulb.ac.be

Received 27 September 2000; revised 9 November and 13 December 2000; accepted 19 December 2000.

Summary. The ant *Plagiolepis pygmaea* forms polygynous (several mated queens per colony) and polydomous (multiple nests per colony) colonies that may be parasitized by the workerless social parasite *Plagiolepis xene*. Earlier laboratory experiments showed that *P. xene* strongly restricts host worker production (Passera, 1972); however, this negative effect seems not to occur under natural conditions. Here, we explored the hypothesis that, in infested natural colonies of *P. pygmaea*, parasite queens affect the distribution of the host queens resulting in the latter inhabiting unparasitized nests of the colony at the period of egg-laying. Our field studies show that the presence of the inquiline ant *P. xene* influences host queen distribution, with a higher level of dispersion within parasitized colonies. In winter, there is a positive association between the number of host queens and the number of parasites in queenright nests. Such a relationship does not occur in summer, so that when egg-laying reaches its maximum activity most queens of the host are found in unparasitized nests. Moreover, the proportion of queenright nests parasitized was dramatically lower than in the winter. A detailed comparison of worker production between parasitized and unparasitized field colonies reveals no difference. Experiments show that reduced worker production in parasitized nests reared under laboratory conditions results from oophagy by the parasitic queens. Overall, our data suggest that the segregation of the host and parasite queens in different nests at the time of egg-laying results in part from host queens avoiding inhabiting parasitized nests to reduce oophagy by the parasite. We discuss the behavioral and ecological implications of our findings.

Key words: Social parasitism, spatial distribution, egg eating, Formicidae.

Introduction

One of the most intriguing phenomena in ants is the occurrence of social parasitism, a way of life that can be temporary or permanent (Wilson, 1971; Hölldobler and Wilson, 1990). The most extreme form of social parasitism is permanent inquilinism. This evolutionary step is reached when the worker caste of the parasitic ant has disappeared. Queens of the parasite infiltrate colonies and produce only male and female sexuals which are reared by the host worker force. Hypotheses accounting for inquiline evolution have been intensively discussed by evolutionary biologists (e.g. Wilson, 1971; Buschinger, 1986; Bourke and Franks, 1991; Nonacs and Tobin, 1992; Heinze, 1995; Ward, 1996; Aron et al., 1999; Bekkevoeld and Boomsma, 2000). By contrast, the consequences of permanent inquilinism on the colony growth and the reproductive success of the host are poorly documented. In a minority of inquiline species, the presence of the parasite causes the death of the host queen, which dramatically reduces the colony life expectancy. Though relatively rare, this strategy occurs in species in which the parasites are relatively short-lived (Buschinger and Winter, 1983; Hölldobler and Wilson, 1990). All the efforts of the host workers are invested in the production of as many parasite sexuals as soon as possible, which will leave the nest to invade a new host colony.

The majority of inquilines, however, co-exist with the host queens which insure the parasites a long-lasting supply of host workers to rear their brood. This occurs especially when the inquiline species parasitizes a polygynous host

* Author for correspondence.

(several mated and laying queens together in a nest). *Plagiolepis xene* parasitizing the polygynous species *Plagiolepis pygmaea* provides a relevant example. The parasites are not expected to inflict too high a damage on the host colony because *P. xene* queens have a life expectancy that probably exceeds one year (L. Passera, unpubl. data.) and they depend on the host workers for dispersal by budding along with the host queens. Budding is a process whereby newly mated queens and workers leave the mother colony and establish a new colony nearby. Such a mode of colony multiplication in *Plagiolepis pygmaea* explains why parasitized colonies are usually clustered in confined biotopes.

