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Polymorphism: a weak influence on worker aggregation level in ants

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Abstract. 1. Aggregation of individuals, a basic behaviour in social species, plays an essential role in many aspects of animal life (reproduction, defence, and alimentation). Understanding how this phenomenon is modulated is important to comprehend the social organisation of the group.

2. In social insects, aggregation is influenced by environmental (e.g. the light level) and social (e.g. polyethism in monomorphic ants) factors. Ants display a great variation of biological characteristics (e.g. queen number, polymorphism, division of labour, etc.) that are likely to influence the level of inter-attraction and so the aggregation.

3. The present research focused on one biological characteristic: the morphological castes (minors, majors), testing the hypothesis that minors will aggregate more than majors due to their greater need to fight against the loss of heat and to increase their self-protection.

4. Aggregation experiments were conducted on two highly polymorphic species, *Atta sexdens rubropilosa* and *Solenopsis interrupta*, using the two extreme morphological castes (majors and minors).

5. All castes exhibited a low level of aggregation: 40–50% of workers assembled for both species, the biggest cluster involving 20% of the total population. The lack of difference between morphological castes in the aggregation shows the weak influence of polymorphism on the interactions between ants.

6. It is concluded that the main factor modulating the aggregation behaviour is polyethism, i.e. the division of labour associated with the presence of an outside-the-nest experience: workers that only take care of the brood, without outside world experience (brood-tenders) assembling more than foraging workers (foragers).

Key words. *Atta sexdens rubropilosa*, *Lasius niger*, polyethism, self-assembling, social interactions, *Solenopsis interrupta.*

Introduction

Living in groups is based on the aggregation of individuals of the same species, which assemble themselves due to different cues (visual, chemical, etc). This way of life brings advantages in term of reproduction, with an increase in reproductive success (insects: Wilson, 2000; social amoebas: Bonner, 1967; birds: Lill, 1974; Aron & Passera, 2000); in terms of defence, with a better protection against predators (social aphids: Turchin & Kareiva, 1989, bees: Millor *et al.*, 1999; fishes: Magurran, 1990; Parrish & Hamner, 1997); and in terms of feeding, increasing the efficiency of search, capture, and use of resources (prey retrieval in ants: Franks, 1986, collective prey capture of neotropical wrasses: Foster, 1987, etc.).

This paper focuses on social insects (ants) that demonstrate the highest level of sociality, namely eusociality. Millions of

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individuals can live together in the same nest; impressive collective structures emerge from their work (nests with great dimensions and elaborate architecture, temperature and humidity control, etc. see Cole, 1994; Anderson *et al.*, 2002; Cassill *et al.*, 2002). The spatial organisation of a nest is complex and depends on many factors that influence individuals (environment, genes, polyethism, etc.). Workers are not homogeneously or randomly dispersed, but they are distributed in small groups (Sendova-Franks & Franks, 1995; Tschinkel, 1999). The brood is assembled in piles and even sorted by ants, the different stages arranged in concentric rings in a single cluster centred around eggs and micro-larvae [*Temnothorax* (*Leptothorax*) *unifasciatus*, Franks & Sendova-Franks, 1992]. Brood-tenders are distributed at high density around the brood in the central zone, whereas foragers are found more on the periphery of the nest, having more individual space than brood-tenders (*Leptothorax fasciatus*, Sendova-Franks & Franks, 1993, 1995). Aggregation is the keystone of this organisation: levels of inter-attractions regulate the level of aggregation of individuals and so the distribution of the individuals (Gordon *et al.*, 1993).

It is important to better understand the aggregation phenomenon and the factors influencing this behaviour in order to learn more about the mechanisms underlying the spatial distribution of insects inside as well as outside the nest. Variation in the pattern of aggregation has been described in an ant species where the polyethism is related to age, between foragers and brood-tenders: the latter caste assembles in a main and stable cluster whereas foragers are more mobile and only aggregate in small and unstable clusters (*Lasius niger*, Depickère *et al.*, 2004a). Moreover, environmental factors influence aggregation: light intensity, for example, decreases the aggregation level of foragers in *L. niger* (Depickère *et al.*, 2004b); temperature also influences the localisation of the brood and so of the workers that take care of it (Cole, 1994; Bollazzi & Roces, 2002).

