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Reproductive hierarchies and status discrimination in orphaned colonies of *Pachycondyla apicalis* ants

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In group-living animals where dominance hierarchies occur, aggression can be reduced if individuals are able to recognize each other. To do this, and to adapt their behaviour suitably when faced with a rival, individuals may rely on two nonmutually exclusive recognition means: they could recognize group members individually and/or their social status. Within insect societies, although conflicts over reproduction resulting in hierarchy establishment are widespread, relatively little is known about the cognitive abilities involved in the regulation of agonistic interactions. We tested whether low-ranking workers of *Pachycondyla apicalis* ants are able to discriminate each other individually and/or if they can discriminate the status of their nestmates. We found no evidence of individual discrimination among subordinates whereas they were able to discriminate their nestmates on the basis of their social and reproductive status. Such a skill may allow them to regulate worker reproduction in queenright colonies efficiently. By considering the structure of the hierarchy and the nature of the dominance relationships in *P. apicalis* societies, we discuss the existence of a more accurate recognition system among the high-ranking workers.

A crucial feature of animal societies that maintain group cohesion is the existence of elaborate recognition systems ranging from group membership to the individual level. Recognition is critical for numerous behavioural interactions between individuals such as territorial defence (Van Dyk & Evans 2007), competitive aggression (Tanner & Adler 2009), pair bonds (Bird & Emery 2008), mate selection (Arbuthnott & Crespi 2009), kin favouritism (Holmes 1995) and dominance hierarchies (Barnard & Burk 1979).

In dominance hierarchies especially, aggression between individuals often constitutes a cost in terms of time, energy and risk of injury (Jaeger 1981; Cole 1986) which can be reduced if individuals are able to recognize each other. To do this, and to adapt their behaviour suitably when faced with a rival, individuals may rely on two nonmutually exclusive recognition means. The first is that individuals may be able to assess the status of group members (Gherardi & Daniels 2003). This requires an ability to discriminate individuals on the basis of cues displayed by the dominants and/or the subordinates depending on an internal state. This ability has been assumed to regulate the dominance relationships in several vertebrate (Rohwer 1977; Meyer et al. 2008) and invertebrate species (Alexander 1961; Winston & Jacobson 1978; Gherardi & Daniels 2003). The second is that individuals could remember the outcome of earlier confrontations with another group member and consequently adapt their behaviour during subsequent encounters (Barnard & Burk 1979). This mechanism of hierarchy maintenance is only possible in species where individual recognition occurs and thus requires an ability to discriminate group members on the basis of their individually distinctive cues. The occurrence of this ability is supported by studies of both vertebrate (Zayan 1974; McLeman et al. 2005) and invertebrate species (Caldwell 1985; Karavanich & Atema 1998) where dominance hierarchies occur.

In social insects, the presence of several reproductive individuals within colonies (queens and/or workers) is a potential source of conflict over reproduction (Trivers & Hare 1975; Ratnieks 1988). When the conflict is expressed, the establishment of a dominance hierarchy between the potential egg-layers is a widespread mechanism (Turillazzi 1985; Bourke 1988; Oliveira & Hölldobler 1990; Röseler 1991; Schwarz & Woods 1994; Heinze et al. 1996; Kolmer & Heinze 2000) to help maintain colony productivity (Johnstone & Cant 1999; Wenseleers et al. 2004; Denis et al. 2008). Indeed, dominance interactions generally govern the partitioning of work with only one or a few dominant individuals monopolizing reproduction whereas subordinates perform the other tasks necessary for the maintenance of the society (Keller & Chapuisat 2001).

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Despite the significance of within-colony conflicts resulting in hierarchy establishment in primitive eusocial insects, relatively little is known about the recognition abilities that may allow efficient regulation of these social organizations. It is generally assumed that agonistic interactions, including dominance and policing behaviour, are crudely regulated by the recognition of the reproductive status (Gobin et al. 1999; Peeters et al. 1999; Liebig et al. 1999, 2000; Sledge et al. 2001; Cuvillier-Hot et al. 2002; Hannonen et al. 2002; Heinze et al. 2002; Dietemann et al. 2003; Stroeymeyt et al. 2007; Brunner et al. 2009; Smith et al. 2009) and that precise recognition systems are improbable (Wilson 1971). However, this assumption has recently been challenged by the discovery of individual recognition abilities in cofounding queens of a social wasp (*Polistes fuscatus*: Tibbetts 2002; Sheehan & Tibbetts 2008) and of two ant species (*Pachycondyla villosa* and *Pachycondyla inversa*: D'Ettorre & Heinze 2005; Dreier et al. 2007) which are characterized by long-term stable dominance hierarchies.

These studies not only highlight the need to acknowledge the occurrence of individual discrimination abilities within insect societies but also provide a theoretical framework allowing prediction of the complexity of the recognition system that can be expected according to the type of social structure. While accurate recognition systems are favoured when a small group of individuals benefit from quickly and accurately recognizing each other (Tibbetts 2002; Chapuisat 2004; D'Ettorre & Heinze 2005), a lack of repeated fights is assumed not to promote their emergence (Dreier & D'Ettorre 2009). This prediction turns out to be true in *Lasius niger* ants where the absence of dominance relationships between the cofounding queens is associated with a lack of individual recognition abilities (Dreier & D'Ettorre 2009).

