

REVISTA BRASILEIRA DE  
**Entomologia**  
A Journal on Insect Diversity and Evolution[www.rbentomologia.com](http://www.rbentomologia.com)

Biology, Ecology and Diversity

**The trade-off between the transmission of chemical cues and parasites: behavioral interactions between leaf-cutting ant workers of different age classes**Juliane F.S. Lopes<sup>a,b</sup>, Roberto da Silva Camargo<sup>a,\*</sup>, Luiz C. Forti<sup>a</sup>, William O.H. Hughes<sup>c</sup><sup>a</sup> Universidade Estadual Paulista, Faculdade de Ciências Agronômicas, Departamento de Produção Vegetal, Laboratório de Insetos Sociais-Praga, Botucatu, SP, Brazil<sup>b</sup> Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas, Pós-Graduação em Comportamento e Biologia Animal, Campus Universitário de Martelos, Juiz de Fora, MG, Brazil<sup>c</sup> University of Sussex, School of Life Sciences, Brighton, UK

## ARTICLE INFO

## Article history:

Received 8 August 2016

Accepted 2 November 2016

Available online xxx

Associate Editor: Rodrigo Feitosa

## Keywords:

Acromyrmex

Age polyethism

Behavioral interaction

Chemicals transfer

## ABSTRACT

Social animals are faced with an intriguing dilemma. On the one hand, interactions between individuals are essential to exchange information and to promote cohesion, while on the other hand such interactions carry with them the risk of catching and transmitting parasites. This trade-off is particularly significant for social insects because low within-colony genetic diversity makes their colonies potentially vulnerable to parasites while frequent interactions are essential to the development of the colonial odor profile necessary for nestmate recognition. Here we investigate whether social interactions between young and old leaf-cutting ant workers show evidence of this trade-off. We find that old workers engage in more selfgrooming and mandibular scraping than young workers, both in keeping with old workers having been more exposed to parasites. In contrast, we find that young workers engaged in more allogrooming than old workers, which seems likely to have a different motivation possibly the transfer of recognition cues. Furthermore, young workers tended to engage in allogrooming with other young workers, although it was the old workers that were most active and with whom allogrooming would seem likely to optimize information or chemicals transfer. This suggests that young workers may be attempting to minimize the risk of parasite transmission during their social interactions. Although limited to behavioral data, these results hint that ant workers may be sensitive to the trade-off between the transmission of recognition cues and disease, and adjust their social interactions accordingly.

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## Introduction

Interactions are fundamental to the organization of all societies. Even in simple societies, individuals share food resources or nesting sites, and exchange information to maintain group cohesion (Wilson, 1975; Kraus and Ruxton, 2002). The transmission of information becomes still more important as social complexity increases. Advanced societies, such as those of humans and social insects, are characterized by a division of labor that is underpinned by information transfer. However, social interactions also carry with them a risk of parasite transmission, which is largely dependent on the interaction rate between infected and susceptible hosts (Anderson and May, 1981; McCallum et al., 2001). Although

this effect will depend on the transmission mode of parasites (Côte and Poulin, 1995), and may be mitigated by decreased inter-group transmission (Wilson et al., 2003), parasites are nevertheless often predicted to be a particular hazard for social animals (Alexander, 1974; Freeland, 1976; Kraus and Ruxton, 2002). Social interactions may therefore involve a trade-off between the need to exchange information and the risk of parasite transmission.

This trade-off may be particularly significant for social insects. Social insect colonies are characterized by low within-colony genetic diversity, which may greatly facilitate the transmission and evolution of any parasite that enters a colony (Hamilton, 1987; Schmid-Hempel, 1998; Boomsma et al., 2005; Hughes and Boomsma, 2006; Morelos-Juárez et al., 2010). Social insects defend themselves against this threat at several levels. Workers have effective individual defenses, consisting of selfgrooming to remove parasites from their cuticle, the prophylactic production of antibiotics to make their cuticles a more hostile environment for any parasites they encounter, and an effective immune response to

\* Corresponding author.

E-mail: [camargobotucatu@yahoo.com.br](mailto:camargobotucatu@yahoo.com.br) (R.S. Camargo).

deal with any parasites that successfully infect them (Hughes et al., 2002; Poulsen et al., 2002a; Rosengaus et al., 2004; Baer et al., 2005; Rosengaus et al., 2007; Okuno et al., 2012). At a second level, social insects also engage in group-level defenses, allogrooming one another to remove parasites, possibly exchanging antibiotic secretions, and dealing hygienically with waste material (Rosengaus et al., 1998; Bot et al., 2001; Hughes et al., 2002). At a third level, social insect colonies are subdivided both architecturally, with nests often consisting of multiple chambers, and demographically, with younger individuals tending to be located at the center of nests and older individuals toward the exterior (Hölldobler and Wilson, 1990; Robinson, 1992). In addition, hazardous tasks such as waste management are often partitioned such that those individuals most exposed to the hazard have least interaction with the remainder of the colony (Hart and Ratnieks, 2001, 2002). Models suggest that the combination of this structuring with group-level and individual defense mechanisms is key to parasite transmission within social insect colonies being minimized (Naug and Camazine, 2002; Pie et al., 2004; Fefferman et al., 2007).

