

Original Article

# Division of labor increases with colony size in the harvester ant *Pogonomyrmex californicus*

C. Tate Holbrook, Phillip M. Barden, and Jennifer H. Fewell

School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe, AZ 85287-4601, USA

Size has profound consequences for the structure and function of biological systems, across levels of organization from cells to social groups. As tightly integrated units that vary greatly in size, eusocial insect colonies, in particular, are expected to exhibit social scaling relations. To address the question of how social organization scales with colony size, we quantified task performance in variably sized colonies of the harvester ant *Pogonomyrmex californicus*. We found a positive scaling relationship between colony size and division of labor in 2 different contexts. First, individual workers were more specialized in older, larger colonies. Second, division of labor increased with colony size, independently of colony age. Moreover, the proportional allocation of workers to tasks shifted during colony ontogeny—older, larger colonies performed relatively less brood care—but did not vary with colony size among same-aged colonies. There were no colony-size effects on per capita activity or the distribution of activity across workers. Size-related changes in task performance were correlated with changes in the rate of encounter between nest mates. These results highlight the importance of colony size for the organization of work in insect societies and raise broader questions about the role of size in sociobiology. **Key words:** biological scaling, encounter rate, group size, social insects, task allocation, task specialization. [*Behav Ecol* 22:960–966 (2011)]

## INTRODUCTION

Biology is largely a matter of size. Body size has profound consequences for the structure, physiology, behavior, ecology, and life history of organisms; these relations are described by biological scaling “rules” or “laws” whose underlying mechanisms can reveal general principles of life (reviewed by Peters 1983; Schmidt-Nielsen 1984; Brown and West 2000; Dial et al. 2008). Just as the size of a multicellular body is determined by the number and size of cells it contains, the size of a social group or colony can be defined by the number and size of individual members it comprises. By extension, the form and function of groups may be shaped by “social scaling” relations, or predictable changes in individual- and group-level properties in response to changes in group size (Jun et al. 2003; Bonner 2004; Yip et al. 2008).

Social scaling patterns, sometimes referred to as “group-size effects,” have been recognized in diverse taxa, for traits ranging from metabolic rate to vigilance (Elgar 1989; Barton 1996; Nakaya et al. 2003; Yip et al. 2008; Pollard and Blumstein 2008, 2011). Colony size appears to play a particularly important role in the structure and organization of eusocial insect colonies, such as those of ants, termites, and some bees and wasps (Tschinkel 1993; Bourke 1999; Anderson and McShea 2001; Jeanne 2003; Hou et al. 2010; Waters et al. 2010). Two features of social insects may increase their

susceptibility to social scaling. First, they exhibit tremendous variation in colony size, from fewer than 10 individuals to tens of millions; colonies grow during ontogeny, and mature colony size varies within and among populations and species (Wilson 1971; Michener 1974; Hölldobler and Wilson 1990). Second, eusocial colonies of all sizes are tightly integrated adaptive units that are, in many ways, functionally equivalent to unitary organisms and may thus experience analogous scaling effects (Wheeler 1911; Wilson 1985; Hölldobler and Wilson 1990, 2009; Seeley 1995, 1997).

Here, we ask whether colony size influences a fundamental attribute of social organization—division of labor—in the harvester ant *Pogonomyrmex californicus*. Broadly defined, division of labor is a statistical pattern in which different individuals perform different functions; it is found, to different degrees, across social groups (reviewed by Michener 1974; Fewell et al. 2009; Holbrook et al. 2009). Division of labor is highly developed in eusocial insect colonies, where it occurs between reproductive and worker castes, and among workers that specialize, over varying time scales, on different nonreproductive tasks (Wilson 1971; Michener 1974; Hölldobler and Wilson 1990, 2009). Functional benefits accrued from division of labor are considered to be of critical importance to the ecological success of social insects (Wilson 1971; Oster and Wilson 1978).

How might division of labor relate to colony size? Ultimate and proximate hypotheses predict that division of labor should increase with colony size. With respect to colony function, the putative benefits of division of labor may be favored more strongly in larger colonies (Bonner 2004), and/or associated costs may select against task specialization in smaller colonies (Oster and Wilson 1978; Herbers 1981; Karsai and Wenzel 1998). Furthermore, self-organizational models of division of labor suggest that increased task specialization may be an

Address correspondence to C.T. Holbrook. E-mail: ctholbrook@asu.edu.

P.M. Barden is now at Richard Gilder Graduate School, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10124, USA.

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emergent consequence of increased colony size (Gautrais et al. 2002; Merkle and Middendorf 2004; Jeanson et al. 2007).