Colonies of *P. pygmaea* are polydomous, i.e. single colonies occupy several, spatially separate nests. The number of nests per colony varies with the season, a process known as seasonal polydomy (Snyder and Herbers, 1991). In spring, colonies split into numerous nests remaining in close proximity to one another. Workers, brood and queens may be exchanged between the multiple nests of a colony. In late summer, the nests recombine with other colony subunits, thus reducing the level of polydomy for overwintering. *Plagiolepis xene* is an obligatory workerless social parasite of the ant *P. pygmaea* (Stumper and Kutter, 1952; Le Masne, 1956). As is typical in inquilinism, *P. xene* is rare and only a few host colonies are parasitized. Overall, less than 1% of the colonies collected over more than 30 years by one of us (L.P.) were found parasitized, with about 30–50% of host colonies being parasitized in infested populations. Like the host species, *P. xene* is highly polygynous: parasitized colonies may contain several tens of reproductive queens of the inquiline, which spread out in the multiple nests of the colony (Passera, 1969). Though virgin females are winged, males are apterous and mating occurs within the host nests (Kutter, 1952; Passera, 1964). Dispersal of the parasites occurs when host colonies reproduce by budding, with *P. xene* queens following the host workers and queens to establish a new colony (Passera, 1969).

In *P. pygmaea*, it has been shown by laboratory experiments that the production of host workers is strongly restricted by the presence of *P. xene* queens (Passera, 1972). However, casual observations suggest that worker population is not different between infested and uninfested colonies under natural conditions. How the parasite queens prevent the production of host workers and how the host species is able to avoid this from happening in the field remains unknown. It has been suggested that parasite queens affect the spatial distribution of host queens, resulting in the latter inhabiting unparasitized nests of the colony at the period of egg-laying (Passera, 1972; Aron et al., 1999). Here, we explored this possibility by investigating the effect of the workerless inquiline ant *P. xene* on the distribution of the host queens *P. pygmaea* in field colonies, both in winter (no egg-laying) and in summer (peak of egg-laying). We analyzed queen distribution within the multiple nests of parasitized and unparasitized colonies of *P. pygmaea*. We also determined within-colony distribution of the parasite in relation to its host. Finally, we investigated how the parasite prevents the production of host workers in experimental units.

Methods

P. pygmaea colonies were collected from the Lauragais region near Toulouse (France). They originated from 3 localities having similar habitats, separated by less than 1 km. The colonies were collected in the soil of south-facing embankments with vertical slopes along roads. Twenty unparasitized and 10 parasitized *P. pygmaea* colonies were collected between 7 January and 21 April 1997 (before queens resumed egg-laying). They were brought to the laboratory for sorting and their contents was censused. Colonies were then kept at 12°C until they were used for subsequent experiments (see egg production). Another set of 8 colonies, 5 unparasitized and 3 parasitized, was excavated in early July, at the time of intense egg laying. In summer, the nests of *P. pygmaea* are very diffuse and queens and workers are scattered just below the surface of the ground which, at the time, is very dry and crumbly, so that nests are collected with difficulty. For this reason, our sample of summer colonies was limited.

Queen distribution in field colonies

The distribution of both host and parasite queens was studied by excavating separately each nest of one colony, and by counting the number of host queens, the number of host workers and the number of parasites in each nest. From the 30 *P. pygmaea* colonies excavated between January and April 1997, 4 parasitized colonies ($\Sigma = 35$ nests, range: 3–19 nests/colony) and 8 unparasitized colonies ($\Sigma = 45$ nests, range: 2–13 nests/colony) were excavated 'nest by nest' during the inactive overwintering period (February – March 1997). The additional 5 unparasitized ($\Sigma = 16$ nests, range: 2–7 nests/colony) and 3 parasitized ($\Sigma = 16$ nests, range: 4–7 nests/colony) summer colonies were excavated in a similar way, and the contents of each nest was determined. Count data from individual nests were pooled respectively for parasitized and unparasitized colonies in order to allow patterns revealed by larger number distribution to be identified and compared.

The aggregativeness of queens counts in nests was analysed by comparing observed distribution to a random Poisson distribution using a χ^2 comparison test. The Morisita's dispersion index was also estimated to confirm observed aggregative trends. This index is one of the best dispersion indices because of its independence of population density and sample size (Myers, 1978). It is defined by the following equation (Morisita, 1962):

$$I_d = n \frac{\sum (x^2) - \sum x}{(\sum x)^2 - \sum x}$$

where I_d is the Morisita's index, n is the number of samples and x represents individual counts. The index $I_d = 1$ for a random distribution, is > 1 for a clumped distribution and is < 1 for a regular distribution. The value $I_d \cdot (\sum x - 1) + n - \sum x$, where n is the number of samples, follows a χ^2 distribution with $n-1$ d.f. allowing to test for departure from randomness.

