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Emergence of increased division of labor as a function of group size

Raphaël Jeanson · Jennifer H. Fewell · Root Gorelick · Susan M. Bertram

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Abstract Empirical evidence suggests that division of labor in insect societies is positively related to group size both within and across taxa. Response threshold models (RTM) have been commonly used to analyze patterns of division of labor. However, these models have been explored empirically and theoretically for only a limited number of tasks, and few studies have examined predictions of the model as colony size and work availability change. We theoretically examine how group size influences division of labor using a fixed response-threshold model. We simultaneously explore how expected by-products of increased colony size, including demand (total work need relative to total work force available) and task number, affect this relationship. Our results indicate that both low demand and high task number positively influence division of labor. We suggest that these changes parallel what is observed within social groups as their size increases, and that, in part, the commonly observed increased division of labor with increasing group size is emergent.

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R. Jeanson (✉)
Centre de Recherches sur la Cognition Animale, CNRS UMR 5169, Université Paul Sabatier,
118, Route de Narbonne,
31062 Toulouse, France
e-mail: jeanson@cict.fr

J. H. Fewell
School of Life Sciences, Arizona State University,
Tempe, AZ 85287-4501, USA

R. Gorelick · S. M. Bertram
Department of Biology, Carleton University,
1125 Colonel By Drive,
Ottawa, ON K1S 5B6, Canada

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Introduction

Division of labor, where different units within a system perform different tasks, is a recurrent property of associations of multiple entities and a hallmark of social living. This fundamental property has been described across a diversity of social taxa, from simple to complex groups. However, empirical evidence suggests that division of labor in social groups increases with increasing group size (Bourke 1999; Anderson and McShea 2001). Larger group size is phylogenetically correlated with more complex and derived sociality, as seen recurrently within the social insects (Oster and Wilson 1978), suggesting that the pattern may reflect selection acting to increase individual specialization. However, there is also a trend towards increased division of labor during social ontogeny, as social groups grow from a few individuals to many (Darchen 1964; Karsai and Wenzel 1998; Thomas and Elgar 2003). In this study, we test the hypothesis that the often assumed positive relationship between division of labor and group size is at least in part emergent, that changes in dynamics as groups increase in size generate higher levels of division of labor. To do this, we produce a model that can be generalized to all social systems from insects to vertebrates and that can explain both phylogenetic and ontogenetic patterns of increasing division of labor with increased group size.

A general rule of systems complexity states that the size of the system dictates the degree of specialization (Bell and Mooers 1997; Bonner 2004). For example, in multicellular organisms, there is a positive relationship between number of cells (indicative of organismal size) and number of cell types, with cell diversity interpreted as physiological division of labor among cell types. In volvocine algae, specialization between somatic cells responsible for movement and reproductive cells is correlated with size (Bonner 1993, 2004). In the algae *Eudorina*, a germ-soma division of labor develops only in colonies that reach 32 cells or more (Bonner 1998). It has been hypothesized that an increase in organismal size selects for additional cell types to satisfy energy requirement imposed by biophysical constraints (McCarthy and Enquist 2005). This trend holds across social systems as well (Anderson and McShea 2001, Bonner 2004). In human societies, there is a positive relationship between the number of organizational traits (crafts and occupations) and group size. In India, the smallest state has a population of 40,000 with 13 occupations, while the largest state has 110 million inhabitants and offers 142 occupations (Bonner 1993). Both for organisms and social groups, increased size impose changes, including enhanced division of labor (Bonner 2004).

Empirical studies showed that the social context, in particular colony size, influences the ergonomics of insect societies. For instance, colony size shapes the exploratory and foraging responses in ants, and an increase in worker number triggers the formation of more efficient foraging networks (Beekman et al. 2001; Mailleux et al. 2003). In wasps, the delay experienced by workers during transfer of materials for nest construction decreases with group size due to the reduction of stochastic fluctuations (Anderson and Ratnieks 1999). Increased colony size can also affect the rate of interactions among workers and thus contribute significantly to the efficient allocation of individuals to different tasks (Pacala et al. 1996; Naug and Gadagkar 1999).

