



## Social parasite pressure affects brood discrimination of host species in *Temnothorax* ants

Olivier Delattre\*, Nicolas Châline, Stéphane Chaméron, Emmanuel Lecoutey, Pierre Jaisson

Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris 13, Villetaneuse, France

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Social parasites exploit complete societies, on which they are dependent. In ants, slave-making species invade, exploit and raid host colonies, impacting their survival and exerting powerful selection pressure on their host species. Recent studies suggest that host ant species may develop a parasite brood intolerance, which could be the first step of a slave rebellion in parasitized colonies. However, enslaved workers of slave-making ants not only raise and feed their parasites, but also accept alien conspecific brood brought during seasonal raids. We compared the agonistic and grooming behaviour (a sign of brood integration) of two sympatric nonhost species (one showing intraspecific parasitism) and of enslaved and free-living host species confronted with alien conspecific worker pupae to assess whether parasite pressure could have decreased brood tolerance in host species. Free-living colonies of species suffering from interspecific or intraspecific parasitism were more aggressive and performed less grooming towards alien conspecific brood than colonies of nonhost species. Moreover, slave workers were not more aggressive towards alien parasites than towards alien conspecific brood but groomed alien parasites more than alien conspecific brood. We discuss how host–parasite coevolution could impact the social recognition mechanisms in host species.

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Interspecific interactions can often lead to coevolutionary 'arms races' (Van Valen 1973; Thompson 1999) in which two or more species directly influence the evolution of each other's life history traits. Adaptations and counteradaptations in response to the reciprocal selection pressures then allow each interacting species to keep up with its opponent (Thompson 1994). Host–parasite interactions are a prime example of how this coevolutionary process may affect the evolution of species, as they result in a mosaic of local adaptations (Thompson 1994). Numerous studies on avian brood parasites, such as cuckoos and cowbirds, which replace their host brood by their own, have shown that host species' counteradaptations are often selected in order to avoid nest parasitism (Rothstein & Robinson 1998; Kruger 2007). Some cuckoo's host species, for example, display more aggressiveness towards parasite than towards nonparasite dummies (Moksnes et al. 1991), or are more aggressive if the parasitism rate is high (Robertson & Norman 1976; Davies et al. 2003). Interspecific social parasitism is another form of parasitism in which two species of social insects coexist in the same nest, one of which is dependent

on the other (Hölldobler & Wilson 1990). In these social parasite species, parasite queens enter the hosts' nests to usurp the host queen, using behavioural and chemical strategies such as appeasement allomones, which reduce aggressiveness from host workers (Lenoir et al. 2001). Afterwards, parasite queens lay eggs that are reared by host workers as if they were related nestmates. Some parasite species, known as dulotic or slave-making ants (Wilson 1975), also conduct periodic raids to steal brood from neighbouring colonies to replenish the enslaved colony labour force (d'Ettorre & Heinze 2001; Mori et al. 2001; Brandt et al. 2005). These ants are obligatory social parasites in which the survival of colonies is dependent on the presence of slave workers (Buschinger 1986; Savolainen & Deslippe 1996). Because invasions and raids impact the targeted colonies' survival (Foitzik & Herbers 2001; Hare & Alloway 2001; Bono et al. 2006a, b; Johnson & Herbers 2006), slave-making ants exert selection pressure on host species that is likely to select for the evolution of defensive traits (Alloway 1990; Foitzik et al. 2001; Blatrix & Herbers 2003; Brandt & Foitzik 2004; d'Ettorre et al. 2004; Achenbach & Foitzik 2009; Tamarri et al. 2009; Scharf et al. 2011).

In ant societies, the first step in withstanding the parasite pressure of dulotic ants could be the closure of potential host colonies. Ants rely on chemical cues, especially cuticular hydrocarbons, to discriminate nestmates from non-nestmates (d'Ettorre & Lenoir 2009). Nestmates share a colonial 'label' that results

\* Correspondence: O. Delattre, Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris 13, 99 avenue Jean-Baptiste Clément, 93430 Villetaneuse, France.

E-mail address: [olivier.delattre@leec.univ-paris13.fr](mailto:olivier.delattre@leec.univ-paris13.fr) (O. Delattre).

from the homogenization of individual odorant chemicals (mainly influenced by each ant's genome, environment and metabolic activity) by constant interindividual exchanges through grooming and trophallaxis (Stuart 1988; Vienne et al. 1995; Boulay et al. 2000). The colonial label is thought to act as a template, ants being considered as nestmates or aliens depending on their odour being, respectively, similar to or different from it (Reeve 1989; d'Ettorre & Lenoir 2009). Nestmate recognition allows ants to restrict affiliative behaviours to nestmates and to reject aliens. However, social parasites have developed physiological and behavioural adaptations to fool the discrimination abilities of host species (Lenoir et al. 2001). For example, parasites can display chemical profiles similar to those of their hosts (Franks et al. 1990; Kaib et al. 1993), with quantitative adjustments depending on the host species (Bonavita-Cougourdan et al. 1997). In that case, host species cannot discriminate parasites from nestmates except by developing a more restrictive tolerance threshold through local adaptation (Reeve 1989). However, such a shift in the threshold could lead to rejection errors, where ants reject nestmates whose cuticular profiles diverge slightly from the colonial label. Host species thus face a trade-off between the costs and benefits of various recognition errors, which will tip the balance between tolerance threshold adjustments according to the level of evolutionary pressure at stake (Reeve 1989).

