Ritualized conflict in *Odontomachus brunneus* and the generation of interaction-based task allocation: a new organizational mechanism in ants

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Intracolonial conflict among ant workers can establish a reproductive hierarchy, with top-ranking individuals often securing oviposition opportunities. Here we show that in the ant *Odontomachus brunneus*, reproduction-based dominance interactions control worker movement and location, and that this, in turn, mechanistically governs task allocation within the colony and establishes a division of labour for nonreproductive tasks. Movement made by a worker towards the brood is mostly preceded by winning a pairwise dominance interaction, and movement away from the brood is mostly preceded by losing a pairwise interaction. Consequently, workers are distributed within the colony such that the more subordinate the individual, the more peripheral her location with respect to the reproductive centre of the nest. Behavioural roles are naturally restricted to particular zones of the colony, therefore, allocation to a particular zone, through dominance interaction, ensures role specialization. This represents a new organizational mechanism, which we call 'interaction-based task allocation'. In characterizing the dominance interactions of this species, we also identify two new behaviours: (1) 'subordinate driving', which involves a dominant individual physically manoeuvring a subordinate, by way of continued aggression, away from the reproductive centre of the nest; and (2) 'antennal shivering', which describes the antennal movements made by a subordinate immediately preceding and during subordinate driving.

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Reproductive division of labour in the eusocial Hymenoptera results in two types of individuals, those that reproduce (e.g. queens and gamergates), and those that perform nonreproductive tasks (workers). Although reproduction is carried out by morphologically distinct queens in most ant species, when multiple queens are present within the nest conflict often results. Under these circumstances, a dominant queen frequently secures the reproductive role by physically, or pheromonally, suppressing reproduction by the other queens (reviewed in Heinze 1993). The workers of most ant genera do possess ovaries of varying functionality, but under normal conditions, worker reproduction is also suppressed by the presence of the egg-laying queen so that workers only perform nonreproductive tasks. This nonreproductive labour is usually divided further among the worker caste, so that workers specialize on functionally related subsets

of tasks (roles) such as brood care, nest maintenance and foraging (Hölldobler & Wilson 1990). The particular specialized role adopted by workers is correlated, to varying degrees, with age. The youngest individuals tend to perform the brood-related tasks, and as workers age, they are more likely to perform tasks away from the brood, such as nest maintenance and eventually foraging. This phenomenon is referred to as 'temporal polyethism' (Franks et al. 1997). In a small percentage of ant species, a second type of polyethism exists in which task specialization is related to an individual's morphological form. This phenomenon is known as physical polyethism (Hölldobler & Wilson 1990) and will not be considered further in this paper. Both reproductive division of labour and polyethism have attracted a great deal of attention from evolutionary biologists and ethologists, but in ants, they have frequently been viewed as separate problems.

There are two competing hypotheses to explain division of labour among worker ants (Franks et al. 1997; Robson & Beshers 1997; Traniello & Rosengaus 1997). The first, 'age-based polyethism', suggests a causal link between age and task such that the actions of each individual are determined by an age-dependent

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behavioural programme. Age-based polyethism is only one of the hypotheses proposed to explain the phenomenon of temporal polyethism, but the two terms are often used interchangeably. To avoid confusion, we adopt the strict definitions outlined above as suggested by Franks et al. (1997).

The competing 'foraging-for-work' hypothesis suggests that task specialization is the product of each individual randomly foraging for work up or down the colony's production line of tasks (reviewed in Bourke & Franks 1995). This differs greatly from the age-based polyethism hypothesis because it does not suggest a causal link between age and task, and adopts the more recent concept of 'task allocation'. That is, the understanding that the colony is organized by simple, dynamic mechanisms that can adjust to changes in the colony's needs and assign workers to tasks accordingly.

A third hypothesis, proposed by West-Eberhard (1981), explains worker behaviour from the perspective of evolutionary origin and ultimate cause. The hypothesis suggests that defeated individuals that are prevented from engaging in direct reproduction should opt to assist with nonreproductive tasks to salvage indirect reproductive benefits. It further suggests that the behavioural role adopted by the individual is determined by which role maximizes reproductive payoff, given the associated inclusive fitness benefits and the individual's declining direct reproductive value. Thus, the pattern of worker behaviour is explained by the ultimate reproductive motivations of the individual. Inherent in this hypothesis is that this motivation explains both reproductive division of labour and the division of labour among workers.