Empirical evidence also indicates that group size positively influences division of labor in social insects (Bourke 1999; Anderson and McShea 2001). For example, small colonies of independent-founding Polistinae wasps typically exhibit less task specialization than swarm-founding wasps characterized by larger colonies (Jeanne 1991a; O'Donnell 1995; Karsai and Wenzel 1998). Workers from large colonies (more than 450 workers) of ponerine ants (*Rhytidoponera metallica*) exhibit a higher degree of task specialization than workers from small colonies (fewer than 80 workers; Thomas and Elgar 2003). Variation in colony size during ontogeny also appears to affect task specialization. At the initial stages of colony foundation, workers tend to be generalists. For example, workers of the wasp *Vespa orientalis* perform all tasks in the first stages of colony development, whereas mature colonies exhibit task specialization and division of labor (Darchen 1964).

Several different models have been put forth to explain the origins of division of labor (reviewed in Beshers and Fewell 2001). Of these, the response-threshold models postulate that division of labor arises from variation among workers in their internal thresholds to external stimuli (Robinson and Page 1989; Bonabeau et al. 1996). When the stimulus for a task exceeds a worker's threshold, this increases the probability that the individual performs the task. Task performance reduces the intensity of the stimulus, consequently reducing the likelihood that the task will be executed by other workers with higher thresholds. The contribution of response thresholds to task organization has been experimentally demonstrated for several tasks, including fanning (Jones et al. 2004), undertaking (Robinson and Page 1988), and foraging in honey bees (Pankiw and Page 2000; Fewell and Page 2000), as well as nest moving (Meudec 1979) and foraging (Stuart and Page 1991) in ants. Response thresholds have also garnered strong theoretical support (Robinson and Page 1989; Bonabeau et al. 1998; Page and Mitchell 1998; Gautrais et al. 2002; Myerscough and Oldroyd 2004; Waibel et al. 2006). These models all reveal that when workers exhibit variable response thresholds, division of labor can result.

Although increasing group size is central to the ontogeny and evolution of social groups, only a handful of theoretical studies to date have examined the impact of group size on division of labor (Gautrais et al. 2002; Merkle and Middendorf 2004). These models incorporated self-reinforcement on individual thresholds, in which individual tendency to perform a task increases or decreases dependent on whether they have performed the task previously. Gautrais et al. (2002) developed a two-task model to investigate how colony size and demand affect task specialization. They concluded that self-reinforcement can drive an increase in task specialization with group size. Merkle and Middendorf (2004) re-examined this model but argued that the results obtained by Gautrais et al. (2002) originated partly from an artifact due to the initial conditions of the simulations. Merkle and Middendorf (2004) revised the threshold reinforcement model to implement a competition between individuals during task selection (i.e., individuals with the lowest threshold for a task are more likely to perform it). This extension of the initial model can generate enhanced task specialization with group size. The addition of self-reinforcement to the response threshold model (RTM) is biologically realistic for many taxa with derived sociality, such as the eusocial insects; it provides a mechanism for temporal variation in individual thresholds that occur as a result of experience, learning and/or aging (Plowright and Plowright 1988; Theraulaz et al. 1998). For instance, it has been experimentally shown that individual response thresholds for bumblebee workers fanning to control nest climate vary with experience (Weidenmüller 2004). However, the inclusion of self-reinforcement into division of labor models necessarily produces a strong positive feedback loop that can mask other effects. Additionally, because it may not be present in all systems, it reduces the generality of the model. So far, no study has examined whether a simple response-threshold model can generate enhanced specialization with increasing colony size without self-reinforcement. In this study, we use a fixed threshold model to simultaneously explore how group size and its correlates, tasks number (i.e., the total number of independent tasks), and task demand affect division of labor.

Empirical research indicates that task number increases both phylogenetically and ontogenetically with increasing group size (Oster and Wilson 1978; Wilson 1976, 1980). Simple mature societies, such as the ponerine ants *Amblyopone pallipes*, tend to perform 5–10 tasks (Traniello 1978), while more complex social groups such as the Myrmicinae or honeybees perform 20–40 tasks (Oster and Wilson 1978; Kolmes 1985; Seeley 1995). For a given species, increased group size can subsequently affect work processing among individuals so that tasks are subdivided or additional tasks are added (Pacala et al. 1996; Anderson and Ratnieks 1999). In the ponerine ant *Ectatomma ruidum*, workers both hunt and transport prey back to the nest when they are in small groups (less than 16 workers); in large groups, hunting and transporting prey are partitioned into two distinct tasks performed by different workers (Schatz 1997). RTM have only just begun to explore how division of labor may be affected by task number and have only focused on how division of labor is influenced by one to five tasks (Bonabeau et al. 1998; Waibel et al. 2006).

