



Regulation of worker egg laying by larvae in a fission-performing ant



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Ants provide one of the best examples of the division of labour in animal societies. In many species, although workers still have ovaries, they refrain from laying (haploid) eggs when a queen is present in the colony and, instead, dedicate themselves exclusively to domestic tasks. In monogynous species, workers generally begin laying eggs once the queen dies, which allows the colony's remaining resources to be invested in the workers' offspring. However, we found that in the fission-performing ant *Aphaenogaster senilis*, worker reproduction was also inhibited by brood pheromones; the presence of larvae, irrespective of their ploidy or origin, inhibited egg laying by orphaned workers in a dose-dependent manner. The end result was that workers allocated resources to the larvae that were present in the colony before starting to lay their own eggs. We also found that, while the number of workers reared was proportional to the number of larvae provided, the number of queens reared tended to plateau at six, regardless of the number of totipotent larvae present. This finding concurs with what has been observed in colonies in the field and fits with what the theory of local resource competition predicts. One explanation is that one of the queens produced is likely to mate and replace her dead mother as the head of the colony. Therefore, by rearing the queen's brood after her death, workers may have an opportunity to prolong the life of the colony.

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The evolution of reproductive division of labour marks the transition from solitary to social life (Buss, 1987; Chapuisat, 2010; Field, Paxton, Soro, & Bridge, 2010; Maynard Smith & Szathmari, 1997; Simpson, 2011). Particularly intriguing is the way in which individuals transmit information about their physiological condition and reproductive potential; by so doing, they influence collective decisions. Colonies of social hymenopterans (ants as well as some bees and wasps) are excellent model systems for studying this phenomenon. Their queens and workers are adapted to carry out highly specialized tasks. While the former have efficient reproductive systems and spend much of their time laying eggs, the latter perform nonreproductive tasks and thus largely control resource allocation. By manipulating food availability and environmental conditions, workers can control whether diploid larvae develop into workers or queens (Oster & Wilson, 1978).

In many species, although workers cannot mate, they do have small ovarioles and can thus potentially lay haploid eggs that will develop into males. Yet, they generally refrain from doing so when a fertile queen is present in the colony (Hammond & Keller, 2004;

Wenseleers & Ratnieks, 2006). In addition, policing mechanisms prevent worker reproduction in queenright colonies (Beekman & Ratnieks, 2003; Ratnieks, 1988). These mechanisms include the selective removal of worker-laid eggs (D'Ettorre, Heinze, & Ratnieks, 2004; Foster & Ratnieks, 2001; Kikuta & Tsuji, 1999; Monnin & Peeters, 1997) and aggressive behaviour directed at egg-laying workers (Monnin & Ratnieks, 2001). These mechanisms are selected for because they enhance colony efficiency either because egg-laying workers spend less time caring for the brood or because they engage in conflicts (Foster & Ratnieks, 2001; Hammond & Keller, 2004; Hartmann, Wantia, Torres, & Heinze, 2003; Iwanishi, Hasegawa, & Ohkawara, 2003; Ohtsuki & Tsuji, 2009; Pirk, Neumann, & Ratnieks, 2003; Teseo, Kronauer, Jaisson, & Châline, 2013; Wenseleers & Ratnieks, 2006). For example, workers that reproduce have significantly shorter life spans than workers that do not reproduce (Tsuji, Kikuta, & Kikuchi, 2012). Moreover, in polyandrous species, workers are less related, genetically to other workers' sons than to the queen's sons (Ratnieks, 1988; Ratnieks & Wenseleers, 2008; Wenseleers & Ratnieks, 2006). Interestingly, it has been suggested that worker policing depends on colony demography and ontogeny (Ohtsuki & Tsuji, 2009). Hence, because worker egg laying in small colonies may hamper colony growth and future reproduction, there may be

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selection for both self-restraint and policing (Bonckaert, van Zweden, D'Ettoire, Billen, & Wenseleers, 2011; Moore & Liebig, 2010).

In many monogynous species, the queen's death puts an end to policing behaviour and triggers ovariole maturation and egg laying in workers (Bourke, 1988; Choe, 1990; Holman, Jørgensen, Nielsen, & d'Ettoire, 2010; Van Oystaeyen et al., 2014). This shift allows the colony to invest its remaining resources in producing workers' sons before it vanishes entirely (Hölldobler & Wilson, 1990). However, in some species that disperse through colony fission (or, more generally, through dependent colony founding), the dead queen may be replaced by one of her daughters (Boulay et al., 2007; Cronin, Molet, Doums, Monnin, & Peeters, 2013). In such species, queens do not participate in large nuptial flights; instead, they mate near the entrances of their nests. If the mother queen is still in the colony, the newly mated queen leaves with a group of workers to create a new colony (walking distance away). However, if the mother queen is dead, the newly mated queen can replace her as the head of the colony. Thus, in fission-performing ants, the life span of the colony may be much longer than that of the queen, provided a replacement queen is produced rapidly enough after the death of the current queen (Bourke & Franks, 1995). In such species, one may expect orphaned workers to allocate resources to the remaining diploid brood so as to produce a few replacement queens (an excessive number would be useless and only increase local resource competition) and as many workers as possible to guarantee colony survival (Bourke & Franks, 1995; Cronin et al., 2013; Pamilo, 1991; Percy & Aron, 2006), even though this investment comes at the expense of laying their own male eggs.

