RESEARCH ARTICLE

Opportunist slave-making ants *Myrmoxenus ravouxi* discriminate different host species from a non-host species

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Abstract Slave-making ants exploit the worker force of host colonies permanently and have to make recurrent raids in order to replenish the slave's stock. Some of these parasite species exploit different host species and few studies so far have been devoted to host species recognition mechanisms. Here, we tried to determine if opportunist slave-making ants using different host species rely on innate or experience-induced preferences to discriminate host from non-host species. We show that *Myrmoxenus ravouxi* slave-making workers are not only more aggressive toward heterocolonial host and potential host species workers when compared with non-host species workers, but also toward heterocolonial host workers than toward heterocolonial conspecifics. Moreover, *M. ravouxi* workers display more antennations and contacts toward the heterocolonial host species when compared with the non-host species. We also show that they do not discriminate between homocolonial and heterocolonial conspecifics. Together, our results suggest that this opportunistic slave-making ant species may have a complex social recognition template based on both innate and experience-based mechanisms.

Keywords Social parasitism · Slave-making ants ·
Social recognition · *Temnothorax* · Coevolution

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Introduction

Slave-making ants invade and periodically raid neighboring colonies of their host species to pillage their brood (Buschinger, 1986, 2009), creating "chimeric" societies of two or more species. With a lifespan of sometimes more than 10 years, these colonies may comprise individuals from different colonies and/or species with no overt conflict. The slave brood is brought back from raided host colonies, following a typical behavioral sequence (Buschinger et al., 1980).

For example, in the slave-making ant *Myrmoxenus ravouxi*, around the end of spring, parasite workers prospect around the nest until they find a host colony. Then, when a scout is successful, it returns to its nest and stimulates her parasite nestmates. This "group recruitment" will launch the raid itself (Winter, 1979). After almost all defenders have fled or have been killed by the parasite workers, the members of the parasite colony (both parasites and slaves) take the brood and bring it back to their nest, where it will emerge. *M. ravouxi* is an opportunistic slave-maker parasitizing more than five *Temnothorax* species (Buschinger and Winter, 1983; Buschinger, 1989, 1997; Seifert, 2007). Such a strategy could represent an adaptive advantage for the parasite, thus accounting for the wider repartition area of *M. ravouxi* within its genus (Buschinger, 1997; Seifert, 2007). Yet, it is still crucial for a slave-making worker to recognize its different host from the non-host species during raids. Indeed, workers from non-host species, more distant phylogenetically (Emery, 1909; Beibl et al., 2005), may not be suitable nurses for the parasite brood. This could increase the mortality rate and impact the parasitized colonies' fitness. Moreover, non-host defenses may be more difficult to overcome for parasite workers, as social parasites often exhibit specific adaptations to their host species (Lenoir et al., 2001; Foitzik et al., 2001,

2003; Brandt and Foitzik, 2004). Therefore, discrimination abilities in parasite species between potential hosts and other species are likely to evolve to be more efficient to discriminate suitable host species.

Members of a colony use a neural template of a common colonial label, which is learned as early as the pre-imaginal development phase in ants (Isingrini et al., 1985), to discriminate nestmates from aliens (Lenoir et al., 1999). Inside the colony, individual chemical cues are blended together in the common label via allogrooming, passive contacts and trophallaxis (Soroker et al., 1994, 2003). This mechanism has been termed the "Gestalt" model by Crozier and Dix (1979).

Experiments with artificial mixed-species colonies of ants have shown that workers were less agressive toward non-nestmates when their colonial odor was more complex (Errard, 1994; Errard et al., 2006). This has been attributed to the fact that a richer colonial label leads ants to form a broader recognition template that increases their tolerance threshold, leading to more frequent acceptance errors (Reeve, 1989; Errard et al., 2006). Slave workers raise and feed parasite brood until their emergence and forage for the entire colony, while slave-making workers are most of the time inactive inside the nest (Buschinger, 1986). Emerging parasite workers may thus learn the colonial label essentially from the interactions with their slave workers. They may develop also a larger colonial template which reduces their ability to discriminate their host from their own species (Errard, 1994; Errard et al., 2006).

Myrmoxenus ravouxi often lives in areas where different host species are present. Nonetheless, parasitized colonies with more than one enslaved species are rare and we do not know if this is because the pillaged brood from a different host species is destroyed by slaves or if parasite workers exclusively raid neighboring colonies of the imprinted host species. Indeed, we know that the species of the actual slave workers may influence slave-maker workers behavior, since expressed preferences for a more common host in a population may yield to adaptive plasticity, particularly during raids (Schumann and Buschinger, 1995). Nonetheless, the authors of this study also demonstrated that workers from the slave-making ant *Chalepoxenus muellerianus*, enslaving two different host species, displayed an innate preference toward their main host species, irrespective of the species they were reared with.