Another expected by-product of increasing group size is a reduction in the need for tasks to be performed relative to the availability of workers to perform them, a parameter referred to as demand (see Gautrais et al. 2002). Because of the added energy and maintenance requirements from increasing the number of individuals in a group, task need should increase with group size at some rate. However, we assume that worker availability to perform tasks should increase faster than the additional task requirements from adding those workers, effectively increasing the proportion of inactive or reserve individuals within the colony. Thus, demand should decrease with group size.

Empirical evidence supports this assertion. Colony investment in patrolling grows at a lower rate than population size in the ant *Lasius niger* (Mailleux et al. 2003). Removal of workers in honeybee colonies leads to an increase in task performance of the remaining individuals (Kolmes and Winston 1988). Experimental removal of worker ants increases the activity (i.e., mean time spent performing tasks) of remaining individuals in *Erebomyrma* (Wilson 1986). Further, individual activity decreases with colony ontogeny in the ant *Ectatomma* (Lachaud and Fresneau 1987).

The reduced demand consequent with increased group size should positively affect division of labor. Assuming that each individual differs in its response threshold for each task, workers with the lowest thresholds should be the first to become active when there is a task need. These workers should therefore become task specialists. However, individuals with higher thresholds for the available tasks should remain inactive for a much higher percentage of their time, as colony tasks are taken care of before their thresholds are met.

Model

Our model was implemented using Monte Carlo simulations in Java (www.jbuilder.com).

Intrinsic variation among individuals in their thresholds

Before each simulation run, a threshold θT_j associated to task T_j was determined for each individual by generating random deviates according to a normal distribution with mean μ (μ=50; arbitrarily chosen) and standard deviation σ. The intrinsic variation ranged from zero (no variation among individuals) to a standard deviation of 15 (extensive variation among individuals). For simplicity, μ and σ were assumed to be identical for all tasks. This does not mean that thresholds for all available tasks for a given individual were identical. Thresholds assigned to a given individual remained constant for the whole simulation run, i.e., there was no self-reinforcement or forgetting.

Group size was 2 to 1,000 individuals.

Task number included 2 to 20 tasks.

Probability of performing task

In the model, any individual can be in two states: inactive or engaged in one task. At each time step, an inactive individual i randomly encounters all available tasks. An individual starts performing the first randomly encountered task for which the intensity of the stimulus is higher than its corresponding intrinsic threshold. The level of stimulus for any given task perceived individually by workers and compared to their individual response thresholds is determined by the total level of the stimulus associated with that task divided by group size.

Probability of stopping task performance

Once engaged in a task, T_j, an individual can spontaneously cease working with probability $1/\tau$ (τ, characteristic time of task performance; $\tau=5$ time steps, arbitrarily chosen). This means that the probability to stop performing a task does not depend upon stimulus intensity and that an individual performs any given task for an average duration of τ. The random duration of task performance within the model adequately captures empirical variation in task performance, including excavation in halictine bees (Jeanson et al. 2005) and nest building in ants (Franks and Deneubourg 1997).

Demand

Demand represents the total colony effort required to complete all tasks relative to the available total effort from workers. In a colony with low demand, worker inactivity will be high because the availability of workers to perform tasks is greater than current stimulus levels across all tasks. In a growing colony, we expect that worker number, and thus total potential work available, increases more rapidly than the increased need for work created by adding colony members. Thus, demand should decrease with colony size. For $\delta<1$, the stimulus across tasks increases less than the maximal amount of work the colony can perform. For simplicity, demand was identical for all tasks. The demand parameters explored were $\delta=0.7$, $\delta=0.9$, $\delta=1$, and $\delta=1.1$.