In many ant species, the worker caste displays high or low polymorphism. Wilson (1980a,b) described the nest of *Atta sexdens* with a spatial segregation of individuals as a function of their morph: minors are mainly localised near the brood, major workers are mainly present at the nest entrance and on the food sources, whereas workers of intermediate size (media) are scattered throughout the whole colony. To this influence of the morph is added a centrifugal movement of workers as a function of their age from the brood (the youngest) to the foraging area (the oldest) (Wilson, 1980a,b). The same spatial pattern and centrifugal movement are observed in *Solenopsis invicta* (Mirenda & Vinson, 1981): minors are more likely to be found near brood piles whereas majors spend more time in the nest periphery. This localisation is influenced by age in both castes, with a centrifugal movement from the brood (youngest) to periphery (oldest) (Mirenda & Vinson, 1981). In this paper, the influence of morphology on aggregation behaviour is studied, independently of worker age.

This influence was studied on two highly polymorphic species: *Atta sexdens rubropilosa* and *Solenopsis interrupta*. These species share some characteristics with the monomorphic species *L. niger* where the aggregation process has been well studied: they are monogynous (facultatively polygynous for *S. interrupta*, Trager, 1991) and terricolous (mainly foraging on the ground and their nest is underground). We hypothesise that the morph of the ant influences its aggregation behaviour, minors being more aggregative than majors. In fact, aggregation should diminish heat loss and increase the protection of the individuals, affecting minors more than majors.

Methods

Ant rearing

The *A. sexdens rubropilosa* colony, originating from Brazil, was composed of fungus, brood, and 500 workers of all physical castes and was reared in a vivarium of 103 × 25 × 43 cm kept at 28 ± 2 °C. The nest was located on one side of the vivarium box, and a cylindrical black plastic box (11 × 12 cm) was placed upside down to constitute the dome of the nest. At the top of the plastic box, a centred hole of 5 cm in diameter was closed by wet cotton fabric stretched over a lattice-work frame to maintain the humidity within the nest. At the base of the box four triangular entrances were each cut at 90° to the base. Inside the nest the fungus was grown inside a jar. The foraging area was located at the other side of the vivarium box. Twice a week, bramble leaves were provided and the leaves were sprayed with water every day.

Solenopsis interrupta colonies (two nests) were collected in Bolivia and reared in plaster nests (Janet type, 20 × 20 cm, 0.5 cm high), each placed in an arena (40 × 37 cm), the borders of which were coated with fluon to prevent escapes. The nest chamber was covered with a red glass plate. Each colony was composed of brood and 2000 workers. They were supplied with water, sucrose solution (1 M) and dead insects twice a week. Nests were moistened regularly and kept at a room temperature of 22 ± 2 °C.

Experimental set-up

The experimental set-up (for *A. sexdens rubropilosa*) was the same as that previously described in experiments on *L. niger* (Depickère *et al.*, 2004a,b). Twenty ants were dropped in the centre of a PVC arena, of dimensions 19.8 cm diameter and 2 cm height, placed on a black paper sheet. This arena's interior edge was coated with fluon to avoid any ants escaping. To avoid any visual signals, a dark cylinder 30 cm high and a dark cover surrounded the arena. Through a centre hole on the cover, the set-up was illuminated by a black chamber bulb (PF712E, 15 W). Another hole on the periphery of the cover allowed a digital camera (Panasonic CCTV Model WV-BP330/G, 0.2 lux sensitivity) to record the ant activity for 90 min. Experiments with *Solenopsis invicta* were carried out at the UMSA University, La Paz, Bolivia, in a similar set-up. Due to the light sensitivity of the digital camera (JVC GR-DVL150E) the only illumination used was that produced by a 25 W white bulb. In order to keep a red luminosity inside the set-up, two layers of red filter paper (Lee Filters®, Ref. 106) were placed between the lamp and the cover of the set-up. The absorption spectrum of the red filter (550–850 nm, maximum at 625–850 nm, Lee Filters Firm, pers.

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comm.) was similar to the emission spectrum of the black chamber bulb (625–700 nm, Jensen, 2000). It can be concluded that both set-ups were comparable.

Experimental method

Two morphological castes were tested for *A. sexdens rubropilosa*: the smallest *gardener-nurses* (called minors in this study) were picked up inside the nest on the fungus and the *forager-excavators* (called majors) were picked up on the foraging area (see Wilson, 1980a for caste determination in *A. sexdens*). Nine experiments were conducted with minors and seven with majors, from February to March 2002. For *S. interrupta*, two morphological castes were used in the experiments: minors (picked up inside the nest) and majors (picked up on the foraging area) (see Mirenda & Vinson, 1981 for caste determination in *Solenopsis invicta*, a species close to *S. interrupta*) and 12 experiments were carried out for each caste.