In this experiment, we chose to test if a highly opportunist slave-making parasite was able to discriminate between non-host, potential host, host and parasite workers (homo or heterocolonial for the last two) to assess if these social parasites rely on innate or experience-induced preferences to discriminate their host species and raid neighboring colonies.

We studied whether *M. ravouxi* could discriminate (1) between a familiar (actual) and non-familiar host species and (2) between a potential (unfamiliar) host species and a non-host species. We monitored slave-making workers' aggressiveness and affiliative behaviors, such as antennations and contacts, to test for host species discrimination when different social stimuli were presented. We also tested whether *M. ravouxi* workers exhibited a different behavior toward their own species. Indeed, the Gestalt model predicts that the colonial odor will be homogenized in a mixed-species colony, making species discrimination difficult (Errard, 1994; Errard and Hefetz, 1997; Errard et al., 2006). However, the behavioral repertoire and the role of slaves and slave makers in parasitized colonies are very different (Buschinger and Winter, 1983; Buschinger, 1986) and species recognition in this context could allow better productivity of parasitized colonies, which could for example increase raid efficiency.

Methods

Species

We chose *M. ravouxi* as our focal species. This species is a slave-making social parasite with a wide distribution in Europe ranging from France to Greece (Buschinger, 1997). It is known to parasitize several species of the diversified genus *Temnothorax* (Buschinger and Winter, 1983, Buschinger, 1989, Buschinger, 1997), among which are *Temnothorax unifasciatus* and *T. rabaudi*. We used the main host (*T. unifasciatus*) and a potential host species (*T. rabaudi*) from an *M. ravouxi* parasitized population to assess if the social parasite was able to discriminate between its host, a potential host and a non-host species (*T. nylanderi*).

We collected the parasite ($N = 12$), parasite-free host ($N = 14$), potential host ($N = 9$) and non-host ($N = 7$) colonies in Vaison-la-Romaine (44°14′N, 5°04′E) in August 2006. Colonies were reared at the laboratory in small plastic boxes ($15 \times 10 \times 5$ cm) with a plaster soil as foraging area, in a nest made from two microscope slides superimposed with a 1-mm free space between them. All colonies were fed once a week with honey and fruit flies. The experiments took place in the late spring, from May to June 2007, after a 3-month wintering period at 8 °C from December to March. The photoperiod was 12/12 h with a night temperature of 15 °C and a day temperature of 22 °C at the time of the experiment. The humidity was kept around 60 %.

Experimental design

We used dyadic presentations to test the discrimination abilities of *M. ravouxi* workers. These comparisons could be categorized in "nestmates versus non-nestmates" and "host versus non-host" recognition tasks (Table 1).

Table 1 Main results with sample sizes and significance degrees

		N	Antennation	Contact	Biting
Nestmates versus non-nestmates	Homocolonial parasite versus heterocolonial parasite	20	NS	NS	NS
	Homocolonial parasite versus homocolonial slave	15	NS	*	NS
	Heterocolonial parasite versus heterocolonial slave	18	NS	NS	*
Host versus non-host	Potential host versus unparasitized host	13	NS	NS	NS
	Non-host versus unparasitized host	13	***	***	*
	Non-host versus potential host	20	NS	NS	**

NS non-significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Our experimental device was a circular arena (3 cm diameter) where two workers (used as stimuli) were tied at opposite sides with a thin nylon filament between their head and thorax. To limit moves and reciprocal interactions, these workers were also anesthetized beforehand with carbon dioxide for 15 s. Then, we introduced a slave-making worker in the arena and covered the device with a thin glass slide. No ant was used for more than one test, as experimental focus or as social stimuli.

Behavioral observations

Our tests lasted for 10 min. We recorded mean antennation and close-contact durations, which we assume are representative, respectively, of the interest for the congener and affiliative behaviors. The intensity of the agonistic response of *M. ravouxi* workers during the tests was assessed using the mean duration of bites. Stinging was also observed but less often than bites, maybe because parasite workers preferentially display this behavior during raids. We discarded the tests were no contact occurred within 2 min.

Comparisons were performed using permutation tests for paired samples. All statistical tests were implemented with StatXact (Cytel Studio, version 8.0.0, 2007).