Worker production in field and laboratory colonies

The possible influence of the parasite on the growth of host colonies was assessed in two ways. First, we compared the mean number of worker cocoons produced in parasitized and unparasitized field colonies, as well as in the parasitized and unparasitized nests of infested colonies. These analyses were carried out on the colonies excavated in early July, which corresponds to the period of intense worker brood production. Because the size of the cocoons of *P. pygmaea* workers and males overlaps with those of *P. xene* sexuals, special attention was given to the identity of the pupae. At this time of the year, nearly all the *P. pygmaea* males had emerged; the remaining male pupae could be identified through the cocoon due to the large size of their eyes. By contrast, the sexuals of the parasite were still in the larval stage. As a result, the number of worker cocoons could be assessed with confidence.

Second, we compared egg production between infested and uninfested *P. pygmaea* colonies under laboratory conditions. Colonies kept under artificial overwintering were divided into experimental units. After having discarded the wintering brood, 9 unparasitized experimental units, each containing 1 *P. pygmaea* queen and 300 workers, and 11 infested units, each containing 1 host queen, 20 to 80 parasitic queens and 300 workers, were set up. All experimental units were fed on honey twice a week, and maintained under summer conditions at $26 \pm 1^\circ\text{C}$. *Plagiolepis pygmaea* main diet consists of nectar of flowers and honeydew of aphids. Previous experiments showed that, under laboratory conditions, both *P. pygmaea* and *P. xene* can be reared for several years and produce sexuals when fed with honey only (Passera, 1969). Queens resumed egg-laying about 1 week after initiation of the rearing at 26°C . The number of eggs laid by *P. pygmaea* queens was counted in both types of experimental units one week later. Eggs from each species are easy to recognize. *P. xene* eggs are more rounded and significantly smaller ($X \pm \text{SD} = 0.28 \text{ mm} \pm 0.019$, range: 0.24–0.33, $n = 78$) than *P. pygmaea* eggs ($X \pm \text{SD} = 0.47 \pm 0.035$, range: 0.41–0.54, $n = 167$; Passera, 1969).

Our results indicated a strong difference in the number of eggs found between both types of units (see results). We therefore investigated whether such a difference resulted from an inhibition of reproduction or a reduction in the egg-laying rate of the host queens due to the presence of the parasite, or from oophagy of the host eggs by the parasite.

Ovarian parameters

Ovarian dissections of *P. pygmaea* queens originating from 10 unparasitized and 15 parasitized experimental units were performed under water 6 weeks after experimental set up. The ovaries were placed in a droplet on a microscope slide and we recorded the number of developing oocytes, the size of the largest oocyte, the size of the longest ovarirole and the number of *corporea lutea* in the base of the ovarioles.

Oophagy

Fifteen eggs, laid by queens of the host ant in uninfested units 3 or 4 weeks after the end of overwintering, were introduced in small, well-fed, experimental units consisting of 200 workers and 26 queens of the parasitic ant ($n = 9$ replicates). Controls consisted of small units containing only 200 queenless workers ($n = 5$ replicates). The number of remaining eggs was censused 3 or 4 days later.

For statistical comparisons, the appropriate parametric or non-parametric test was employed (Zar, 1984). All significance levels refer to two-tailed tests.

Results

Queen distribution in field colonies

For both parasitized and unparasitized *P. pygmaea* colonies, most nests sampled were free of queens and occupied by workers only. The distribution of *P. pygmaea* queens in nests of parasitized and unparasitized colonies during overwintering was found to be significantly different from a random Poisson distribution (parasitized colonies: $\chi^2 = 23.75$, $\text{df} = 3$, $p < 0.001$; unparasitized colonies: $\chi^2 = 8.74$, $\text{df} = 3$, $p = 0.032$). Rather, queens showed a clear aggregative trend (Morisita's dispersion index in nests of parasitized colonies: $I_d = 2.43$, $n = 35$, $p < 0.001$; in nests of unparasitized colonies $I_d = 1.84$, $n = 45$, $p < 0.001$).