West-Eberhard's (1981) hypothesis was based on eusocial wasp behaviour where aggressive interaction among foundresses determines the reproductive division of labour and defeated foundresses engage in nonreproductive tasks. In some species of wasps, these interactions continue even after colony founding and can involve all members of the colony, not just queens or top-ranked individuals. Furthermore, in some species, rank also correlates to task such that subordinate individuals spend more time foraging and dominant individuals spend more time on the comb (reviewed in Jeanne 1991). Until recently, it was thought that aggressive intracolonial interaction in ants only occurred between queens of polygynous or pleiometrotic species (reviewed in Heinze 1993). However, it is now known that in many species physical conflict does occur between all members of the colony, creating a reproductive hierarchy among the workers. This type of interaction is important for determining which individuals secure direct reproductive opportunities within the colony and is especially common in primitive groups (e.g. Cole 1981; Ito & Higashi 1991; Ito 1993; Peeters 1993; Heinze et al. 1994; Heinze & Hölldobler 1995; Heinze et al. 1997). Although these studies have primarily focused on the establishment of a reproductive division of labour, Ito & Higashi (1991) also reported that, for *Pachycondyla sublaevis*, low-ranking individuals were more likely to be foragers. This suggests that conflict in ants may be important for establishing both a reproductive division of labour and a division of labour for nonreproductive tasks, as in many eusocial wasps.

Our study describes the ritualized dominance interactions among workers of the ant *Odontomachus brunneus*. Particularly, we focus on how this type of interaction affects the spatial distribution of individuals, and how this, in turn, mechanistically affects task allocation within the colony. We also examine the reproductive condition of focal workers to determine whether this influences the outcome of dominance interactions.

METHODS

Field Collection and Culture Methods

Odontomachus brunneus is the sole member of its genus in northern Florida. Seven colonies were collected between April and June 1997 from the sand hills longleaf pine forests of the Apalachicola National Forest.

We maintained colonies in the laboratory at a constant temperature of 30°C. Each colony was housed in a plaster nest (7.5 × 9.0 cm), which was subdivided along the long side by a wooden splint, creating two interconnecting chambers. A single entrance/exit was provided and the nest was covered with glass. The glass was then covered with a red film filter, as this species shows unusual sensitivity to light (personal observation). Each nest was placed in its own tray whose sides were coated with Fluon® so that the ants could not escape. In all colonies, the ants arranged themselves so that the chamber furthest from the entrance contained the brood, creating three very distinct zones: the 'brood zone', the 'broodless zone' (constituting all areas within the nest, excluding the brood zone) and the 'foraging zone'. These easily identifiable zones were used to note the location of focal workers.

All colonies were fed daily on live mealworms, water and sugar water. Additionally, each colony was supplied with soil particles to provide a pupation medium for final-instar larvae.

Sampling and Marking Workers

Three of the seven colonies were chosen for observation based on their health (i.e. the successful eclosion of new workers and a large brood pile). From each, we took a stratified sample of 15 workers so that five individuals came from each of the three zones within the colony. Each worker was then marked uniquely by placing coloured fine-gauge wire around the legs and petiole. We then reintroduced these individuals to their own colonies; all individuals returned to their previous zone. All colonies were allowed to adjust to laboratory conditions for at least 6 weeks before any focal workers were marked, and the colonies were left for an additional week after marking before observations began.

Observations

Each marked worker was observed for four 15-min periods, giving a total of 60 min of observation per worker. For each colony, the 15 focal workers were observed over four complete rounds and the order of the individuals within each round was randomized. The four rounds for each colony were spread evenly over a period of 5 days, such that round 1 was started on Monday and round 4 was completed on Friday. Each focal worker was followed continuously within the 15-min observation period with the use of a freely moving microscope, and all behavioural data were recorded on audio tapes. These behavioural data included the tasks performed by the individuals, detailed descriptions of all dominance interactions, the zone in which the behaviours were performed, and all movement between zones.

Ovarian Dissections

Once behavioural observations were complete, we removed the focal workers from the colony and killed them by rapid freezing. After thawing, the workers were dissected in insect Ringer's solution to determine the condition of their ovaries. We categorized ovarian condition as one of the following: (1) swollen at the base and healthy with/without developing oocytes; (2) slender at the base and healthy without developing oocytes; and (3) withered and unhealthy without oocytes.