While parasites select for social insects to minimize their social interactions, the need for information transfer conversely requires these to be frequent to, in particular, develop the necessary cues to allow nestmate recognition. Although other pheromones may play a secondary role in some taxa (Hughes et al., 2001; Hernandez et al., 2006), the primary cues used for nestmate recognition are normally non-volatile cuticular hydrocarbons (CHCs) (Lahav et al., 1999; Howard and Blomquist, 2005; Guerrieri and D'Ettorre, 2008; Martin et al., 2008). Individuals transfer these CHCs between one another by allogrooming or trophallaxis to produce a colony-specific blend or 'gestalt' odor which allows nestmates to be distinguished from non-nestmates (Soroker et al., 1995; Boulay et al., 2000; Lenoir et al., 2001; Soroker et al., 2003) so CHCs constitutes a great source of information and when they are transferred not just the gestalt odor is obtained but so the information about individual colony origin. Colony specific odors that maintain colony insularity by rejecting any individual that carries a different odor are well known in social insects (Breed, 1983; Wilson, 1971). Individuals eclose with an individually-distinctive profile of cuticular hydrocarbons and acquire the gestalt odor rapidly over the days following eclosion (Morel et al., 1988; Dahbi et al., 1998; Kaib et al., 2000; Cuvillier-Hot et al., 2001). Individuals continue to biosynthesize cuticular hydrocarbons throughout their life, so continually need to interact with nestmates to maintain and to contribute to their gestalt colony odor formation and avoid redeveloping an individually-distinctive profile (Boulay et al., 2000; Boulay and Lenoir, 2001).

As with other group-living animals, social insect workers therefore need to balance the need for social interactions to transfer chemical cues with the risk of the same interactions transmitting parasites. Here we investigate whether some social behaviors in leaf-cutting ants show evidence of such a trade-off. Four behaviors were examined: allogrooming, selfgrooming, mandibular scraping and antennation.

Allogrooming is the principal mechanism by which CHCs are transferred between leaf-cutting ants because this species only rarely engage in trophallaxis (Moreira et al., 2006). Also it is an important mechanism of disease resistance, but carries with it the risk of disease transmission (Rosengaus et al., 1998; Hughes et al., 2002; Fefferman et al., 2007). Although allogrooming may also serve to increase immunity (Traniello et al., 2002; Ugelvig and Cremer, 2007), it seems probable that this benefit will normally be outweighed by the risk of infection. Selfgrooming both plays a role in disease defense removing fungal spores and other contaminants from the cuticle (Hughes et al., 2002) and in the development of the gestalt odor. Mandibular scraping most probably has a hygienic function in which the effective action is in one direction (Basibuyuki

and Quicke, 1999) and transfers dirt material that has accumulated on the mandibles from the cleaned to the cleaning part (Lopes et al., 2005). Antennation was measured as a general measure of social activity. We compared all four behaviors between young and old workers.

Young workers are most valuable to the colony because of their long expected life. Their tasks are generally limited to within, and often at the center of the nest (Robinson, 1992; Camargo et al., 2007), so they may be less exposed to parasites than older workers which engage in moving soil, waste management or foraging (Schmid-Hempel, 1998; Boomsma et al., 2005). This contrast in exposure is likely to be particularly strong for leaf-cutting ants because young workers reside exclusively within the fungus garden. The ontogenetic differences lead to several hypotheses: mandibular scraping will be more common in old workers than young workers because the former are more likely to be contaminated with soil or food debris; selfgrooming will be more common in old workers than young workers because the tasks of the former (soil moving, waste management, foraging) carry more risk of parasite exposure; allogrooming will also be more frequent for old rather than young workers for the same reason, and in addition will tend to be within age categories in order to limit transmission by dividing interaction networks (Naug and Camazine, 2002; Pie et al., 2004; Fefferman et al., 2007). In contrast, information transfer would predict similar rates of selfgrooming and allogrooming for old and young workers because both groups need to develop and maintain their CHC profile. Furthermore, information transfer would be optimized by allogrooming between age categories in order to prevent them developing distinct CHC profiles which would interfere nestmate recognition.

## Materials and methods

The study was conducted with two colonies of *Acromyrmex crassispinus*, collected at Jaguariaíva-PR (24°32' S; 49°57' W), and two colonies of *Acromyrmex rugosus*, collected at Botucatu-SP (22°52'20" S; 48°26'37" W), both locations being in southeast Brazil. *A. crassispinus* is found mainly in pine forests and uses monocotyledonous as fungus substrate while *A. rugosus* occurs in grassland and disturbed habitat using dicotyledonous plants as substrate (Verza et al., 2007). The two species otherwise have very similar ecology and life-history, with both nesting within the soil and reaching a similar size at maturity with one or two fungus gardens. Here, they were chosen for easy access and rearing capability of these species. Also, both species show the classic pattern of alloethism for *Acromyrmex*, with a continuous size-frequency distribution around two modes, normally termed small workers and large workers (Wetterer, 1999; Hughes et al., 2003). Small *Acromyrmex* workers reside within the fungus garden where they care for the brood and fungus. Large workers also remain within the fungus garden while young, where they serve as a substrate for the culturing of antimicrobial bacteria to protect the fungus garden (Currie et al., 1999, 2003; Poulsen et al., 2002b). Medium and large old-aged workers work outside the fungus garden and nest, foraging for vegetation, removing waste and building the nest (Camargo et al., 2007).

Here, we considered that young workers (light brown color) were 1 week old, and old workers (dark brown color) were more than 3 and 4 weeks old. This assumption is based on study from Camargo et al. (2007), where leaf-cutting ants start to participate in activities outside the nest by 3 or 4 weeks of age, and defined as "outside workers". Thus all of them should be older than 1 month. On the other hand young worker as defined as "inside workers" and all of them should be younger than 1 week.

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