Status discrimination through fertility signalling allows ants to regulate reproductive conflicts

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Dominance hierarchies allow group-living animals to regulate the partitioning of reproduction, but the recognition systems underlying dominance interactions remain equivocal. Individual recognition, a cognitively complex recognition system, is often posited as an important mechanism for the regulation of linear dominance hierarchies because of its high level of precision. However, providing it actually allows a fine-scale discrimination of the individuals' statuses, status discrimination may offer an alternative, simpler, recognition system allowing the same level of precision while saving the memory-related costs associated with individual recognition. With the aim of disentangling the cognitive mechanisms underlying the formation and maintenance of hierarchies, we here studied the within-group recognition systems in the ant Neoponera apicalis, where orphaned workers compete over male parentage in a linear hierarchical structure. Overall, we found that status discrimination abilities were in fact sufficient for the establishment and stabilization of linear hierarchies. The observed level of accuracy allowed fine-scale discrimination of all top rankers' hierarchical status, and thus translated into a functional individual discrimination of all competing workers at the top of the hierarchy. Low-ranking workers did not exhibit such fine-scale status discrimination. We moreover showed that a putative signal of fertility, 13-methylpentacosane, precisely labelled the workers' position in the hierarchy, thereby providing the recognition cue likely to explain the individuals' discrimination abilities. This signal could therefore play a key role in the regulation of the reproductive conflict in this species. In contrast with the traditional view, our study shows the implication of a cognitively simple but equivalently efficient recognition system during the emergence and stabilization of a linear dominance hierarchy.

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The existence of recognition systems is a central feature of group living. Recognition is used in a wide range of social interactions, thereby allowing group members to adapt their behaviour according to the age, sex, kinship, group membership, hierarchical status, reproductive status, species and neighbourhood of the individuals with which they interact (Sherman, Reeve, & Pfennig, 1997; Thom & Hurst, 2004; Tibbetts & Dale, 2007). Understanding the exact nature of the recognition mechanisms across taxa, their contexts and associated costs and benefits is therefore a major challenge in the biological sciences (Wiley, 2013).

Dominance hierarchies are widespread throughout the animal kingdom. These hierarchies are characterized by asymmetries among group members in the partitioning of resources (Zanette & Field, 2009), and can induce important fitness consequences by mediating access to reproduction, food resources or susceptibility to diseases (Ellis, 1995). Nevertheless, the overt aggression often associated with these hierarchies can also bear important costs in terms of time, energy, physical injuries or vulnerability to predators (Hsu, Earley, & Wolf, 2006; Rutte, Taborsky, & Brinkhof, 2006). Reducing these costs may imply the use of ritualization mechanisms, as is frequently observed in hierarchical contests (Hemelrijk, 2000; Hsu et al., 2006; Tibbetts & Dale, 2007). These mechanisms allow the individuals to adapt their behaviour towards encountered nestmates without the need for overt aggressive interactions, and therefore play a key role in the stabilization of dominance hierarchies.

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Numerous empirical and theoretical studies have proposed a variety of intrinsic and extrinsic factors that may be responsible for the formation and maintaining of dominance hierarchies (Dugatkin & Earley, 2004; Hsu et al., 2006). These factors include pre-existing differences between competing individuals (Parker, 1974), the value of the contested resource (Maynard Smith & Parker, 1976) and the influence of previous experiences on the outcome of future encounters (Dugatkin & Earley, 2004; Hsu et al., 2006; Rutte et al., 2006). Game-theoretical studies have shown that hierarchy formation could rely on self-organizing processes, such as winner and loser effects (Dugatkin & Earley, 2004; Hsu et al., 2006; Rutte et al., 2006), without the need for any particular recognition mechanism. In this case the outcome of past encounters influences the chance of winning or losing in future interactions in a self-reinforcing manner, i.e. regardless of the identity or rank of the opponent. However, dominance interactions are often highly directed (Chase & Seitz, 2011; Hsu et al., 2006; Tibbetts & Dale, 2007), indicating that individuals actually recognize the status of their opponents, through either direct or indirect (i.e. memory-based) rank perception (Hemelrijk, 2000; Tibbetts & Dale, 2007). Recognition systems are therefore an important feature of dominance interactions, although not mutually exclusive with self-organizing processes. However, the recognition systems underlying dominance interactions remain equivocal (Hsu et al., 2006), particularly since they very often translate into a linear hierarchical structure.

Individual recognition has often been posited as an important mechanism for the regulation and stabilization of linear dominance hierarchies (d'Ettorre & Heinze, 2005; Dale, Lank, & Reeve, 2001; Thom & Hurst, 2004; Tibbetts, 2002; Tibbetts & Dale, 2007). In this indirect rank perception system (Hemelrijk, 2000), individuals remember earlier interactions with specific group members and adjust their dominance behaviour in subsequent encounters with these same individuals (Dale et al., 2001; Tibbetts, 2002). Despite the complexity of this cognitive mechanism, recognizing individual identity is therefore supposed to provide high benefits by matching the level of precision required for the maintenance of linear hierarchies (Thom & Hurst, 2004).