Stimulus intensity

Each time a task T_j is performed by an individual, the stimulus intensity S_j is decreased by an amount α ($\alpha=3$, arbitrarily chosen). For each time step, the level of the stimulus S_j associated to task T_j is increased by β_j:

$$\beta_j = \alpha \frac{N}{T} \delta \tag{1}$$

where N is the group size (number of individuals), T the tasks number, and δ the demand. The rate of stimulus regeneration is identical for all tasks and does not vary over time.

Each simulation lasted 5,000 time steps. At the beginning of each simulation, the intensity of the stimulus was set to zero. The stimulus intensities associated with each task were updated at the beginning of each time step.

For each time step and each individual, the order of tasks was randomly determined. In total, 100 replicates were performed for each condition tested.

Data analysis

We quantified the intensity of division of labor (DOL) with an index developed by Gorelick et al. (2004) that derives from Shannon's (1948) mutual entropy index. The DOL statistic measures the degree to which different individuals within a group specialize on different tasks and the degree to which each individual is a specialist. By definition, inactive workers do not contribute to colony work; instead, inactivity is the null condition that thresholds are not met. Consequently, inactivity was not considered as a task when computing DOL statistics. To calculate DOL, we generated a matrix of task performance, in which each cell contains the frequency with which a specific individual was observed performing a specific task. The matrix was normalized so that the total of all cells added to one. From this matrix, we calculated Shannon's index, H_{tasks} for the distributions of individuals across tasks (see Gorelick et al. 2004 for detailed methodologies) and mutual entropy for the entire matrix. Mutual entropy divided by the Shannon's index H_{tasks} yields an index that ranges from 0 (no division of labor) to 1. For each condition explored, the DOL statistics were averaged across all simulations runs ($n=100$).

Results

Our model explored how variability of response thresholds ($\sigma=0$, 5, 15), group size (2 to 1,000 individuals), task number (2, 5, 10, and 20 tasks), and demand ($\delta=0.7$, 0.9, 1, and 1.1), influenced division of labor. We found a general pattern in which division of labor increased with increasing group size, but only within certain parameter limits.

Consistent with the assumptions of the threshold model, variation in response thresholds was a requirement for division of labor. No division of labor arose when response thresholds did not vary among individuals ($\sigma=0$). Division of labor appeared at the lowest tested variance ($\sigma=5$), and changing variances above this level did not have a strong effect (Fig. 1).

With variance in thresholds, division of labor became strongly influenced by group size, task number, and demand. The three variables showed an interaction effect. The influence of task number and group size on division of labor changed as demand moved above or below one, the point at which total task need matches total worker availability (see Eq. 1). When need for work exceeded the amount of work that could be performed ($\delta>1$), division of labor again did not arise (Fig. 1). Under this scenario, stimulus intensities associated with all tasks were above the amount of work the group could perform at each time step. The stimulus intensity of each individual task, therefore, quickly rose above the threshold of any individual so that all workers became equally likely to perform any task at each time step, regardless of thresholds.

Division of labor became more positively affected by group size and task number as demand moved below one.