Results

Antennations

Myrmoxenus ravouxi workers antennated heterocolonial workers from the host species *T. unifasciatus* longer than workers from the non-host species *T. nylanderi* (Fig. 1; Permutation test; $t = -2.848$, $P = 4.8.10^{-4}$). Other comparisons were not statistically different ($P > 0.368$).

Contacts

Myrmoxenus ravouxi workers stayed more in contact with their parasite sisters than with their slaves (Fig. 2; Permutation test; $t = 2.384$, $P = 0.0134$). They also remained for
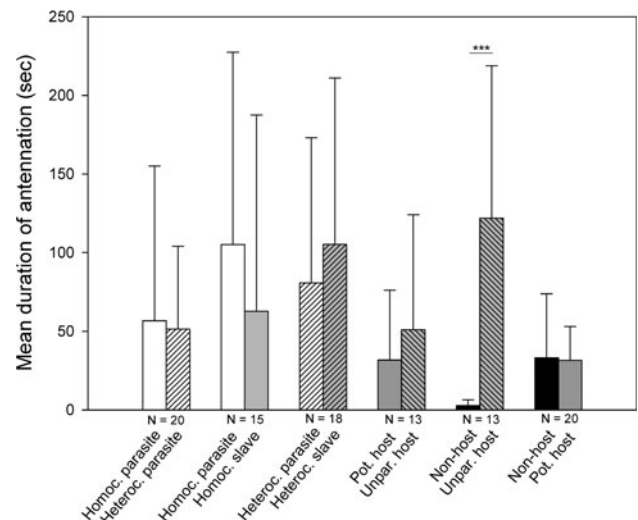

Fig. 1 Mean duration of antennation in seconds ($\pm$SE) of *M. ravouxi* workers during test choices with homocolonial and heterocolonial *M. ravouxi* parasites (Homoc. parasite and Heteroc. parasite), homocolonial and heterocolonial *T. unifasciatus* slaves (Homoc. and Heteroc. slaves), unparasitized *T. unifasciatus* hosts (Unpar. host), potential *T. rabaudi* hosts (Pot. host) and *T. nylanderi* non-hosts (Non-host). ***$P < 0.001$

more time in contact with heterocolonial free-living host workers from the host species *T. unifasciatus* than with workers from the non-host species *T. nylanderi* ($t = -2.169$, $P = 9.8.10^{-4}$). Other comparisons were not significant ($P > 0.127$).

Bites

Myrmoxenus ravouxi workers were more aggressive toward *T. unifasciatus* heterocolonial host workers than toward *M. ravouxi* heterocolonial parasite workers (Fig. 3; permutation test; $t = -1.831$, $P = 0.0312$). They also bit more *T. unifasciatus* heterocolonial host workers than *T. nylanderi* non-host workers ($t = -1.96$, $P = 0.0156$). Finally, they aggressed more workers from the potential host species *T. rabaudi* than workers from the non-host species *T. nylanderi* ($t = -2.198$, $P = 9.8.10^{-3}$). Other comparisons were not statistically different ($P > 0.125$).
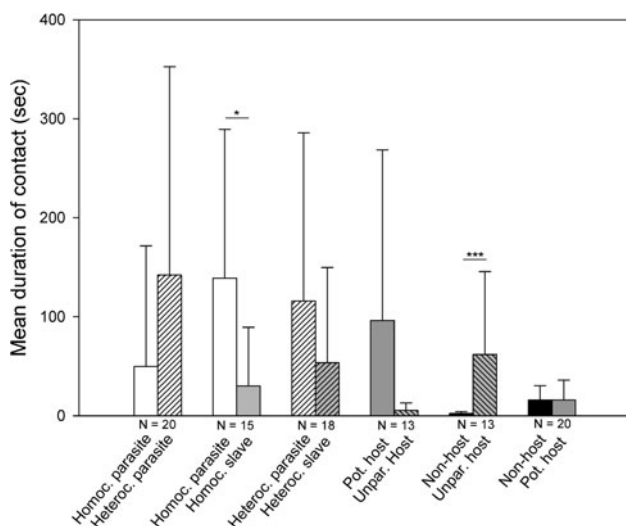
Fig. 2 Mean duration of contact in seconds (±SE) during test choices with homocolonial and heterocolonial *M. ravouxi* parasites (Homoc. parasite and Heteroc. parasite), homocolonial and heterocolonial *T. unifasciatus* slaves (Homoc. and Heteroc. slaves), unparasitized *T. unifasciatus* hosts (Unpar. host), potential *T. rabaudi* hosts (Pot. host) and *T. nylanderi* non-hosts (Non-host). *$P < 0.05$, ***$P < 0.001$
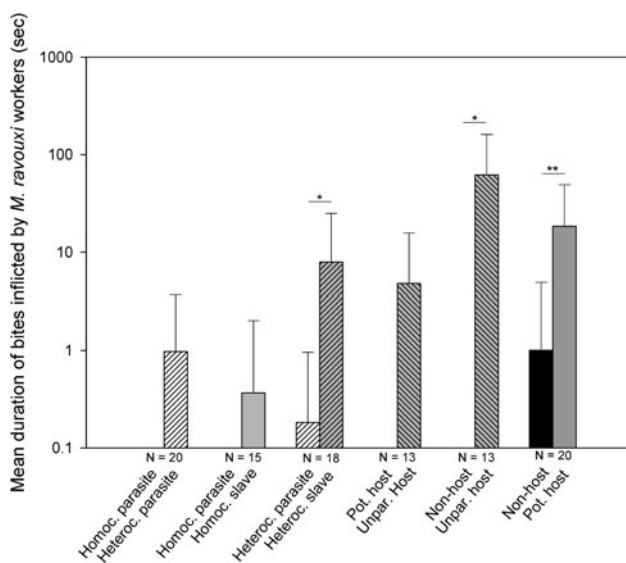