As shown in figure 1 (white dots), most *P. xene* queens were found in nests without *P. pygmaea* queens, whatever the

season. Up to 68 parasite queens were found clumped in a single nest. The number of parasites was independent of the number of host workers in this nest ($r^2 = 0.01$, N.S.). From the 35 nests collected in the winter, 16 contained at least 1 *P. pygmaea* queen; 13 of the queenright nests ($\approx 80\%$) were found parasitized (Fig. 1, black dots). The number of parasites was positively associated with the number of host queens in queenright nests ($r^2 = 0.77$, $F = 48.23$, $\text{df} = 15$, $p < 0.001$). This correlation remained significant even when the extreme value (10 host queens, 22 parasites) was excluded ($r^2 = 0.52$, $F = 14.55$, $\text{df} = 14$, $p = 0.002$). Queens of the parasite showed a strong aggregative trend ($I_d = 3.09$, $n = 35$, $p < 0.001$). Such a trend was observed both in nests inhabited by *P. pygmaea* queens ($I_d = 1.99$, $n = 16$, $p < 0.001$) and nests uninhabited by the host queens ($I_d = 2.60$, $n = 18$, $p < 0.001$).

The aggregative behaviour of the parasite also occurred in summer ($I_d = 2.69$, $n = 16$, $p < 0.001$). At this period of the year, however, the proportion of queenright nests parasitized was lower than in the winter, with only 2 queenright nests over 8 (= 25%) being found parasitized (Fisher's exact test, $p = 0.021$) (Fig. 1, inset). No significant relationship occurred between the distribution of the parasite and the hosts queens in summer ($r^2 = 0.27$, $F = 2.25$, $\text{df} = 7$, $p = 0.18$). Moreover, from the 54 host queens collected directly from the field in the winter (January–March; $N = 45$ nests from 4 colonies), 49 (90.7%) were located in nests containing at least 1 parasite. This proportion dramatically decreased in summer (July; $N = 16$ nests from 3 colonies), with only 3 (9.26%) over the 18 host queens excavated sharing a nest with one or more parasites ($\chi^2 = 33.3$; $p < 0.001$). Therefore, when egg-laying reaches its maximum activity, the queens of the host were more likely to be found in nests free from parasite queens.

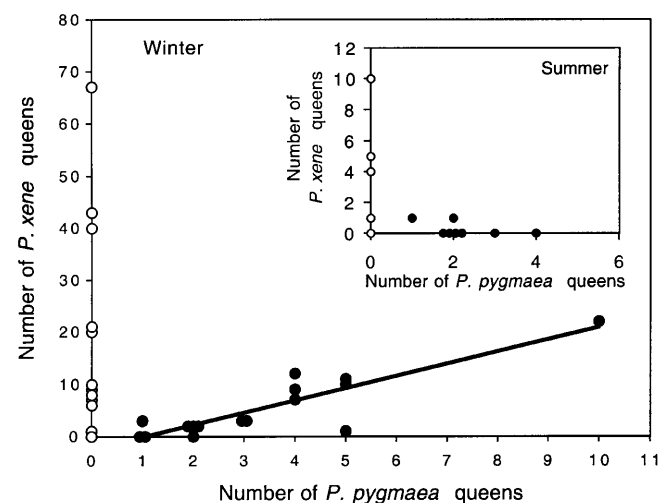


Figure 1. Distribution of the number of parasitic queens *P. xene* (white dots) per nest of its host *P. pygmaea* as functions of the number of host queens (black dots) in the nests, in the winter. Linear regression on queenright nests: $y = 2.33x - 2.43$, $r^2 = 0.77$, $n = 16$, $p < 0.001$. Inset: same situation in colonies excavated in summer ($r^2 = 0.27$, $n = 8$, $p = 0.184$)

Worker production in field colonies

No difference occurred in the number of workers produced between nests belonging to unparasitized (median: 30.5, interquartile range: 58.5) and parasitized colonies (median: 53, interquartile range: 31.2) (Mann-Whitney test, $U = 106.5$, $p = 0.43$). The comparison between the number of worker cocoons reared in nests uninhabited and inhabited by the *P. xene* queens in the 3 parasitized colonies confirmed this result (unparasitized nests: median: 59, interquartile range: 32.75; parasitized nests: median: 45, interquartile range: 26.75) (Mann-Whitney test, $U = 24.0$, $p = 0.44$). Thus, the presence of the inquiline parasite *P. xene* does not alter the rearing of new cohorts of workers in natural colonies of *P. pygmaea*.