RESULTS

Description and Characterization of Dominance Interactions

All dominance interactions were characterized by a sequence of discrete agonistic behaviours. All agonistic behaviours were seen in both marked and unmarked individuals; however, in any given interaction, the sequence could stop at any point. The full sequence of agonistic behaviours is described below and illustrated in Fig. 1.

Rapid antennation

Interactions began with 'antennal duelling', in which two workers met head-on and clashed antennae at high speed for approximately 3 s. Rapid antennation also occurred in a side-on form, in which one worker rapidly antennated the thorax or gaster of a second worker. This second form of initial contact often led to antennal duelling.

Yielding/dominating

After an antennal duel, one individual would yield by folding its antennae and crouching such that its legs were bent at an acute angle and its coxae touched the substrate. The dominant individual would continue rapid antennation to the head and thorax of the subordinate whilst raising its body such that its femurs were parallel to the substrate.
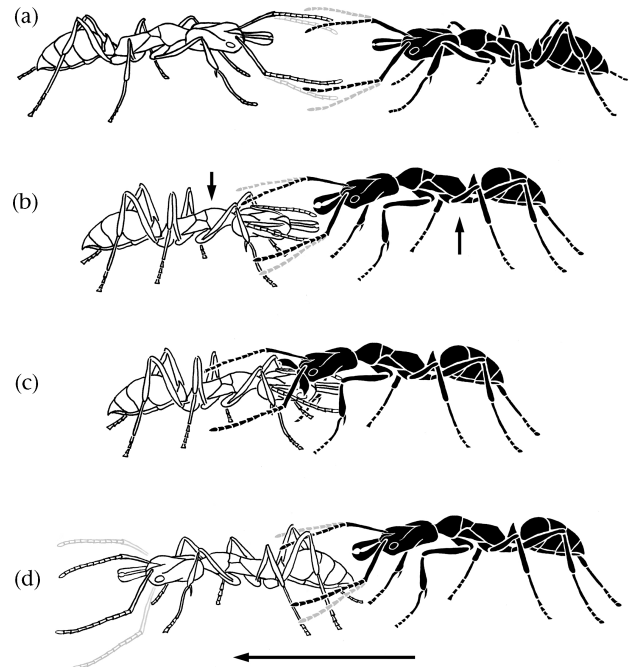

Figure 1. A dominance interaction between two workers of the ponerine ant *O. brunneus*. Illustrations show the main agonistic behaviours that comprise the dominance interaction: (a) 'rapid antennation', the initial exchange where the outcome of the interaction is decided, (b) 'yielding/domination', where body posture indicates the dominant and subordinate individual, (c) 'aggressive grooming', where aggression from the dominant can escalate, and (d) 'transition behaviours', where the actions of the dominant are directly responsible for the reallocation of the subordinate to a zone further away from the brood. Drawings by Scott Powell.

Aggressive grooming

Once the outcome of the interaction had been determined, the aggression displayed by the dominant often escalated. The dominant began grooming the subordinate, but continued rapid antennation to the head and thorax whilst maintaining a raised body posture. The dominant also periodically bit the subordinate and occasionally grasped her by the thorax, lifting her clear of the substrate. In extreme cases, the dominant attempted to sting the subordinate, but no injuries or deaths ever resulted from such behaviour.

Transition behaviour

At any point on the ascending scale of aggression, the subordinate would attempt to escape contact with the dominant by crawling away. At this point, 'antennal shivering' would frequently occur: the subordinate rhythmically vibrates her antennae such that they drum the substrate. The action of the antennae during antennal shivering is distinct from that of antennal duelling because of the rhythm, the slower speed of movement, and because the antennae were spread wider. As the subordinate moved away, the dominant frequently engaged in 'subordinate driving', which involved continued aggression from behind that appeared to guide the subordinate's direction of movement. The dominant

increased aggression by biting and grasping the subordinate's legs and gaster if she turned towards the brood, thus ensuring the subordinate was 'driven' away from the reproductive centre of the nest. Once subordinate driving was initiated, the dominant usually continued the driving action until the subordinate was fully ejected from the zone in which the interaction began. The dominant would then return to her original zone and the subordinate remained in the more peripheral location. If the driving action was relinquished, the subordinate occasionally turned back towards the brood and avoided being moved to a more peripheral zone.