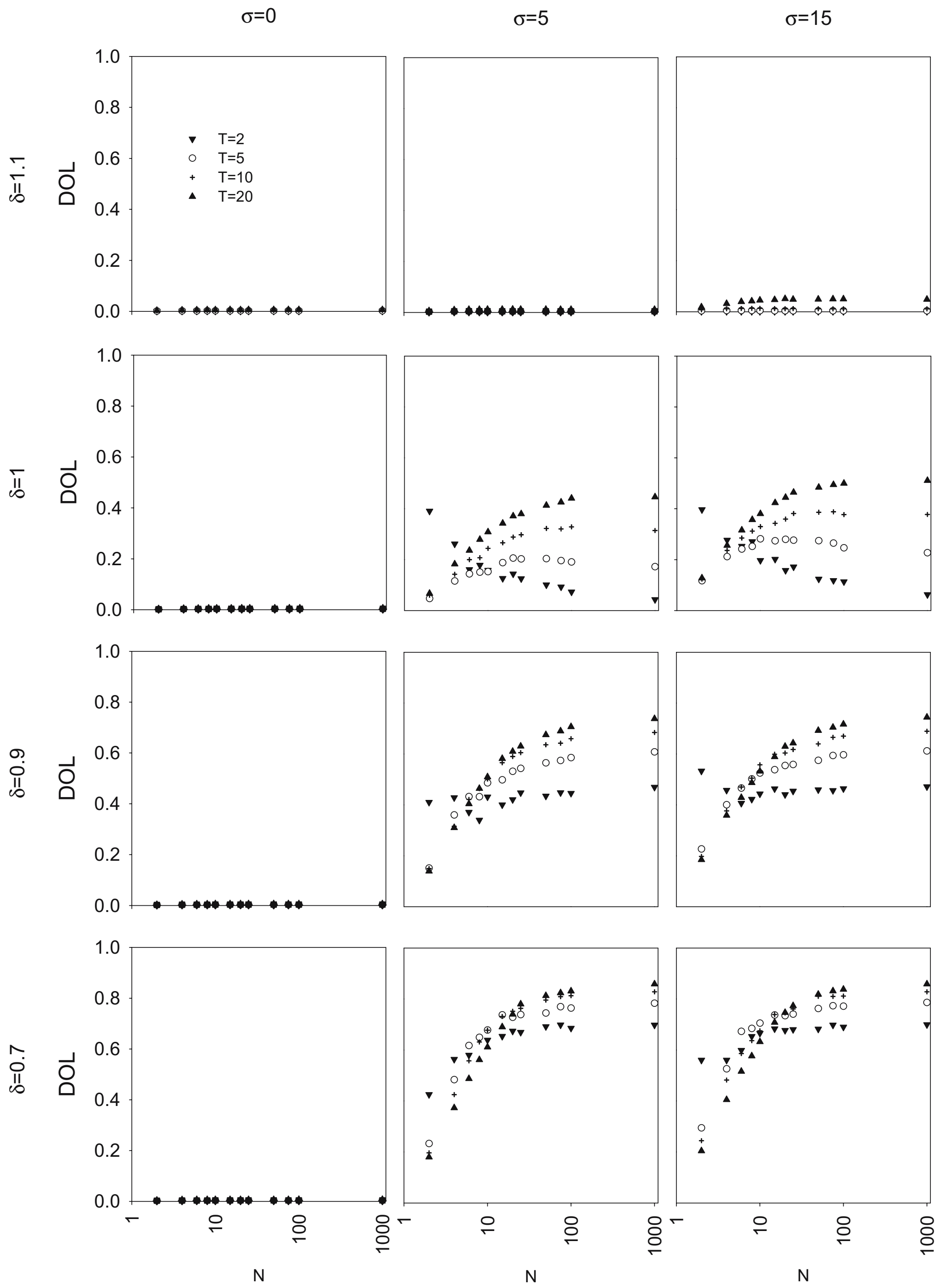

Fig. 1 Influence on division of labor of variance in response thresholds (σ), task demand (δ), and task number (T) as a function of group size (N)

The effect of task number on division of labor was generally positive, but the impact of number of tasks on division of labor was dependent on demand. At a demand of one and a low number of tasks (2–5), division of labor actually decreased with increasing group size (see below). However, it increased with group size when 10 or 20 tasks were available (Fig. 1). The importance of a high task number for division of labor became less intense as demand dropped below one (δ=0.9, 0.7; Fig. 1); at δ<1 division of labor increased with both increasing task number and increasing group size, plateauing between 100 and 1,000 individuals.

The increasing importance of task number as demand increases is consistent with model dynamics. At δ=1, tasks are filled only when all individuals are active, which often does not occur because not all individuals encounter tasks with stimulus levels above their thresholds. At this demand level, increasing group size actually negatively affects division of labor because it increases the likelihood that some individuals will have, by chance, high thresholds for

