



Long-term dynamics in proximity networks in ants

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Social insects rely extensively on interactions to coordinate their activities. Some studies have recently explored several attributes of insect colonies from a network perspective, providing evidence of variation in connectivity patterns among group members. The temporal stability of interaction networks, however, has rarely been examined. In this study, ants of the species *Odontomachus hastatus* were individually equipped with passive microtransponders to collect their spatial positions in artificial nests automatically. Colonies were surveyed for 3 consecutive weeks to build weighted networks of proximity between ants. The analysis revealed important interindividual differences in connectivity patterns and showed that proximity networks were stable over time. The removal of the queen did not impact the patterns of association between workers, confirming that she did not contribute to shaping network structure. Ants forming long-lasting associations with a small number of nestmates exhibited a reduced tendency to move. In contrast, mobile workers were more likely to interact homogeneously with their nestmates and did not display any privileged associations.

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Social network analysis has recently generated considerable interest for understanding animal sociality (Croft et al. 2008; Wey et al. 2008; Krause et al. 2009). A set of quantitative tools developed in the context of graph theory can be applied to gain insights into the organization of social groups. Animal networks are usually explored with individuals modelled as nodes and social relationships as edges (Croft et al. 2008). Social network analysis offers an ideal framework for quantifying relationships among group members and for exploring the mechanisms shaping social structures. Several metrics are available to probe networks at complementary levels of analysis including the identification of the position and role of individuals, the investigation of the existence of subgroups or the characterization of the overall network structure (Wey et al. 2008). This approach is also relevant for comparative studies quantifying differences in social organization across taxa (Sundaresan et al. 2007; Kasper & Voelkl 2009).

In social insects, interactions among nestmates play a central role and define pathways for the propagation of various signals. Some studies have recently examined various aspects of their organization from a network perspective (division of labour: Fewell 2003; Naug 2009; Bhadra et al. 2009; nest architecture: Buhl et al. 2004; Perna et al. 2008; food transfer: Sendova-Franks et al. 2010;

pathogen transmission: Otterstatter & Thomson 2007; Naug 2008). Several attributes of networks arise via the existence of nonrandom relationships among group members and the presence of highly interactive individuals. For instance, an important interindividual variability in interaction rate has been documented in the harvester ant, *Pogonomyrmex barbatus*, in the chamber closest to the nest entrance where a few workers displayed many interactions while most had few contacts (Pinter-Wollman et al. 2011). This variation in connectivity is believed to increase information flow within colonies because highly interactive individuals lessen the number of interactions required to connect distant workers.

The construction of networks for social insects usually relies on the aggregation of data accumulated over time. This approach proves fruitful in gaining insights into the overall network properties but it fails to inform on its dynamics. If the structure of interaction networks grants the colony efficient coordination and organization, the patterns of connectivity should be relatively persistent over time in the absence of global perturbations. The temporal stability of interaction networks, however, has rarely been examined. A reason for this probably lies in the difficulty of surveying colonies and monitoring interactions over long periods of time (Moreau et al. 2011). Using a topological approach, Blonder & Dornhaus (2011) recently investigated network dynamics in the ant *Temnothorax rugatulus*. The observation of colonies for short periods (30 min) did not show any persistence in interaction patterns between two independent sequences: ants heavily engaged in interactions showed few contacts 3 weeks later, and vice versa. However, a purely topological description of networks

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ignores important attributes encountered in real-world systems. In the case of social networks, edges can be assigned a weight corresponding to the strength of associations or the intensity of interactions. A number of techniques and metrics have been developed to probe the architecture of weighted networks (Barrat et al. 2004). For nodes with a given degree, different situations can arise (Barthélemy et al. 2005). An individual can interact uniformly with each of its partners or, in contrast, it can display dominant interactions with some privileged partners and weak contacts with others. The analysis of the heterogeneity in the distribution of weights is thus expected to offer a different picture of the temporal persistence of associations.

In this context, the objective of this study was to provide a longitudinal analysis of the structure of proximity networks in monogynous colonies of the ponerine ant *Odontomachus hastatus* with a particular emphasis on the role of the queen. Populations of *O. hastatus* display geographical variations in queen number. In southeast Brazil, polygyny is frequent and reproduction is partly mediated by dominance interactions among queens (Oliveira et al. 2011). For this study, ants were collected in French Guiana where colonies are monogynous and contained an average of 300 individuals (median = 277, range 54–873, $N = 15$). *Odontomachus hastatus* exhibit a queen–worker dimorphism and there is no indication of reproduction by workers. Although dominance behaviours among workers exist in *Odontomachus* (*O. brunneus*: Powell & Tschinkel 1999), such agonistic interactions have not been reported in *O. hastatus*. The relatively large size of individuals of *O. hastatus* (body length: 1.5 cm) is well suited to exploit the recent advances in radiofrequency identification (RFID) by equipping ants with passive microtransponders. This methodology allows the automatic collection of individual spatial positions over several consecutive days in artificial nests (Moreau et al. 2011). I combined topological information and the distribution of edge weights (duration of associations) to ask whether ants were uniformly connected or whether, in contrast, they displayed privileged associations with a few nestmates. Using data collected over 3 consecutive weeks, I examined the temporal persistence of proximity patterns among ants. I evaluated whether the queen occupied a special position in the network and tested experimentally whether her removal impacted network structure. Finally, I investigated the relationship between space use and individual variation in connectivity.