Using a fission-performing ant species, *Aphaenogaster senilis*, we examined the collective reproductive decisions of orphaned workers in relation to the presence of totipotent larvae. In this species, the queen signals her presence to workers by means of contact pheromones (Ruel, Hefetz, Cerdá, & Boulay, 2013). When the workers perceive this signal, they refrain from laying eggs and rear almost all young larvae as workers (Boulay, Cerda, Fertin, Ichinose, & Lenoir, 2009; Boulay et al., 2007). However, if the queen disappears, workers rear a few larvae as new queens, which allows requeening (Chéron, Doums, Federici, & Monnin, 2009). The mechanism of larval caste determination is unknown in this species but probably involves nutritional and hormonal factors (Barroso, Amor, Cerdá, & Boulay, 2013; Ledoux, 1977). To investigate a trade-off between egg laying by orphaned workers and raising already existing larvae to adulthood, we sought to answer the following questions. First, we asked whether larvae number affected larval fate and/or egg laying by workers in queenless colonies. To date, the presence of larvae has been shown to inhibit egg laying by workers in two ant species, *Cerapachys biroi* (Teseo et al., 2013) and *Pachycondyla villosa* (Heinze, Trunzer, Oliveira, & Hölldobler, 1996), and in the honeybee *Apis mellifera* (Arnold et al., 1994; Mohammedi, Paris, Crauser, & Le Conte, 1998; Oldroyd, Wossler, & Ratnieks, 2001; Traynor, Le Conte, & Page, 2014). In *P. villosa*, young larvae were also observed eating worker-laid eggs (Heinze et al., 1996). Second, we asked whether worker-laid eggs suffered higher mortality in the presence of larvae, either directly as a result of larval predation or indirectly through worker policing. Third, we asked whether egg laying by workers was affected by the sex of the larvae. Male larvae might be predicted to have no effect on worker egg-laying decisions since males do not contribute to colony survival. Fourth, we asked whether young diploid larvae inhibited egg laying by workers via chemical signals. Thus far, most studies on reproductive inhibition in workers have focused on queen pheromones; larval pheromones have largely been ignored, particularly in ants. Finally, although orphaned workers may collectively decide to rear diploid larvae

before producing sons, some individuals might none the less selfishly lay eggs before all the larvae reach the pupal stage. Therefore, the fifth question we asked was whether orphaned workers punished potential cheaters when larvae were present. By answering this series of questions, we aimed to determine whether and how orphaned ant workers trade individual reproduction for raising existing larvae to adulthood and, potentially, to queens.

METHODS

Model Species and Rearing Conditions

Aphaenogaster senilis is a common species distributed along the western Mediterranean Basin. All the stock colonies used in this study were collected in Doñana National Park (southwestern Spain). In this area, colonies are active from March to December. At least three larval stages have been identified in this species (Boulay et al., 2009). All three stages are present in the colonies year round, but the first instars are more abundant from September to April and the second and third instars from March to July. New workers are produced from May to November (Boulay et al., 2009). Males are produced in large numbers in colonies with more than 500 workers; this process occurs mostly in the summer, although males can be found until November. Virgin queens are produced in much smaller numbers. They can be found in queenless colonies throughout the year and in large queenright colonies (of greater than 2000 workers) in July and August (Boulay et al., 2007).

Each colony used in this study had a queen and 1000–2500 workers. They were housed in plastic boxes (dimensions: 13 × 32 cm and 15 cm high) that contained three or four test tubes (dimensions: 2 × 20 cm). The groups used in the following experiments were placed in test tubes half filled with water blocked by a cotton plug. The test tubes were connected to a 9 × 9 cm circular arena, whose inner walls had been coated with Fluon to prevent ants from escaping. Both the stock colonies and the experimental groups were kept at 25 ± 1 °C and fed mealworms, *Tenebrio molitor*, twice a week. Under these laboratory conditions, colonies continually produced worker pupae but only rarely generated males. Experiments 1, 2, 3 and 5 were conducted using colonies that had been kept in the laboratory for 2–5 months. Experiment 4 was conducted using colonies that had been kept in the laboratory for 3 months to 2 years.

Experiments

The first experiment aimed to determine whether orphaned workers delayed producing their own sons because of the presence of queen-derived larvae. Five queenless groups composed of 200 workers were created from each of 10 large stock colonies. The groups received 160, 120, 60, 20 or no first-instar larvae from the same stock colonies. They were all checked 24 h after set-up to confirm that no eggs had been introduced unintentionally. The experimental groups were then kept in the above-mentioned rearing conditions. The groups were checked three times a week for 11 weeks; all the pupae produced were collected, and their sex and caste were determined. Worker-laid eggs and surviving workers were counted at weeks 7 and 11. This experiment was conducted in November 2011 with colonies collected 2 months earlier.

The second experiment aimed to determine whether the larvae directly or indirectly increased the mortality of worker-laid eggs. Three experimental groups of 50 workers were created from each of 15 stock colonies. The first group received 30 freshly laid workers' eggs and 60 first-instar larvae from the same stock colony, the second group received 30 freshly laid workers' eggs but no

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