At the beginning of the experiments, 20 ants were dropped onto the centre of the arena. Their activity was recorded during 90 min and a snapshot was taken at 30 s, at 1 min and after every minute up to 40 min and then every 5 min (51 snapshots in total). The Cartesian position of each ant in the arena was recorded for each snapshot. Ant aggregation was defined when two or more workers were at a distance (thorax to thorax) of less or equal to 1 cm from each other. This distance was chosen because it gave the best agreement between visual observation and automated analysis. Using processing programs, the following were calculated: (i) the radial distribution of ants in the set-up: the arena was divided into five rings of 2 cm and the worker density was calculated for each ring; (ii) the number of aggregated ants and so the aggregated fraction (number of aggregated ants/total number of ants in the arena); (iii) the number of clusters and their size (in ants number): clusters were ranked in decreasing order for each experiment and for each time point. Then, for each rank, a median size of cluster was calculated; (iv) the spatial stability of the biggest cluster: the distance between the centroid of the biggest cluster at time $t-1$ and the centroid of the biggest cluster at time t was calculated for each experiment giving a median distance. All data are expressed in terms of median and quartiles 1 and 3 and were analysed by non-parametric statistics.

Results

In both species, workers placed at the centre of the arena were seen to rapidly disperse themselves throughout the whole arena. After 90 min, in *A. sexdens rubropilosa*, minors were distributed throughout the whole arena whereas majors were more present at the periphery of the arena (85% of the majors and 60% of the minors in this zone) (Fig. 1). For *S. interrupta*, both castes were concentrated on the peripheral ring, with 85% of the workers in this zone.

The pattern observed for both species was statistically different from that formed by a random distribution of ants within the arena and which took into account the experimental radial distribution of ants (χ^2-test: *Atta*: minors: $\chi^2_4 = 41.1, P < 0.005$; majors: $\chi^2_4 = 24.6, P < 0.005$; *Solenopsis*: minors: $\chi^2_4 = 10.6, P < 0.05$; majors: $\chi^2_4 = 13.3, P < 0.01$), revealing an active aggregation of workers (for the method see Depickère *et al.*, 2004a).

The fraction of aggregated individuals in *Atta* shows that 50% of the minors and 40% of the majors were aggregated during the whole experiment (Fig. 2). Nevertheless, at 90 min, no statistical difference appeared between the aggregated fractions of both castes (Mann–Whitney U-test: $U = 14, N_{\text{minors}} = 9, N_{\text{majors}} = 7$, NS). In *Solenopsis*, 40% of the workers were aggregated for both castes during the whole experimental period (Fig. 2).

In both species, minors and majors showed a similar aggregation pattern of small clusters (Fig. 3) over the whole experimental time. Whatever the species, the biggest cluster assembled only 15–20% of the workers in both castes at 90 min (Fig. 3, *Atta*: Mann–Whitney U-test: $U = 16.5, N_{\text{minors}} = 9, N_{\text{majors}} = 7$, NS; *Solenopsis*: Mann–Whitney U-test: $U = 65, N_{\text{minors}} = 12, N_{\text{majors}} = 12$, NS). It should be pointed out that for *Atta*, the median size of the biggest clusters for minors is greater than for majors during the first 30 min. It suggests that minors have aggregated before dispersing.

Temporal changes in the distance between the centroid of the biggest cluster at time $t-1$ and the centroid of the biggest cluster at time t gave an approximation of the spatial stability of this cluster. In minors of *Atta*, this distance was low at the beginning of the experiments and then started to increase at 40 min (Fig. 4). This suggested that minors, dropped at the centre of the arena at $t = 0$, took long to disperse. This is corroborated by Fig. 3a where it can be observed for minors of *Atta* that the median size of the biggest cluster remained high during the first 30 min before decreasing (start of the exploratory phase). In majors, the distance remained high during the whole experimental period (Fig. 4). In *Solenopsis*, for both castes, no spatial stability was observed and the distance remained high (Fig. 4).