METHODS

Animals and Experimental Set-up

In French Guiana, colonies of *O. hastatus* typically nest in root clusters of epiphytic plants or between fronds of young palm trees (Gibernau et al. 2007). Four queenright colonies (colonies A–D) were collected at Petit Saut (5°03'N, 53°02'W) where all colonies sampled were monogynous ($N = 15$). Using Superglue, I glued RFID tags to the thorax of 55–58 workers plus the queen. The RFID tags and reader were purchased from Lutronic (<http://www.nonatec.net>). Each tag is 6 mm long and weighs ca. 6 mg (about 1/3 of the weight of an ant). The body length of a worker is about 1.5 cm. Tagged ants were gently introduced into the foraging area of an artificial nest (18 × 24 cm and 1 cm high) which was divided with a plastic strip into two compartments. Each compartment could accommodate all the ants and was covered with a transparent plastic plate to prevent ants from escaping. One compartment (18 × 12 cm) was termed the foraging area. This area was connected to a second compartment (18 × 12 cm) which was partitioned into two interconnecting chambers. This second compartment (hereafter, nest) was covered with a red film filter (Fire E#19, Rosco,

London, U.K.). The floor of all compartments was covered with plaster and a top layer of soil. A quantity of brood (10–15 eggs, 10–15 larvae of different sizes, 5–10 pupae), comparable to that found in natural colonies of similar size (R.J., unpublished data), was added. Ants were maintained in a climate room at 25 °C. Each trial began when the queen and brood entered the nest and lasted 7 days. Ants were fed twice a week with live house flies, *Lucilia sericata*, and vitamin-enriched food provided in a cup placed in the centre of the foraging area; water was provided ad libitum. The queen was present on the first and third weeks but removed on the second week. Workers that died or lost their tags during the course of trials (range 5–7) were excluded from the analysis. The exclusion and reintroduction of the queen necessitated removing the top of the nest. Because this manipulation may have disturbed ants, the first hour of each week was not included in the analysis.

The detection field of the transponder reader was 3.5 cm and the reading distance equalled approximately 1.5 cm. An apparatus was designed to move the reader across the surface of the set-up. The RFID reader was mounted on a device moving on a rail along the X axis. This rail could move independently on a second rail along the Y axis. Movements along each rail were driven by stepper motors piloted by a microcontroller via motor drivers (Moreau et al. 2011). The step displacement along the X axis was chosen to allow an overlap of the detection field of the reader. When the reader detected a tag, the microcontroller sent its number, time and the spatial coordinates of the reader to a computer. On average, each ant was detected every 250 s (duration of a forward or backward path of the reader). Mobile ants could be detected at distinct locations during the course of the reader (for details see Moreau et al. 2011). For each tag, the median efficiency of detection, defined as the number of detections divided by the total number of scans, equalled 1.21 (first–third quartiles 1.07–1.35, $N = 602$). The positions of ants between consecutive detections were obtained by interpolation assuming that ants move along a straight line (about 60% of interpolations concerned positions less than 5 cm apart). I checked that linear interpolation allows a confident estimation of the rate of association among ants. In groups of 55 individuals, I generated spatial positions for each ant to simulate individual paths and locations within the experimental set-up (1 position/s). These simulated paths were first used to characterize the patterns of associations among individuals. For each ant, I next randomly sampled 2400 positions along its simulated paths to reproduce the experimental sampling rate (ca. 1 position/250 s). On these sampled positions, I applied the same procedure as on experimental data to determine the patterns of association. There were significant correlations in the numbers of associations for each pair of ants between both data sets (10 iterations; Pearson correlation: all $r > 0.99$, all $P < 0.001$). This confirmed that the interpolation between successive positions provided a confident estimation of the patterns of association between ants. Interpolated positions were used for all subsequent analyses.

Data Analysis

Criterion for defining an association

The use of RFID tags allowed me to detect whether ants were next to each other at the same time (i.e. colocalization) but not to determine whether they were actively interacting (i.e. antennal–body contact). Two ants (body length 1.5 cm) were considered to be associated if the distance between their thorax (i.e. position of the RFID tag) was less than or equal to 2 cm. Under this assumption, an ant can be associated simultaneously with several nestmates. Although it is reasonable to assume that the rate of interactions correlates with the amount of time spent in contact, the terms association and proximity are used hereafter to avoid any

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