Occasionally, workers close to one another adopted submissive and dominant postures without physical contact. These responses were very similar to the yielding/dominating posturing seen following an antennal duel and were treated as analogous. The analogy was based on the similarity of the behavioural response and the fact that, occasionally, contact was subsequently made and followed by 'aggressive grooming'.

All workers displayed extreme subordinate posturing without physical contact when close to their queen. In all three colonies, the queen maintained a dominant body posture at all times.

Dominance Interactions, Direction of Movement and the Spatial Distribution of Workers

A test-of-fit of log-linear models was used to examine the relationships between the following three factors: (1) the direction of movement between zones with respect to the reproductive centre; (2) the outcome of dominance behaviour prior to movement between zones; and (3) the colony. Initially, we measured the outcome of dominance behaviour prior to movement in two different ways: (1) as the last interaction prior to movement and (2) as the net result of all dominance interactions within a zone prior to a movement. Both measurements yielded almost identical results. Therefore, the analysis using the last interaction prior to movement is given here because it can be presented more clearly. The best-fitting log-linear model was one with an interaction between the direction of movement and the outcome of dominance behaviour prior to movement (G_6=7.95, N=287, P=0.24). The high P value indicates a good fit between the model and the observed data, suggesting that movement away from the reproductive centre was preceded by losing a dominance interaction, and movement towards the reproductive centre was preceded by a win. The log-linear analysis also indicated no significant colony effect, and when the data for all three colonies were combined, it showed that 98% (95% confidence interval (CI) of 94–99.6%, N=137) of focal worker movement towards the brood was preceded by a win. In contrast, 95% (95% CI of 90.2–97.8%, N=150) of focal worker movement away from the brood was preceded by a loss in a dominance interaction.

For each focal individual, it was easy to identify an 'allocated zone' as the zone in which a worker spent most of her time because of the spatially limiting actions of her nestmates. The more dominant the individual, the closer
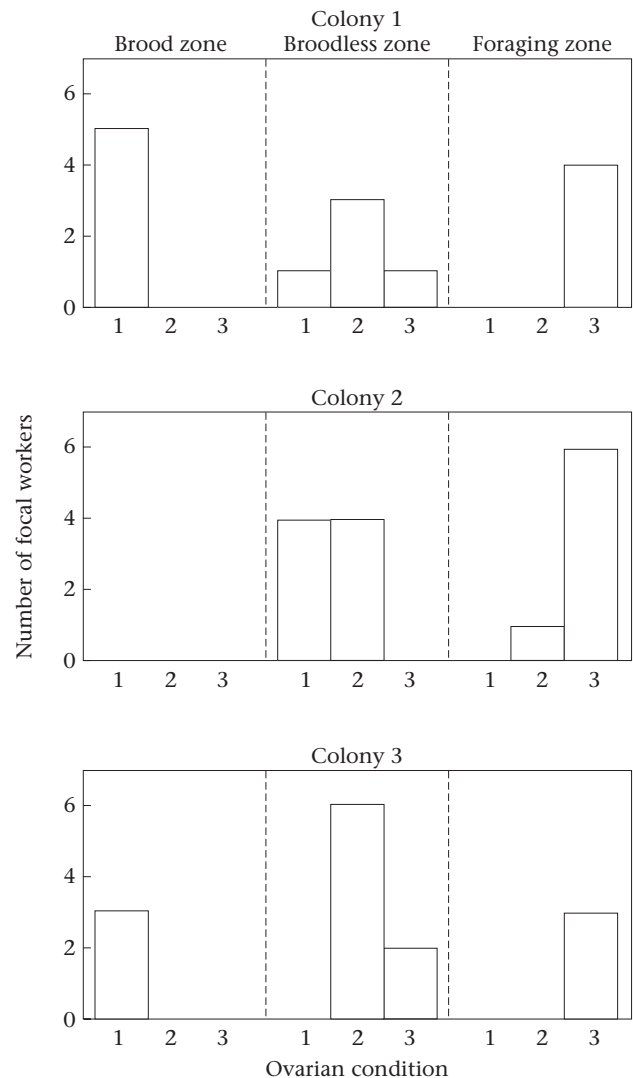

Figure 2. The relationship between the ovarian condition of focal workers and the zone in which they spent most of their time (allocated zone), for all three colonies. Ovarian condition was categorized as either: (1) swollen at the base and healthy with/without developing oocytes; (2) slender at the base and healthy without developing oocytes; or (3) withered and unhealthy without oocytes.

her allocated zone was to the brood. If a worker moved out of her allocated zone towards the reproductive centre, she quickly lost interactions with more dominant workers and was pushed back to her initial location. In all three experimental colonies, all 15 focal workers were involved in dominance interactions.