Discussion

Aggregation levels in ants seems to be variable between species, depending on the environmental and individual ant characteristics. In this study, both *A. sexdens rubropilosa* and *S. interrupta* have a low level of aggregation: 40–50% of the workers in the arena were aggregated after 90 min. However, this level is high enough to claim the existence of an inter-attraction and thus aggregation.

Two morphs of worker, minor and major, were identified and tested. Both morphs of both species showed a high wall-following behaviour, being found especially on the periphery of the arena. Majors and minors in both species displayed the same pattern: four or five clusters where the biggest assemblage contained 15–20% of the total number of individuals. These clusters were not stable in space. Minors of *A. sexdens rubropilosa* took longer to disperse at the beginning of the experiments, suggesting low levels of exploration.

Is aggregation influenced by polymorphism? The analysis of the results reveals a weak variation in the level of aggregation according to the morphological caste. Added to this is the result obtained in *L. niger*, a monomorphic ant where several patterns of aggregation were highlighted between ants of the same morph

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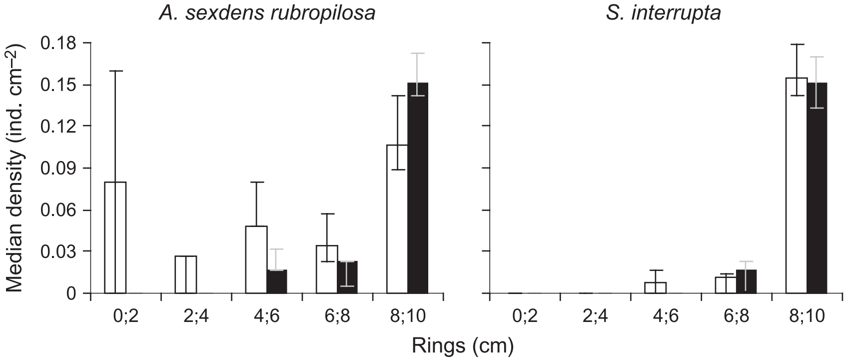

Fig. 1. Median density (and quartiles 1 and 3) of minors (open bars) and majors (filled bars) of both species in the five rings of 2 cm dividing the arena (0 = centre of the arena).

but belonging to different ethological castes (brood-tenders vs foragers, Depickère *et al.*, 2004a). Polymorphism does not appear to be a predominant factor controlling the level of aggregation.

Can polyethism explain the results in polymorphic ants as in *Lasius niger* (Depickère *et al.*, 2004a)? In fact, the division of labour is linked with two notions: the knowledge (or not) of the outside-the-nest environment, and the level of activity/mobility of the individual. In both polymorphic species studied, majors have a greater role in exterior tasks such as the defence of the nest (*Solenopsis*: Wilson, 1971), foraging and prey retrieval (*Solenopsis*: Mirenda & Vinson, 1981; *Atta*: Wilson, 1980a), exploration (*Atta*: Wilson, 1980a), and nest construction (*Solenopsis*: Wilson, 1978; *Atta*: Wilson, 1980a). Minors in both species perform interior tasks such as fungus (for *Atta*) and brood caring (for both species) but also exterior tasks: minors of *Solenopsis* have a greater role in foraging on sugar food source (Mirenda & Vinson, 1981) whereas minors of *Atta* are involved in parasol riding (Wilson, 1980b: minors riding on the leaf pieces carried by majors, in a protective role against parasitoids). To summarise, minors and majors perform tasks in and outside the nest, especially in *Solenopsis*, and have a high level of activity. Ethologically, they are closer to the foragers than the brood-tenders of *L. niger*. A conclusion is that the experience of the outside world seems to decrease the aggregation level of the caste. A possible mechanism could be linked to associative learning between the presence of light and the need to move/disperse (for foraging, for defence, etc). Furthermore, the activity rate and mobility level of individuals due to polyethism is also believed to influence the aggregation level. Indeed, the dimorphic ant *Pheidole pallidula* (presence of majors and minors) is an extreme case where the morphologically specialised caste of majors is weakly active in daily inside-the-nest tasks (Sempo *et al.*, 2006). As a result, majors become more aggregative than minors in this species.