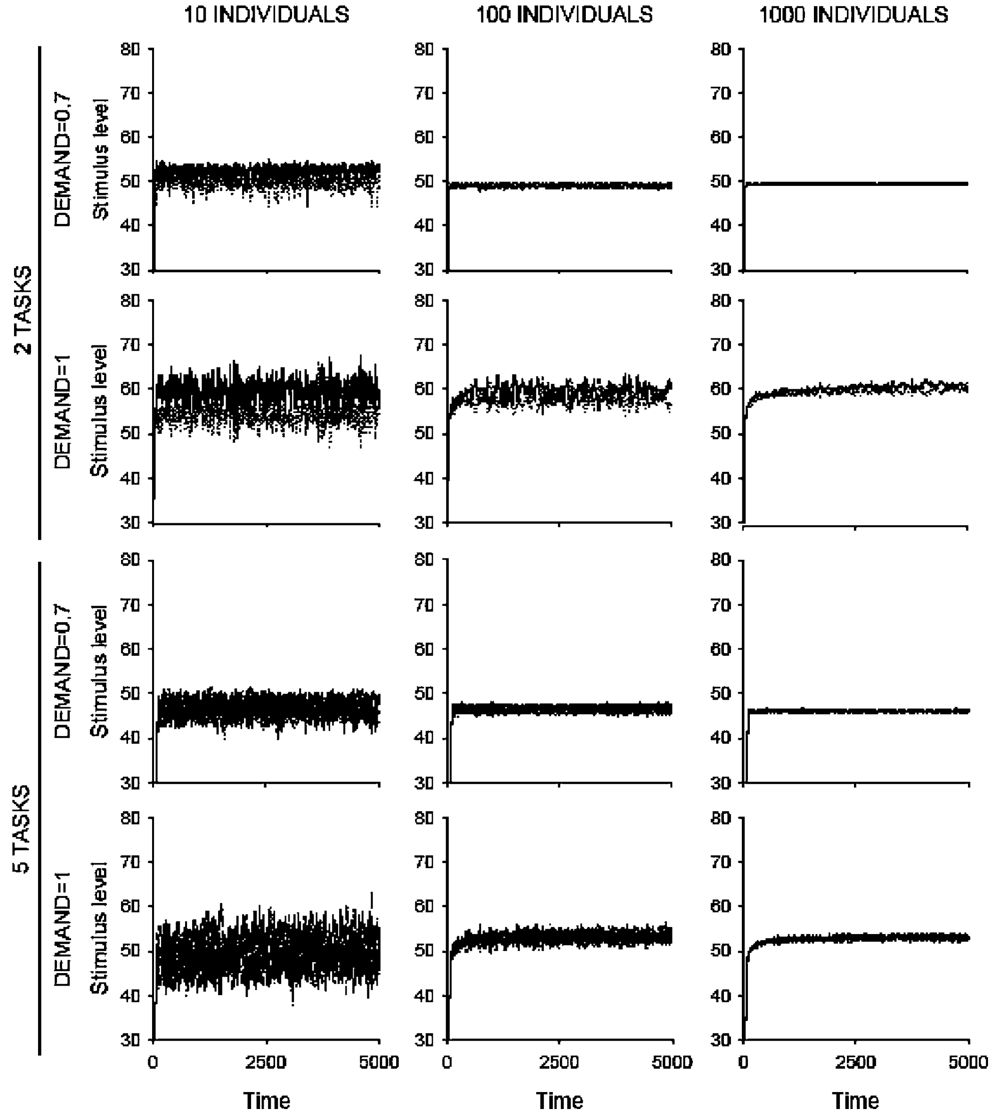

Fig. 2 Representative patterns of the stimulus levels over time for 10, 100, and 1,000 individuals with two and five available tasks for a demand of 0.7 and 1. Variance=5. One simulation per condition is indicated

all tasks. They remain inactive over multiple iterations until the stimulus level of some task reaches their internal thresholds. While they are inactive, stimuli for multiple different tasks accumulate and eventually exceed the thresholds of all individuals. As each individual with lower thresholds ends a task bout, they are equally likely to start performing any other task because the stimulus level of all tasks is high. Thus, task specialization is reduced. Increasing task number offsets this effect by distributing individual stimulus levels across a larger number of tasks.

As demand decreases below one, fewer individuals are needed to perform the available tasks. Although individuals with high thresholds for all tasks may remain inactive, their presence is not detrimental to task specialization because all work is completed at each time step and so stimulus levels do not accumulate. Consequently, most individuals switch between inactivity and activity for the tasks for which they have the lowest thresholds. Overall, the interplay between lower demand and inter-individual variability in the response thresholds enhances division of labor.