Location and Ovarian Condition

Figure 2 shows the relationship between the ovarian condition of focal workers and their allocated zone. One focal worker was lost (escaped or died) from both colony 1 and colony 3 before ovarian condition could be assessed. For all three colonies, the focal workers with the most developed ovaries occupied positions closer to
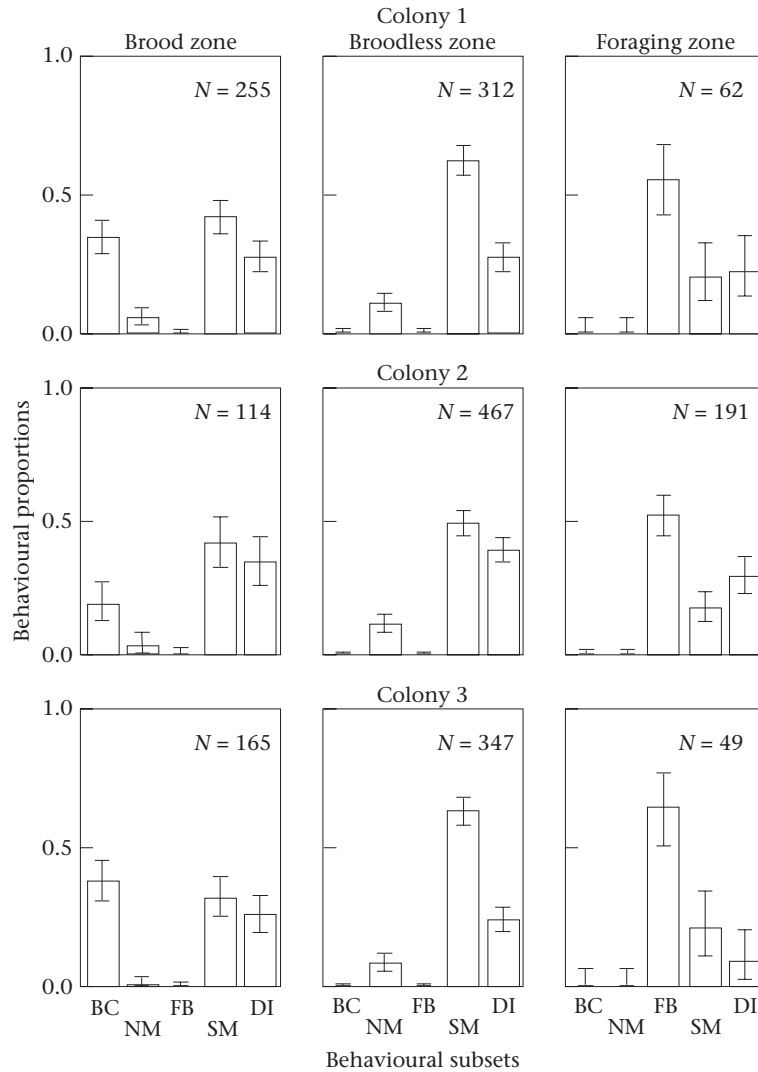
Figure 3. The proportions (with 95% confidence intervals) of particular behavioural subsets performed in the three spatial zones of the colony, for all three colonies. All observed behaviours were categorized into one of five subsets: brood care (BC), nest maintenance (NM), foraging behaviour (FB), self-maintenance (SM), or dominance interaction (DI).

the brood, whilst individuals that had an allocated zone further away from the reproductive centre of the nest (i.e. the foraging zone) had less developed ovaries.

For most of the focal individuals, their allocated zone stayed constant over the 5-day observation period with only occasional and brief movement out of this zone. A few individuals shifted to a more peripheral zone over the 5 days; for these workers the latter allocated zone was used as it represents a more accurate estimate of social status at the time of dissection.