Egg production in experimental units

Far more eggs laid by the *P. pygmaea* queen were collected in unparasitized units ($X \pm SD = 68.3 \pm 40.3$, $n = 9$) than in parasitized ones ($X \pm SD = 1.5 \pm 1.3$, $n = 11$) (Mann-Whitney test, $U = 0.0$, $p < 0.001$; Fig. 2). Three explanations may account for such a difference in the production of eggs in the presence and absence of the parasite: (1) egg laying of

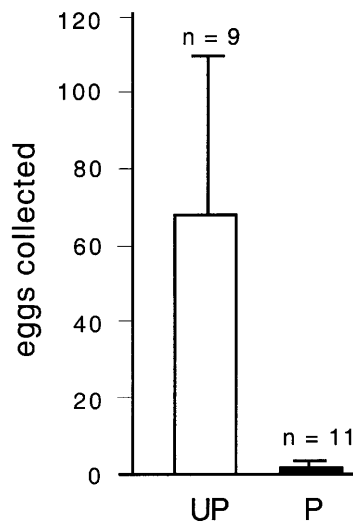


Figure 2. Mean number \pm S.D. of eggs laid by *P. pygmaea* queens in unparasitized (UP) and parasitized (P) experimental units. n: number of experimental units

P. pygmaea queens is inhibited by the parasite, (2) part of food is given to the parasites, so that host queens would be starved and therefore less fertile, or (3) eggs of *P. pygmaea* are eaten by *P. xene* (oophagy).

All the ovarian parameters assessed after dissection showed that vitellogenesis was similar for *P. pygmaea* queens reared in parasitized and unparasitized units (Table 1). Neither the number of developing oocytes, nor the number of *corpora lutea*, the length of the largest oocyte or the length of the longest ovariole differed significantly between both treatments. Differences in egg production may thus not be explained by an inhibition of vitellogenesis in the host queens by the parasite *P. xene*. The absence of difference in ovarian parameters (especially concerning the number of developing oocytes, the number of *corpora lutea* and the length of the longest ovariole) also makes very unlikely the hypothesis of a reduction of host queens fertility due to starvation in parasitized units.

From the 15 eggs of *P. pygmaea* introduced in the experimental units, the number of eggs still present after 3 or 4 days in parasitized units ($X \pm SD = 2.7 \pm 2.1$, $n = 9$) was significantly lower than that found in control, unparasitized units ($X \pm SD = 12.4 \pm 1.8$, $n = 5$) (Mann-Whitney test, $U = 0.0$, $p < 0.003$; Fig. 3). These data indicate oophagy by the parasite queens and are in agreement with laboratory observations. At several occasions, the queens of *P. xene* were seen

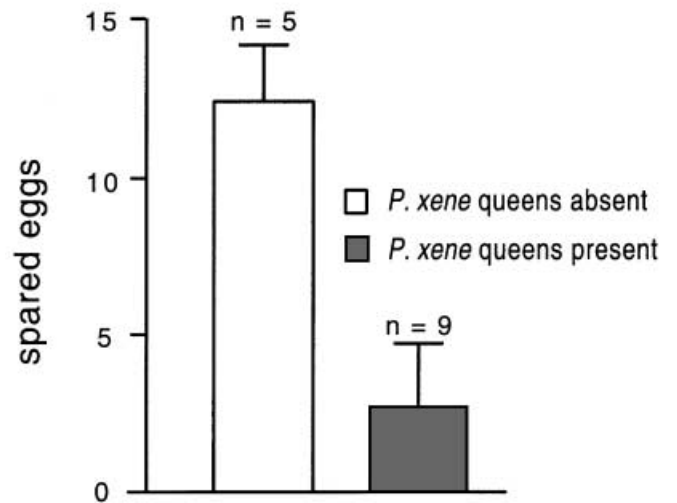


Figure 3. Fifteen eggs of the queen host were introduced into experimental parasitized or unparasitized units of orphaned workers. Bars showed the number of eggs found in the experimental units 3 or 4 days later (means \pm S.D.). n = sample size

Table 1. Mean number \pm S.D. of developing oocytes and *corpora lutea* at the base of the ovariole, and mean length \pm S.D. of the largest oocyte and the longest ovariole in queens of *P. pygmaea* heading colonies parasitized or unparasitized by the workerless inquiline ant *P. xene*. n = sample size