The magnitude of fluctuations in stimulus levels throughout the course of the simulation is also important to division of labor because high fluctuations in stimulus levels rapidly change the probabilities of individuals choosing a specific task. We found significant effects of group size on fluctuations in stimulus levels (Fig. 2). These fluctuations consistently decreased with increasing group size and with decreasing demand. The decrease in stimulus variance with larger group size partially offsets the negative affect of group size on division of labor seen under some parameter conditions. Increasing group size decreases relative variance in the distribution of thresholds among workers, increasing the likelihood that similar subsets of workers would be distributed across each of the different tasks. This effect is similar to that of increased population sampling decreasing the likelihood of sampling error via

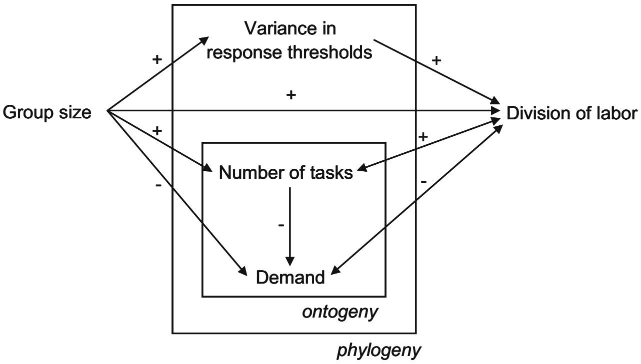

Fig. 3 Influence of group size on division of labor. All three effects can account for phylogenetic differences on the intensity of division of labor; both variations in the number of tasks and demand are also involved during colony ontogeny. *Plus and minus symbols* depict positive and negative influences respectively

random effects. Similar effects contribute to the reduction of queuing delays and improve task partitioning efficiency during foraging in wasps (Anderson and Ratnieks 1999).

Overall, our simulation results indicate that positive or negative effects of task number and group size on division of labor are interdependent with level of demand. A demand above one prevents task specialization regardless of group size and task number. For a demand of one, the increase in division of labor with group size is highly dependent on task number, and division of labor can be negatively affected by group size when task number is low. However, this dependence is less important as demand decreases; at demand levels below one, both group size and task number positively affect division of labor.

Discussion

In this study, we examined how increased group size and its correlates (number of tasks and demand) affected the intensity of division of labor. We assumed that individuals responded to task stimuli when the stimulus exceeded their fixed threshold and that their thresholds did not vary with experience. Given these simple assumptions, we found that division of labor increased with group size under most conditions, but was dependent on parameters that are likely byproducts of increased group size.

Previous theoretical findings revealed that task specialization should increase with group size. These findings not only used similar assumptions to ours but also incorporated self-reinforcement (Gautrais et al. 2002; Merkle and Middendorf 2004). Our results suggest that self-reinforcement is not necessary to drive the positive relationship between group size and division of labor, making the threshold model more universally applicable across social systems, as well as other biological systems that show changes in group size and behavioral differentiation.

Our model output supports the assertion that by-products of increasing group size, namely demand and task number, can positively influence division of labor. The increasing number of tasks and reduced demand modeled here likely parallel variations in group size as colonies grow ontogenetically (Fig. 3). However, their relative influence on division of labor may differ depending on colony life-history stages. Changes in task number are likely to be strongest during early colony ontogeny, at a stage where group size is lower. As colonies mature, the number of tasks performed within the colony should plateau. Once colonies express the number of tasks typical of mature groups, but continue to grow, reductions in demand should become a stronger influencing force on division of labor. The changes in task number within the model match observational data. The number of available tasks is directly linked to the number of individuals in the group, as need, and opportunity for new tasks arise during colony ontogeny. For example, in fungus-garden ants, the first workers tend to brood. Foraging only begins when the colony has reached a critical size (Fernandez-Marin et al. 2003). Nectar collection in the wasps of the genus *Vespula* is partitioned in mature colonies but not in young colonies (Jeanne 1991a). Comparisons across taxa also suggest enhanced task partitioning with colony size. For instance, the evolution toward larger colonies parallels increased division of labor in swarm-founding wasps (Jeanne 1991b; O'Donnell 1995). In eusocial halictine bees and bumblebees, colonies of a few dozen individuals do not partition food collection and storage (Anderson and Ratnieks 1999; Michener 1974). However, in honeybee colonies, foraging and storage involve different workers (Seeley 1995).