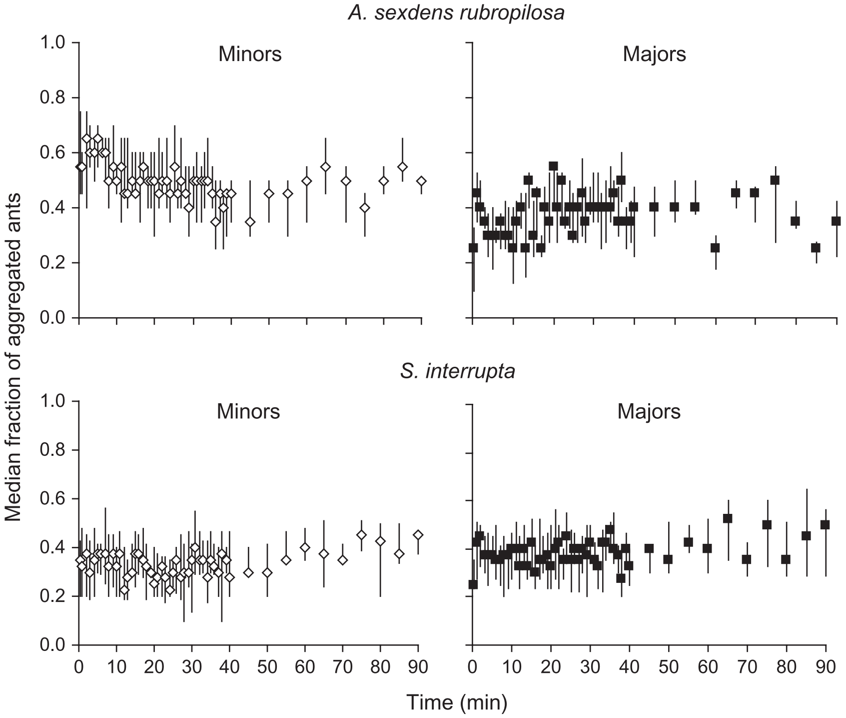

Fig. 2. Median fraction (and quartiles 1 and 3) of aggregated ants for both species and both castes.

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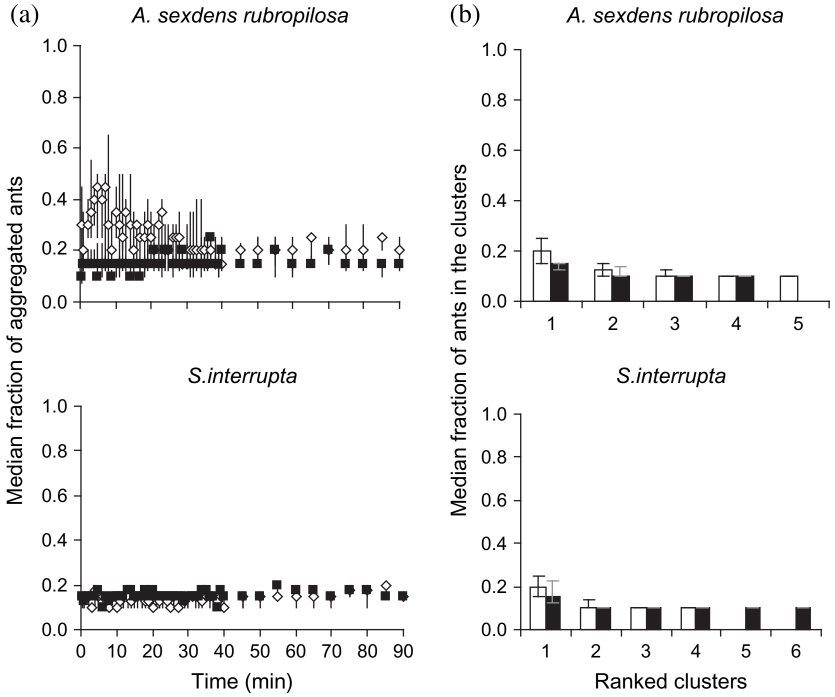

Fig. 3. Median size (and quartiles 1 and 3) of clusters for minors (white) and majors (black) of both species. (a) Temporal changes in the median size (according to the total population) of the biggest cluster; (b) median size of clusters ranked in descending order at 90 min.