Task Performance

To establish the spatial pattern of task performance in *O. brunneus* colonies, we examined the relationship between zone and behaviour with log-likelihood ratio tests (*G* tests). For all three colonies, a significant relationship between zone and behaviour was found (colony 1: $G_8=364.0$, $N=629$, $P<0.0005$; colony 2: $G_8=447.0$, $N=$ 772, $P<0.0005$; colony 3: $G_8=383.2$, $N=561$, $P<0.0005$). Dominance interactions and self-maintenance behaviour (e.g. grooming and eating) were performed in all zones, but the three main behavioural roles (brood care, colony maintenance and foraging behaviour) were only performed in particular zones (Fig. 3). As expected, brood care was exclusively limited to the brood zone, foraging behaviours were exclusively limited to the foraging zone, and nest maintenance behaviours were exclusively limited to the two regions inside the nest and were mostly performed in the broodless zone.

DISCUSSION

In this study, we described the ritualized dominance interaction among workers of the ponerine ant *O. brunneus*. In particular, we investigated how these interactions affected the movement and location of workers within the colony, and how this, in turn, influenced task

allocation. Movement made by a worker towards the brood was mostly preceded by winning a pairwise interaction, and movement away from the brood was mostly preceded by losing a pairwise interaction. Consequently, workers were distributed within the colony such that the more subordinate the individual, the more peripheral her location with respect to the reproductive centre of the nest. Behavioural roles are naturally restricted to particular zones of the colony, therefore, allocation to a particular zone, through dominance interaction, ensured role specialization. In addition, the dominance interactions seem to have a reproductive basis because social rank (proximity of allocated zone to the brood) was strongly related to ovarian condition. Thus in *O. brunneus*, reproduction-based dominance interactions generate a division of labour as a consequence of the interplay between the emergent spatial pattern of workers and the natural spatial distribution of particular behavioural roles. This represents a new organizational mechanism, which we name 'interaction-based task allocation'. This mechanism is especially interesting because it shows that division of labour, a pattern of behaviour that appears cooperative at the colony level, can actually be generated from selfish interactions at the individual level.

In the characterization of the dominance interactions of *O. brunneus*, we also report two new behaviours. The first, subordinate driving, represents the upper boundary of intracolonial aggression in this species and involves a dominant individual physically manoeuvring a subordinate, by way of continued aggression and physical contact, away from the reproductive centre of the nest. The second new behaviour, antennal shivering, describes the antennal movements made by a subordinate immediately preceding and during subordinate driving. Subordinate driving is the first reported instance where the aggressive actions of one worker have a consistent directional effect on a nestmate's movement.

Dominance interactions among queens have been widely documented in ants. These interactions, which are often physical, seem to play a key role in determining which queen achieves reproductive dominance, affecting the reproductive division of labour in the colony (e.g. Medeiros et al. 1992; Heinze 1993). It has recently been shown that workers also establish reproductive hierarchies through physical interaction (e.g. Cole 1981; Ito & Higashi 1991; Ito 1993; Peeters 1993; Heinze et al. 1994; Heinze & Hölldobler 1995; Heinze et al. 1997). To our knowledge, this is the first study in ants to demonstrate that reproductive dominance interactions among workers can function as a mechanism of task allocation. This suggests that reproductive conflict may function as a mechanism of both reproductive and nonreproductive division of labour. In addition to the data presented here, the reproductive basis of the dominance interaction among workers is supported by our observation that dominant workers will quickly begin oviposition after the queen's death.

In agreement with West-Eberhard's (1981) hypothesis, we showed that the reproductive capability of workers is important in the social organization of *O. brunneus* because of the establishment of a reproductive hierarchy.

However, we also showed that the role adopted by each individual is driven by the actions of nestmates, not by individualistic considerations of inclusive reproductive value. This suggests that alternative behavioural mechanisms may underlie the ultimate cause proposed by West-Eberhard (1981). Put simply, in *O. brunneus*, despite the ultimate reproductive motivations of the individual, task allocation within the colony is achieved through a mechanism of social interaction. The central importance of social interaction and the resulting spatial pattern of individuals make this organizational mechanism novel.

In almost every species of ant studied, a correlation between age and task has been found; a phenomenon defined as temporal polyethism. So overwhelming are the reports of this correlation that any mechanism seeking to explain colony organization must account for it. In most of the known ant genera, workers still posses ovaries, and these ovaries have been widely reported to senesce (Hölldobler & Wilson 1990). We propose that in 'interaction-based task allocation', ovarian condition functions as the means of comparison in the social interactions that organize the colony. As an individual's ovarian condition declines with age, her social status decreases and she is allocated, through social interaction, to progressively more peripheral zones and consequently different roles. Thus, colony organization established by this mechanism will create an age–task correlation. In the few highly derived genera that have completely sterile workers, it is possible that a mechanism of social interaction still underlies task allocation even though the ultimate motivations may have changed.