Our results also reveal that division of labor is negatively associated with demand (the need for work to be completed relative to the number of available workers). This theoretical finding is supported by empirical evidence. In the wasp *Ropadilia marginata*, behavioral observations indicate that an increase in demand is met by an increase in the number of active workers and eventually; as the need for work increases further, workers increase their task generalization (Naug 2001). Work requirements should increase with worker number, as new space and resource requirements are added. However, additional work requirements should not match the increase in potential work output and efficiency from adding individuals. Decreasing demand generates an increase in the proportion of inactive workers. Our model suggests that this promotes division of labor. Changes in the demand associated with completing all tasks could also contribute to the behavioral ontogeny of task specialization. For instance, variations in the demand for hygienic behaviors induced by changing the genotypic composition of honeybee hives—and consequently the number of individuals competent to perform this task—

alter the ontogeny and persistence of task specialization (Arathi and Spivak 2001).

Our model makes the testable expectation that the presence of inactive workers is a by-product of decreasing demand with colony size. However, maintaining a pool of inactive workers might be adaptive, insofar as this provides reserve workers to face unexpected fluctuations experienced by colonies (Anderson and McShea 2001). In the context of foraging, inactive workers can be recruited to reduce the delay for load transfer between foragers and receivers. Thus, a pool of inactive workers might act as a buffer to minimize queuing delay experienced by workers and thereby enhance task partitioning efficiency (Anderson 2001; Anderson and Ratnieks 1999; Jeanne 1991b; O'Donnell 1998). A correlation between individual inactivity and group size can also originate from more efficient worker allocation induced by the parallel treatment of work via task partitioning. In enhancing the overall efficiency in task performance, large group size can favor a reduction in individual work load. Thus, an increase in task number or an increase in task partitioning with group size might reduce demand, in turn promoting task specialization (Fig. 3).

Phylogenetic differences in the variance in response thresholds could also account for the increased division of labor with group size reported across taxa (Fig. 3). However, the relative significance of colony size in the evolution of specialization is also influenced by the ecological and evolutionary variations between basal and more derived clades (Traniello and Rosengaus 1997). Comparative analyses on mating frequency in various ant species reveal a positive relationship between colony size and polyandry (Cole 1983; Boomsma and Ratnieks 1996; Murakami et al. 2000; Fjerdingstad and Crozier 2006). Although the expression of the underlying diversity in variance of thresholds within a group might depend on colony size, one could also expect that the range of thresholds among workers depends upon the number of queens producing workers (i.e., pleometrosis and polygyny) and/or the number of males the queen(s) mated with (degree of polyandry). Genetic diversity among individuals should promote the expression of different thresholds and enhance division of labor (Robinson and Page 1989; Bonabeau et al. 1996; Beshers and Fewell 2001; Myerscough and Oldroyd 2004). Across taxa, the interplay between group size and enhanced division of labor may thus benefit from multiple mating of queens (Oldroyd and Fewell 2007).

In this study, we focused on behavioral differentiation among workers assuming the existence of a single physical caste, but our conclusions could be extended to species with morphological castes. Workers of different physical castes differ in their response thresholds such as in the dimorphic ant *Pheidole pallidula* where minors and majors exhibit different thresholds for foraging and defense (Detrain and Pasteels 1991, 1992). Moreover, the number of physical castes is believed to be positively correlated with group size (Wilson 1980; Bonner 1993; Fjerdingstad and Crozier 2006). In increasing the variance in response thresholds among workers, the morphological diversification could thus further contribute to the increased specialization in large colonies.

In conclusion, our model provides insight into possible mechanisms contributing to division of labor. An increase in division of labor could parallel an increase in group size directly via the distribution of thresholds within groups and indirectly via by-products of increased group size (i.e., task number and demand; Fig. 3). These indirect effects of increased group size could, therefore, have shaped early social evolution and driven social systems characterized by highly cooperative large groups.

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