However, linear hierarchies can also theoretically emerge and be maintained through direct rank perception (i.e. status recognition; Hemelrijk, 2000). Individuals in this case base their decisions on the characteristics signalling an opponent's absolute fighting abilities (resource-holding potential; Parker, 1974), such as age, size, weight or dominance badge (Chase & Seitz, 2011). In contrast to individual recognition, there is thus no need for the opponents to be familiar (Tibbetts & Dale, 2007). Status recognition could therefore save the costs of memory characterizing individual recognition (Thom & Hurst, 2004). However, a critical assumption for the involvement of such a recognition system in the formation and stabilization of linear hierarchies is that it allows a fine-scale discrimination of ranks, but this has never been demonstrated.

Dominance hierarchies are commonly found in social insects (e.g. ants: Cuvillier-Hot, Lenoir, Crewe, Malosse, & Peeters, 2004; Heinze, Hölldobler, & Peeters, 1994; Heinze, Stengl, & Sledge, 2002; Liebig, Peeters, Oldham, Markstädter, & Hölldobler, 2000; Monnin & Peeters, 1999; bees: Ayasse, Marlovits, Tengö, Taghizadeh, & Francke, 1995; Bull, Mibus, Norimatsu, Jarmyn, & Schwarz, 1998; wasps: Sledge, Boscaro, & Turillazzi, 2001; Tibbetts, 2002), and this is particularly true when the colonies comprise several individuals with equivalent reproductive potentials competing to gain access to reproduction. Workers in hopelessly queenless colonies thus typically compete with one another over male parentage (Bourke, 1988; Ratnieks, Foster, & Wenseleers, 2006), with a resulting linear or near-linear hierarchical structure of dominance relationships regulating the partitioning of reproduction (Heinze et al., 1994; Heinze et al., 2002; Peeters & Liebig, 2009), as in the Neotropical ant Neoponera (formerly Pachycondyla; Schmidt & Shattuck, in press) apicalis (Oliveira & Hölldobler, 1990). This species shares all the traits typically characterizing Ponerinae ants, i.e. small societies, a limited queen−worker dimorphism and a high potential for worker reproduction (Fresneau, 1994), and is therefore a good model system for studying the recognition mechanisms involved in the formation and maintenance of dominance hierarchies.

A previous study has shown that low-ranking individuals are able to discriminate top-ranking from low-ranking workers, suggesting a capacity to recognize the social status of their nestmates (Blacher, Lecoutey, Fresneau, & Nowbahari, 2010). However, these recognition abilities have never been investigated in top-ranking workers. Since they are the individuals actually involved in the reproductive competition, the costs of mistaking ranks for those of adjacent-ranking nestmates are, in contrast to low rankers, potentially high. We could hypothesize that a more precise recognition system (e.g. individual recognition) is necessary for an efficient discrimination among top-ranking individuals (Tibbetts & Dale, 2007), but this could also be achieved without a necessarily greater level of cognitive complexity in the eventuality of fine-scale status discrimination. Assessing top rankers' cognitive abilities therefore remains a crucial step in understanding the recognition mechanisms underlying the formation and stabilization of the hierarchical structure in these social groups (Elwood & Arnott, 2012; Wiley, 2013). Here we tested the possibility of fine-scale status discrimination without the need for individual recognition by studying the cognitive abilities of N. apicalis top- and low-ranking workers. Furthermore, the nature of the recognition cues involved in these dominance interactions remains unknown, but they probably involve chemical communication. Chemical signals, mainly cuticular hydrocarbons, are widely acknowledged to be of primary importance in the communication of dominance and especially reproductive status in social insects (Liebig, 2010; Monnin, 2006). We therefore also analysed the individuals' chemical profile to investigate the nature of the putative recognition cues at the basis of these dominance interactions.

METHODS

Ants

Colonies of N. apicalis were collected in the Kérenroch forest, Petit Saut (5° 04′15.8″ N, 53° 02′36.3″ W), French Guiana in March 2007 and have been kept in the laboratory in France ever since. Ants were housed in plaster nests (18 × 14 cm) connected to a foraging area of the same dimensions, where food (crickets and honey/apple mixture) was provided twice a week and water ad libitum. Each colony had a queen, more than 70 workers and brood at every developmental stage. Nests were maintained at a temperature of 27 ± 2 °C, a relative humidity of 60 ± 5% and a 12:12 h light:dark cycle. Ant collection, husbandry and experimental procedures used in this study fulfilled all the legal requirements concerning insect experimentation of France.

Dominance Hierarchy

From our stock colonies, we created six experimental colonies by isolating 40 randomly chosen workers and placing them in a