These three species are characterised by a polyethism related to worker age (*Lasius*: Lenoir, 1979; *Atta*: Wilson, 1980a,b; *Solenopsis*: Mirenda & Vinson, 1981). According to the hypothesis presented in the present study, young workers of each morphological caste in *Solenopsis* and *Atta* might well assemble because they mainly take care of the brood and do not have experience of the outside world. The older workers of each morphological caste might present a lower aggregation, attributed to their greater experience of the outside world. This hypothesis requires testing to confirm that the level of aggregation evolves

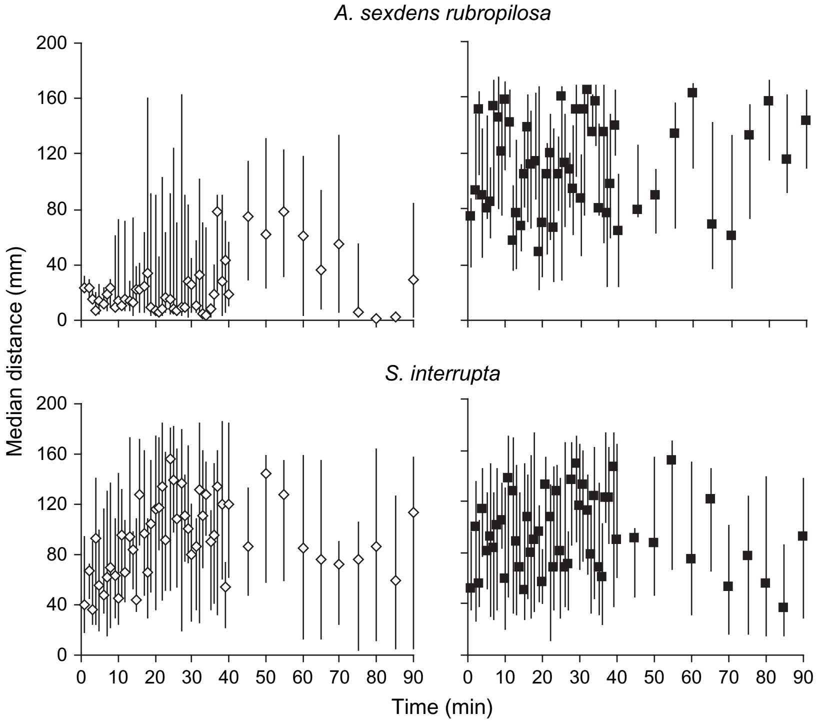

Fig. 4. Median distance (and quartiles 1 and 3) between the centroid of the biggest cluster at time $t - 1$ and the centroid of the biggest cluster at time t, for minors (white) and majors (black) of both species.

with age and experience of outside world. A real control of the outside-the-nest experience (individual marking and control of the number going outside) would be necessary to verify if this factor is really the key factor influencing aggregation behaviour. It would also be of interest to test the individuals in different luminosity conditions, such as under light and in darkness, to see if there is a different behaviour as seen in *L. niger* where brood-tenders aggregate in both conditions whereas foragers show a low clustering level under light conditions (Depickère *et al.*, 2004b).

In conclusion, all aggregation experiments conducted on the different species seem to suggest a relation between the level of aggregation and polyethism, and certainly individual history, according to the contact with the environment, the ecology of the species, etc. This study represents a first step in the research of mechanisms at work in the spatial organisation of social insects such as ants. More monomorph and polymorph species should be studied to confirm the hypothesis on the relationship between levels of aggregation and polyethism. The conditions used in these experiments are far removed from the natural life of ants. Nevertheless they are a necessary exercise before exploring more natural conditions (variation in the density of individuals and available space, presence of brood, of inside-nest odour, etc.) and verifying the conclusions of this study. A further and final step would be to explore whether the link between polyethism and spatial distribution is found in all ant species, from the most primitive to the most evolved species (Wilson, 1971; Baroni Urbani *et al.*, 1992; Astruc *et al.*, 2004).

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References

Anderson, C., Theraulaz, G. & Deneubourg, J.L. (2002) Self-assemblages in insect societies. *Insectes Sociaux*, **49**, 99–110.

Aron, S. & Passera, L. (2000) *Les Sociétés Animales: Evolution de la Coopération et Organisation Sociale*. De Boeck University, Brussels.

Astruc, C., Julien, F.J., Errard, C. & Lenoir, A. (2004) Phylogeny of ants (Formicidae) based on morphology and DNA sequence data. *Molecular Phylogenetics and Evolution*, **31**, 880–893.

Baroni Urbani, C., Bolton, B. & Ward, P.S. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). *Systematic Entomology*, **17**, 301–329.

Bollazzi, M. & Roces, F. (2002) Thermal preference for fungus culturing and brood location by workers of the thatching grass-cutting *Acromyrmex heyeri*. *Insectes Sociaux*, **49**, 153–157.