We showed that ritualized conflict among *O. brunneus* workers organizes the colony through the establishment of a social hierarchy. Contrary to previous understanding, similar dominance interaction among workers occurs in a number of ant genera, and seems especially common in primitive groups (e.g. Cole 1981; Ito & Higashi 1991; Ito 1993; Peeters 1993; Heinze et al. 1994; Heinze & Hölldobler 1995; Heinze et al. 1997). Such overt aggression, however, is not present in most of the more derived groups, so how can hierarchical interaction and its organizational properties still exist? A number of alternative nonmutually exclusive forms of interaction are likely. The first, and most obvious, is that the vigour of the antennal contact seen in dominance interactions has declined so that hierarchical information is still exchanged through the antennae, but the interaction is far more subtle. In all species of ants, the continuous antennal contact that occurs among nestmates functions as a means of communication (Hölldobler & Wilson 1990), thus easily allowing for the communication of hierarchical information. Secondly, hierarchical interaction can occur via pheromonal communication. We showed that *O. brunneus* queens adopt a dominant posture at all times, and that all workers adopt a subordinate posture when close to her without the need for physical contact. This can most readily be attributed to pheromonal communication of reproductive dominance, a reported phenomenon that is widely accepted. Occasionally, workers changed posture in a similar manner when in the proximity of each other. Like the

non-physical and unapparent hierarchical interaction that is accepted to occur between ant queens and workers, there may be similar and commonplace subtle dominance interaction among workers. These interactions may not be obvious to researchers.

In many ant species, especially those from the more derived groups, food is shared orally among group members by liquid food exchange or stomodeal trophallaxis (Hölldobler & Wilson 1990). This may serve as another alternative hierarchical interaction in the absence of physical conflict. Stomodeal trophallaxis primarily serves to distribute nutrients among group members, however, it is also thought to have a number of other functions. Although it appears to be a highly cooperative behaviour, food is frequently not shared equally. In a number of ant species, dominant individuals solicit liquid food from subordinates such that they gain a disproportionately large share of the colonies nutrition, suggesting that trophallaxis has a hierarchical component (e.g. Cole 1981; Franks & Scovell 1983; Bourke 1988). Furthermore, Liebig et al. (1997) suggested that food sharing might have evolved as an appeasement behaviour during aggressive interactions. Thus, trophallaxis not only represents another alternative form of hierarchical interaction in the absence of overt dominance interactions, but it may even be evolutionarily linked to intracolonial conflict among workers.

The new mechanism of task allocation presented here still requires rigorous empirical and theoretical testing before its generality can be satisfactorily assessed. Despite this, it is possible to highlight what it can contribute, even at this early stage. First, the mechanism is based on behavioural interactions that are almost universally observable in primitive groups, namely, reproductive conflict. This mechanism then may explain why task specialization is so widespread in the eusocial Hymenoptera. Put plainly, a seemingly cooperative division of labour may be an inevitable product of the interplay between the natural location of behavioural roles within Hymenopteran societies and the emergent distribution of individuals produced by reproductive conflict. Second, a complex pattern of colony organization is achieved from simple rules of interaction in pairwise encounters, suggesting that the system is self-organizing. Clearly, the dynamics of the mechanism are not yet understood, but observations on O. brunneus suggest that the rate of social interaction might act to reallocate workers in accordance with changing colony needs. For example, under conditions of limited food supply, the rate of interaction and level of aggression within the nest drastically increased. This caused a marked increase in the number of individuals being pushed into the foraging arena, resulting in an increase in the size of the foraging force.

Finally, we must consider the limits of interaction-based task allocation. What it provides is an evolutionarily consistent, potentially self-organizing mechanism for establishing and maintaining a simple division of labour in the colony. Task allocation in Hymenopteran societies can be extremely complex in the more derived groups and is most likely a multilayered process. Clearly,

it is very likely that secondary organizational mechanisms may have evolved that increase the ergonomic efficiency of the colony. Thus, interaction-based task allocation is not mutually exclusive with other explanations of colony organization, we simply propose that it represents the base mechanism upon which other adaptations have been built.

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