Fig. 3 Mean duration (logarithmic scale) of bites in seconds (±SE) during test choices with homocolonial and heterocolonial *M. ravouxi* parasites (Homoc. parasite and Heteroc. parasite), homocolonial and heterocolonial *T. unifasciatus* slaves (Homoc. and Heteroc. slaves), unparasitized *T. unifasciatus* hosts (Unpar. host), potential *T. rabaudi* hosts (Pot. host) and *T. nylanderi* non-hosts (Non-host). *$P < 0.05$, **$P < 0.01$

Table 1 summarizes our different results.

Discussion

In heterospecific encounters, slave-making workers displayed more aggressive behaviors against workers from host

and potential host species than against non-host workers. Moreover, parasite workers did not bite more workers from the host than from the potential host species. Taken together, these results suggest that *M. ravouxi* workers discriminate host species from non-host species, but not their host species from a potential host species. Our colonies were kept isolated in the laboratory from autumn to spring, so that no familiarization effect to any species could affect the behavioral response of our workers during the tests (Heinze et al., 1996; Knaden and Wehner, 2003; Sanada-Morimura et al., 2003). Therefore, *M. ravouxi* workers' discrimination between host—familiar or not—and non-host species is at least partially independent of previous experience.

Because slave-making ants depend on their host species during the entire colony's life, raids are necessary to replenish the worker force as the slave stock decreases with time. Thus, the selection pressure is strong on parasite societies to be able to find and pillage host colonies and to discriminate suitable host from non-host species (Foitzik et al., 2001, 2003; Hare and Alloway, 2001; Blatrix and Herbers, 2003; Brandt and Foitzik, 2004; Fischer and Foitzik, 2004; Brandt et al., 2005; Fischer-Blass et al., 2006). Therefore, a genetically based recognition template of potential hosts appears all the more adaptive than it can allow host shifting or raiding on different species according to the most commonly available host species. Indeed, *M. ravouxi* exploits at least six different hosts (Buschinger, 1989; Seifert, 2007). Phylogenetic data suggest that these host species are closely related to each other, and that the *Myrmoxenus* genus has already a long independent evolutionary history from the *Temnothorax* genus (Beibl et al., 2005). We can thus hypothesize that this slave-making species derived from and/or parasitized a common ancestor to its group of host species (Emery, 1909; Baur et al., 1995; Parker and Rissing, 2002; Sumner et al., 2004). These species may share some common cuticular compounds, which may be used by the slave maker to recognize them as potential hosts. Moreover, *M. ravouxi* olfactory system may have been selected for better discrimination of host species, as a consequence of a coevolutionary process (Thompson, 1994) between this slave-making ant and its host species. However, the fact that we recorded no difference in aggressiveness of *M. ravouxi* workers for the host-potential host comparisons could also be interpreted as a consequence of a standardized environment, as we kept in isolation our colonies for 6 months prior to the tests. Some studies indeed demonstrated that diet and environment could influence the colony odor (Crosland, 1989; Liang and Silverman, 2000; van Zweden et al., 2009b; see Sturgis and Gordon, 2012). Still, van Zweden et al. (2009a) also showed that a homogenized environment will not affect the discrimination ability of ants, suggesting that heritable cues play the most important part in nestmate recognition (van Zweden et al., 2010).