Bonner, J.T. (1967) *The Cellular Slime Molds*. Princeton University Press, Princeton, New Jersey.

Cassill, D.L., Tschinkel, W.R. & Vinson, S.B. (2002) Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta*. *Insectes Sociaux*, **49**, 158–163.

Cole, B.J. (1994) Nest architecture in the western harvester ant *Pogonomyrmex occidentalis (Cresson)*. *Insectes Sociaux*, **41**, 401–410.

Depickère, S., Fresneau, D. & Deneubourg, J.L. (2004a) Dynamics of aggregation in *Lasius niger* (Formicidae): influence of polyethism. *Insectes Sociaux*, **51**, 81–90.

Depickère, S., Fresneau, D. & Deneubourg, J.L. (2004b) The influence of red light on the aggregation of two castes of the ant, *Lasius niger*. *Journal of Insect Physiology*, **50**, 629–635.

Foster, S.A. (1987) Acquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, *Thalassoma lucasanum*. *Environmental Biology of Fishes*, **19**, 215–222.

Franks, N.R. (1986) Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **18**, 425–429.

Franks, N.R. & Sendova-Franks, A.B. (1992) Brood sorting by ants: distributing the workload over the work surface. *Behavioral Ecology and Sociobiology*, **30**, 109–123.

Gordon, D.M., Paul, R.E. & Thorpe, K. (1993) What is the function of encounter pattern in ant colonies? *Animal Behaviour*, **45**, 1083–1100.

Jensen, J.J. (2000) A note on quality of light. URL http:/www.durst-pro-usa.com/quality_of_light.htm, accessed September 2003.

Lenoir, A. (1979) Le comportement alimentaire et la division du travail chez la fourmi *Lasius niger* (L.). *Bulletin Biologique de la France et de la Belgique*, **CXIII**, 1–314.

Lill, A. (1974) Sexual behaviour in the lek-forming white-bearded manakin (*Manacus manacus trinitatis*). *Zeitschrift fur Tierpsychologie*, **36**, 1–36.

Magurran, A.E. (1990) The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici*, **27**, 51–66.

Millor, J., Pham-Delegue, M., Deneubourg, J.L. & Camazine, S. (1999) Self-organized defensive behavior in honeybees. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 12611–12615.

Mirenda, J.T. & Vinson, B. (1981) Division of labour and specification of castes in the red imported fire *Solenopsis invicta* Buren. *Animal Behaviour*, **29**, 410–420.

Parrish, J.K. & Hamner, W.M. (1997) *Animal Groups in Three Dimensions*. Cambridge University Press, Cambridge.

Sempo, G., Depickère, S. & Detrain, C. (2006) Spatial organization in a dimorphic ant: caste-specificity of clustering patterns and area marking. *Behavioral Ecology*, **17**, 642–650.

Sendova-Franks, A. & Franks, N.R. (1993) Task allocation in ant colonies within variable environments (a study of temporal polyethism: experimental). *Bulletin of Mathematical Biology*, **55**, 75–96.

Sendova-Franks, A.B. & Franks, N.R. (1995) Spatial relationship within nests of the ant *Leptothorax unifasciatus* (Latr.) and their implications for the division of labour. *Animal Behaviour*, **50**, 121–136.

Trager, J.C. (1991) A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *Journal of the New York Entomological Society*, **99**, 141–198.

Tschinkel, W.R. (1999) Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: distribution of workers, brood and seeds within the nest in relation to colony size and season. *Ecological Entomology*, **24**, 222–237.

Turchin, P. & Kareiva, P. (1989) Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*, **70**, 1008–1016.

Wilson, E.O. (1971) *The Insect Societies*. Belknap, Harvard University Press, Cambridge, Massachusetts.

Wilson, E.O. (1978) Division of labor in fire ants based on physical castes (Hymenoptera: Formicidae: *Solenopsis*). *Journal of the Kansas Entomological Society*, **51**, 615–636.

Wilson, E.O. (1980a) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) I. The overall pattern in *A. sexdens*. *Behavioral Ecology and Sociobiology*, **7**, 143–156.

Wilson, E.O. (1980b) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) II. The ergonomic optimization of leaf cutting. *Behavioral Ecology and Sociobiology*, **7**, 157–165.

Wilson, E.O. (2000) *Sociobiology: The New Synthesis*. Belknap, Harvard University Press, Cambridge, Massachusetts.

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