In this study, we extended the investigation of recognition systems in social insects by studying the within-colony recognition abilities of low-ranking workers in *Pachycondyla apicalis* ants. Although infertile workers may play an important part in the maintenance of social cohesion (Ratnieks 1988; Van Zweden et al. 2007), their cognitive abilities have never been studied. *Pachycondyla apicalis* colonies are headed by a single queen that generally monopolizes reproduction. However, competition for male production occurs among workers and gives rise to overt aggressive behaviour between them (Oliveira & Hölldobler 1990; Dietemann & Peeters 2000). These agonistic interactions lead to the set-up of a reproductive hierarchy where worker reproduction is monopolized by the dominant one which lays most of the eggs and by a few high-ranking individuals that lay occasionally. Since the numerous low-ranking workers are not much involved in agonistic interactions (Oliveira & Hölldobler 1990), we predicted that individual discrimination does not occur among them. On the other hand, as subordinates may benefit from police worker reproduction, we predicted that they are able to discriminate the reproductive status of their nestmates.

METHODS

Ants and Rearing Conditions

We used three colonies of *P. apicalis* collected in March 2007 in the Kerrenroch forest, Petit Saut (5°04′09.7 N), French Guiana. *Pachycondyla apicalis* societies are small (mean number of workers ± SD = 87 ± 75, $N = 85$) with a single queen (Fresneau 1994). These colonies were installed in plaster nests (Fresneau 1994) and reared at 26 ± 2 °C, 65% humidity, 12:12 h light:dark photoperiod. Nests consisted of various chambers covered with a glass roof and red Plexiglas to allow observations. They were connected to a foraging arena (18 × 14 cm). Ants were supplied twice weekly with crickets, honey/apple mixture and water ad libitum.

Experiments

The experimental procedure included three phases. First, we observed the set-up of the reproductive hierarchy in newly orphaned colonies to determine the social status of each individual. Then, through habituation/discrimination experiments we tested whether individual and status discrimination occur. Finally, we dissected all ants to check whether the social rank of the individuals was correlated with their ovarian development.

Reproductive hierarchy

In each colony, 41 workers randomly collected in the nest were individually labelled with dots of paint and numbers glued on the thorax for subsequent identification and returned to their colony. Because orphaned conditions promote the set-up of a reproductive hierarchy among workers (Dietemann & Peeters 2000), these 41 workers were then isolated in a new nest a week later.

Daily scanning observations and video recording were performed during 14 consecutive days (2 h a day for each colony, with several sessions of 15–60 min during the diurnal phase of the colony) starting from the day the orphaned colony was established. We recorded bites and antennal boxes (i.e. when a worker intensely pummels the head of a target individual), agonistic behaviours representative of the dominance relationships (Ito & Higashi 1991; Heinze et al. 1996). Each individual that performed an agonistic behaviour, as well as the one that was targeted, was recorded in a matrix, a method classically used to determine the hierarchical order in social insects (Monnin & Peeters 1999). Only one interaction for each pair of workers in a given direction was carried forward in the matrix. Indeed, taking into account many repeated interactions on the same day does not provide additional information about hierarchical relationships (Peeters & Tsuji 1993). The dominance behaviours within a pair were mostly unidirectional, but when this was not the case, the dominant individual was determined according to the following criteria (in order of importance): (1) dominant in more than 50% of the interactions, (2) performed most of the bites, (3) dominated the last interaction observed. The rank order was determined by arranging the matrix in an order that minimized the number of inconsistencies (i.e. when an individual is assigned at a lower rank than an individual that it dominates). The top-ranked individuals that additionally performed more than 75% of the aggressive acts were considered to be high-ranking individuals and the remainder low-ranking individuals.

Discrimination experiments

The day following the phase of social status determination, we tested the ability of low-ranking workers to discriminate other low-ranking nestmates individually and/or their nestmates on the basis of their status within the group. To do this, we used and video recorded a procedure of habituation/discrimination commonly used for vertebrates (see for example: Johnston 1993) and adapted for ants (Nowbahari 2007; Foubert & Nowbahari 2008). During the habituation phase, the tested ant (taken randomly from the group of low-ranking workers) was exposed to a nestmate previously anaesthetized with CO_2. This procedure was repeated four times in succession (each time 4 min long) at 5 min intervals. Five minutes after the end of the habituation phase, we carried out the discrimination test (4 min long) which consisted of exposing the tested ant to two anaesthetized nestmates: the individual previously met during the habituation tests (familiar ant) and another nestmate (unfamiliar ant). Since the length and occurrence of antennating behaviour are commonly used to quantify the interest shown by an ant towards a social stimulus (Boulay et al. 2000), only these behavioural indices were subsequently analysed. We predicted a significant reduction in investigation time across the