Parasite workers antennated and stayed more in contact with their host species workers than with the non-host workers, displaying non-agonistic and affiliative behaviors toward them. This may be related to the fact that the recognition template of *M. ravouxi* workers comprises some of the familiar host species-specific chemical cues. In the study of Schumann and Buschinger (1995), *C. muellerianus* workers imprinted on the potential host label inspected potential host species nest entrances more often than workers imprinted on the main host species, so that an effect of experience could not be entirely rejected. In our experiment, *M. ravouxi* workers were certainly more familiar with the species-specific chemical cues of *T. unifasciatus*, and their recognition template is likely to include them, at least partially. This could explain here the more frequent affiliative behaviors displayed toward the host species. Heterocolonial workers from their host species may elicit affiliative or aggressive behaviors depending on whether they are perceived under or over the tolerance threshold of parasite workers (Reeve, 1989). Nonetheless, the experimental design used here offer a choice between different social stimuli at the same time. This forced the contrast between stimuli and may have influenced the behavioral decisions because of these stressful conditions, but gives us an interesting insight into the discrimination abilities of *M. ravouxi* workers.

We did not record any difference in aggressiveness of parasite workers toward their slaves and their sisters. Within parasitized colonies, parasite and slaves are likely to share common cuticular compounds and to display the same colonial label (Franks et al., 1990; Kaib et al., 1993; Bonavita-Cougourdan et al., 1996, 1997; d'Ettorre et al., 2002; Brandt et al., 2005; reviewed in Lenoir et al., 2001). Homocolonial slaves are perceived as nestmates by *M. ravouxi* workers (see Lenoir et al., 1999). Nonetheless, it has been demonstrated that in experimental mixed-species colonies, different species can keep distinct profiles (Errard et al., 2006). Here, *M. ravouxi* workers displayed an affiliative preference for their nestmate sisters, as they stayed more in contact with them than with the slaves of their colony. Consequently, this test clearly showed that *M. ravouxi* workers discriminated their sisters from their slaves in these experimental conditions.

Parasite workers did not behave differently toward conspecific heterocolonial workers than toward their sisters, but, in the presence of a parasite and a slave of another colony, they were also more aggressive toward slaves. It reinforces the idea that parasite workers' discrimination between species inside a parasitized colony could be the consequence of them having a colonial template where species-specific cues play a major role, thus allowing the discrimination of host slaves, which display a slightly different chemical signature than the parasite workers. The high weight of parasite species-specific cues in the matching process between the perceived odor and the template, combined to the permissive tolerance threshold imposed by the mixed colony condition, could then explain the high tolerance for homospecific congeners, be they from another colony or not. This ability could even be beneficial, since relying on specific cues may for instance enable *M. ravouxi* workers to avoid agonistic interactions when encountering heterocolonial homospecific workers during raiding periods. Although Schumann (1992) observed occasional intraspecific raids in *C. muellerianus* in a field study, since then very few studies have been devoted to intraspecific slavery in slave-making ants (Le Moli et al., 1993; Kronauer et al., 2003). Moreover, it seems difficult to disentangle the mechanisms of such a behavior without repeated field observations coupled with population studies. Territorial conflicts could lead to attacks of neighboring colonies, and the brood could then be opportunely brought back into the nest (Wilson, 1975; Alloway, 1980; Stuart and Alloway, 1982; Pollock and Rissing, 1989; Foitzik and Heinze, 1998; see Buschinger, 2009). But Le Moli et al. (1993) recorded almost no aggressive behavior between residents and invaders in *Polyergus rufescens*, and pillages did not last. This could be interpreted as an "error" in the raiding attempt, with invaders not completing the entire cycle of their raids. Indeed, during the raiding period, one may hypothesize that scouts could trail territorial marks of a colony to find a suitable target (Franks et al., 2007a, b; Cao and Dornhaus, 2012). In parasitized colonies, because foragers are enslaved host workers only (Buschinger, 1986), these marks may contain species-specific host chemical cues that could be mistakenly lead parasite workers to initiate a raid, as observed by Schumann (1992) and Le Moli et al. (1993), on a parasite colony. Because parasitized colonies' chemical label includes both species-specific cues of host and parasite species, it thus support the idea that host species-specific cues may also have a heavier relative weight either in the perceptual component or in the decision process of slave-making ants, which increases the efficiency of raids by facilitating the recognition of host species.

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