A second line of defence could also theoretically stem from the enslaved workers' behaviour. Enslaved ants could indeed 'rebel', with at least three available options (Gladstone 1981). First, they could leave the parasite colony and go back to their nest. Second, they could refuse to work in the parasitized society, or just leave it. Last, they could engage in male production within the parasite nest. All three options have been considered before, and researchers have concluded on both theoretical and empirical grounds that no selection pressure could easily lead to the propagation of such 'rebel behaviour' in a host population (Gladstone 1981). Another neglected possibility has recently been proposed, which consists in enslaved workers destroying parasite brood, or indirectly affecting its probability of survival because of poor care (Achenbach & Foitzik 2009). Achenbach & Foitzik (2009) experimentally demonstrated that some host species of *Temnothorax* ants indeed selectively destroyed parasite brood in parasitized colonies of *Protomognathus americanus*. They proposed that such behaviour could directly impact the growth and survival of the parasite society, therefore decreasing the parasite pressure on the neighbouring host colonies. This could indirectly increase the inclusive fitness of slaves if their relatedness with free-living hosts from the surrounding nests is high (Achenbach & Foitzik 2009).

Selective destruction of parasite brood means that host species' workers can discriminate parasite offspring inside a parasitized colony (Johnson et al. 2005; Achenbach et al. 2010). Such discrimination of parasite brood by enslaved workers is highly unlikely, as ants learn their colonial template during the days following emergence (Jaisson 1975; Jaisson & Fresneau 1978). Therefore pillaged brood emerging inside the parasitized colony should develop a recognition template that includes parasite species-specific cues, which could explain why slave workers care for parasite brood (Le Moli & Mori 1987). Moreover, parasite brood may be attractive for their host species because of close phylogenetic relationship, brood mimicry and the possible existence of an attractiveness pheromone (Mori et al. 1996; Johnson 2000). Consequently, it may be difficult for slave workers to discriminate and destroy parasite brood, unless host species develop original recognition mechanisms. For example, discrimination could rely on specialized sensory sensillae on the antennae that respond only to species-specific parasite cuticular hydrocarbons (Hansson 1999). Another hypothesis would imply a prominent influence of

preimaginal learning (Isingrini et al. 1985) or genetic factors (Grafen 1990; El-Showk et al. 2010) during the template formation process in host species. Since slavemaker ants focus on pupae during raids (Buschinger et al. 1980), both mechanisms would minimize the impact of postemergence experience on template formation, in the parasitized nest, therefore enhancing discrimination of heterospecific (and maybe conspecific) non-nestmates. Rejections may also be the result of a lower colonial tolerance threshold, either as a consequence of previous encounters with parasite workers (Pamminger et al. 2011) or as a product of the selection of a more restrictive threshold in parasitized populations of host species (Fürst et al. 2012). With a more restrictive tolerance threshold (Reeve 1989), host workers would be aggressive even towards conspecific raided brood. In that case, raided brood from neighbouring host colonies may not reach emergence if rejected by slave workers, thereby reducing parasitized colonies' fitness as well.

We investigated how parasite pressure could affect conspecific brood discrimination in a *Temnothorax* host species of the European slave-making ant *Myrmoxenus ravouxi*. We expected the tuning of recognition systems to have evolved differently in sympatric species of a slave-making ant, that is, host species workers should be less tolerant to non-nestmate brood than those of the nonhost species. Therefore we compared brood discrimination of one sympatric *Temnothorax* host and two sympatric nonhost species of the dulotic social parasite *M. ravouxi*.

## METHODS

### Ethical Note

No specific permits were required for the study. *Myrmoxenus ravouxi* is listed as a vulnerable species by the IUCN, but is not a protected species in France, except in protected areas where no ants can be collected. The sites where we collected our species were not privately owned or protected in any way.

### Species

*Myrmoxenus ravouxi* is found widely in Europe (Buschinger 1997), where parasite workers conduct raids periodically at the beginning of the summer. It is a very opportunistic parasite (Buschinger 1989; Seifert 2007), using different species as hosts (*Temnothorax unifasciatus*, *Temnothorax nigriceps*, *Temnothorax affinis*, *Temnothorax rabaudi* and some others). All *M. ravouxi* parasite colonies collected in our study had *T. unifasciatus* as hosts, even if free-living (i.e. unparasitized) colonies of *T. rabaudi* were also found in the study collection site. We also collected two other species that often live in sympatry but are never used as hosts: *Temnothorax parvulus* and *Temnothorax nylanderi* (Buschinger 1989). The latter suffers from chronic intraspecific parasitism, maybe because of competition for nest sites (Foitzik & Heinze 1998, 2000). We did not perform genetic analyses on our colonies of *T. nylanderi* from the Fontainebleau site to test for effective intraspecific parasitism. None the less, the colony density was high with approximately two colonies per m<sup>2</sup>. Moreover, *T. nylanderi* was the only *Temnothorax* species found in the collection site in dead tree branches. In such a population, colony invasions and fusions are likely to occur as the result of competition for nest sites. Intraspecific or interspecific parasitism has not yet been reported in *T. parvulus* (Buschinger 1997); therefore, we assumed that this species does not experience social parasitism. *Temnothorax parvulus* was particularly interesting to consider in our study since it is one of the more common sympatric nonhost species of *M. ravouxi*.

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