	Parasitized units (n = 15)	Unparasitized units (n = 10)	t-test
No. of developing oocytes	17.4 \pm 5.3	15.2 \pm 5.4	t = 1.8, p > 0.25
No. of <i>corpora lutea</i>	9.2 \pm 1.8	9.3 \pm 2.2	t = 0.7, p > 0.90
Length of largest oocyte	0.39 \pm 0.03	0.36 \pm 0.08	t = 1.63, p > 0.10
Length of longest ovariole	4.11 \pm 0.5	4.57 \pm 1.6	t = 0.81, p > 0.40

devouring *P. pygmaea* eggs and chorions of empty eggs were frequent on the egg pile. On the contrary, aggression of larvae or cocoons of *P. pygmaea* by the parasite was never observed.

Discussion

To the best of our knowledge, this study is the first to investigate the effect of an inquiline parasite on the spatial distribution of the host queens within natural colonies of ants. Given the scarcity of the parasite and the polydomous structure of host colonies, our data were based on a large number of nests from a limited number of colonies. Our results show that the workerless inquiline parasite *Plagiolepis xene* affects the distribution of the host queens within colonies of *P. pygmaea*. In winter, before host colonies undergo their seasonal cycle of subdivision and queens spread out among the colony subunits and resume egg-laying, host queens show a clumped distribution and the greater part of them still share the same nests with their parasites. This aggregative trend also occurs in *P. xene*. The larger the number of host queens in queenright nesting units, the larger the number of parasites found in the same unit.

The small number of parasitized colonies found in summer (see methods) did not allow to compare accurately host queen distribution between infested and uninfested *P. pygmaea* colonies. However, our data indicate that at this period of the year, i.e. at the peak of egg-laying, a behavioral shift occurs with most of the queens of the two species living apart in distinct nests. First, no relationship occurred between the number of parasites and the number of host queens in queenright nests. Second, the proportion of queenright nests parasitized was dramatically lower than in the winter. Two interpretations may account for the segregation of the host and parasite queens in different nests at the time of egg-laying: (i) segregation of queens could merely result from the natural dispersion of the hosts into the numerous nests following colony subdivision in spring; (ii) segregation could be induced by the presence of the parasite, that is, host queens could flee from parasitized nests. Both processes may have generated a distribution pattern such as observed in our data and their respective influence is difficult to discriminate. However, the lower proportion of queenright nests parasitized in summer (Fig. 1) indicates that the hypothesis of parasite avoidance may not be ruled out, but the question remains open. In particular, the proximate mechanisms by which host queens are able to detect the presence of the inquilines remain unknown. Previous experiments have shown that host workers are unable to recognize and eliminate the brood of the inquiline (Aron et al., 1999). On the other hand, attempts to introduce virgin or newly mated queens of *P. xene* into host colonies, parasitized or not, always resulted in killing of the parasite (Passera, 1964).

The segregation of the host and parasite queens in different nests at the time of egg-laying may have important consequences on worker production and ultimately colony growth and reproduction. Previous studies showed that queenright cultures of *P. pygmaea* containing queens of their

social parasite *P. xene* are subjected to a strong decrease in the production of new host workers, with parasitized cultures producing 6–7 times less worker cocoons than unparasitized ones (Passera, 1972). These results are consistent with those reported here showing that eggs are far less numerous in parasitized than in unparasitized experimental units. Such a difference does not result from the parasitic queens preventing or repressing egg-laying by the host. Investigation of ovarian activity indeed revealed that egg production proceeds as in queens reared in unparasitized units. Rather, the disappearance of the eggs in parasitized units is clearly due to oophagy by queens of the parasite. Oophagy of the host eggs is therefore most likely a prime factor responsible for the decrease of worker production in laboratory colonies of *P. pygmaea*. Interestingly, worker production was not different between parasitized and unparasitized colonies under natural conditions. This suggests that most of the eggs laid by host queens are spared from oophagy in parasitized field colonies. The absence of oophagy under natural conditions probably results from queens being physically separated from the parasite at the time of egg-laying. Cannibalism of larvae or pupae of the host by the parasite was never observed. Although this possibility may not be completely excluded, the fact that as many pupae of the host were reared in nests inhabited by the parasite as in those free of parasite in parasitized colonies suggest that it probably rarely occurs. A few other examples are known in which the inquiline queens eat eggs laid by the host queen(s). Females of the workerless parasite *Doronomyrmex (Leptothorax) kutteri* were seen to eat eggs of its host *Leptothorax acervorum* (Kutter, 1969; Franks et al., 1990). Haskins and Haskins (1964) showed that in colonies of *Myrmecia vindex* parasitized by the inquiline ant *M. inquilina*, all host brood disappeared after several months and only sexuals of the parasite were reared. This was believed to result from oophagy by the parasitic queen, but there was not direct evidence for that assertion. In this species, however, parasitized field nests produce host workers. The authors hypothesized that the production of host workers in the field resulted from the ability of the host queen to move away from the parasite in order to protect their eggs from oophagy. The inquiline ant *Solenopsis daguerrei* steals the food offered to the host queen *S. richteri*, leading to a decline in egg production and depopulation of the host colonies (Silveira-Guido et al., 1973; Calcaterra et al., 1999). Thus, even when inquiline ants do not execute the host queen, they may strongly reduce colony growth.

It is noteworthy that in all parasitic ant species mentioned above, female sexuals leave the mother nest on their own at sexual maturity and disperse by flight to reproduce before they infiltrate new host colonies (*M. inquilina*: Haskins and Haskins, 1964; *D. kutteri*: Buschinger, 1965; *S. daguerrei*: Silveira-Guido et al., 1965). Thus, dispersal of the parasites does not involve host workers. This contrasts with *P. xene*, in which dispersal of the newly mated queens is strongly dependent on the host workers since the young parasitic queens dealate in the nest where they mate, then follow workers and host queens leaving the mother nest to establish a new colony by budding (Passera, 1964). Dispersal on the wing is excep-

tional in this species (Espadaler and Lopez-Soria, 1991). Breeding and dispersal of the parasite therefore require a large worker force. Since budding occurs only when the colony produces many new host queens (Passera, 1969), reproductive success of the parasite is linked to the reproductive success of the host species.

The oophagy exhibited by *P. xene* may seem odd at a first sight because it appears to conflict with the interests of the parasite, which benefits from long-lasting supply of host workers. However, eggs eaten by the parasite does not comprise an essential nutritional element of its diet (see methods), as is the case for other inquiline species such as *Myrmecia inquilina* (Haskins and Haskins, 1964). It has been shown that queenless colonies of *P. pygmaea* containing *P. xene* and fed exclusively with honey, produced new sexuals of the parasite without difficulty (Passera, 1964, 1969). Oophagy of *P. pygmaea* eggs could therefore be more directed to decrease the competition for food between larvae of both species than to feed the parasite. Furthermore, at the time of egg-laying the host and parasite queens are scattered in different nests, so that oophagy occurs locally in some nests and does not weaken much the worker force of the colony.

Overall, this study shows that queens of the parasite *P. xene* eat the eggs of their host *P. pygmaea*, resulting in a decrease of worker production in parasitized nests under laboratory conditions. By contrast, no difference occurred in the number of workers produced between parasitized and unparasitized field colonies. Our field data strongly suggest that such a difference stems from the spatial distribution of both species under natural conditions. They indicate that queen distribution among nests of the polydomous host *P. pygmaea* is influenced by the presence of the inquiline parasite *P. xene*, with host and parasite queens segregating in different nests at the time of egg-laying. The proximate mechanisms involved in this process remain unknown. Further studies aimed at determining how host queens are able to detect the presence of the inquilines, if parasite colonies escape some costs by increased budding and whether infected colonies comprise a higher number of nests units are needed to settle this issue.

Acknowledgements

We thank E.L. Vargo, V. Fourcassié, Y. Roisin and J. Lauga for their comments on a first draft of the manuscript. Two anonymous reviewers provided constructive criticisms on a previous version of the manuscript. Special thanks to P. Bouissou for his help during the collection of the colonies used in this study. This work was partly supported by a FNRS research grant no. 1502299 to S. Aron, a FRIA grant to M. Gilbert and Tournesol exchange programme no. 00/002 to S. Aron and L. Passera.

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