Despite a rich theoretical literature, empirical evidence of colony-size effects on division of labor is scarce. Interspecific surveys of wasps and ants reveal loose, positive correlations between colony size and task specialization (Karsai and Wenzel 1998; Jeanne 2003) or the degree of worker polymorphism, which roughly approximates division of labor (Anderson and McShea 2001; Bonner 2004; but see Fjerdingstad and Crozier 2006). Within social insect species lacking physical worker subcastes, various estimates of task specialization increase with colony size and/or age (*Polybia occidentalis*: Jeanne 1986; *Pog. barbatus*: Gordon 1989; and *Rhytidoponera metallica*: Thomas and Elgar 2003), although there is only a weak effect on division of labor in the ant *Temnothorax albipennis* (Dornhaus et al. 2009). None of those studies, however, distinguished between effects of colony size and colony age, which are typically correlated but may differ in their relative influence on colony organization (Wilson 1983). Moreover, between-colony comparisons may fail to detect ontogenetic changes in behavior, due to confounding sources of variation.

We examined how the organization of work scales with colony size within and among colonies of *Pog. californicus*, which are founded independently (without workers) by one or more queens and grow to contain up to several thousand monomorphic workers at maturity (Johnson 2000). First, we conducted a longitudinal study of growing colonies, to test for early ontogenetic changes while controlling for between-colony variation. Second, we observed unmanipulated same-aged colonies that varied in size due to differences in growth rate, providing a natural experiment for measuring effects of colony size, independent of colony age. In each case, we quantified nonreproductive division of labor, along with 2 related components of work that may be size dependent: 1) the proportional allocation of workers to tasks, which can shift according to colony needs (Gordon 1996; Mailleux et al. 2003; Thomas and Elgar 2003; Tschinkel 2006), and 2) per capita activity, which is predicted to decrease in larger colonies, in conjunction with the scaling of task demand and/or energy use (Jeanson et al. 2007; Hou et al. 2010; Waters et al. 2010). Finally, the rate of encounter between nest mates is hypothesized to scale with colony size and to underlie size-related changes in task organization (Gordon 1996; Pacala et al. 1996); therefore, we analyzed variation in per capita encounter rate as a function of colony size.

## MATERIALS AND METHODS

### Collections and colony maintenance

Newly mated *Pog. californicus* foundresses were collected on 4–6 July 2007 and 4 July 2008, in Pine Valley, San Diego Co., California (lat 32°49'20"N, long 116°31'43"W, 1136 m elevation). Because queens of that population are pleometrotic (found colonies cooperatively), laboratory colonies were initiated with 2 (in 2008) or 3 (in 2007) randomly chosen queens each. Some queens died during colony founding; the number of queens per established colony ranged from 1 to 3 and did not differ significantly between years ( $t$ -test:  $t_{19} = 1.96$ ,  $P = 0.06$ ). Colonies were reared at 30 °C in plastic nest containers supplied with water (in test tubes plugged with cotton) and ad libitum Kentucky bluegrass seeds and previously frozen crickets or mealworms.

### Longitudinal study: 3 months versus 1 year

To test for ontogenetic changes in the organization of work during early colony growth, we quantified task performance in 7 colonies 3 months after colony founding and again at 1 year of age. All colonies were founded in 2008. One week

before each observation period, each colony was transferred to an observation nest consisting of 2 plastic containers (11 × 11 × 3.5 cm each) connected by clear vinyl tubing (0.6 cm diameter). One nest container was lined with plaster to retain moisture; colonies kept all brood in this chamber. The other nest container opened, via a 0.6-cm-diameter entrance/exit, into a 55 × 36 cm foraging arena supplied with water (in a test tube plugged with cotton) and ad libitum Kentucky bluegrass seeds. Nests were maintained at 28–30 °C under ambient light.

Two days before each colony was observed, all “mature” (darkly pigmented) workers were transferred to a holding container, from which 36 individuals (or all individuals when there were fewer than 36) were essentially randomly selected and marked with a unique color combination on the head, mesosoma, and gaster using Sharpie oil-based paint markers. Different samples of workers were selected at 3 months and 1 year. “Callow” (lightly pigmented) workers were not marked or observed, to avoid potentially confounding effects of worker age structure on division of labor. Each individual was weighed to the nearest 0.1 mg before marking (in other lab colonies, wet mass scales with head width<sup>2,4</sup>; log-log regression:  $R^2 = 0.76$ ). All workers, marked and unmarked, were returned to the nest approximately 40 h prior to observation; colonies qualitatively resumed predisturbance behavior within several hour.

We conducted 30 scan samples per colony (Altmann 1974), separated by at least 15-min intervals, between 8:00 and 17:00 h for 1 day. To stimulate foraging, we supplemented seeds with previously frozen fruit flies in proportion to the number of workers (~1 fly per 10 workers) at 8:00 h. During each sample, we systematically scanned from one corner of the brood chamber to the far end of the foraging arena, noting the behavioral state and location of each marked worker at the instance when she was first seen; after this initial sweep, we searched for specific individuals that had been overlooked. Some individuals could not be found during all 30 scan samples, but each marked worker was observed at least 25 times. Behavioral acts were grouped into 5 major tasks:

Allogrooming: grooming another worker or queen.

Brood care: antennating, grooming, manipulating, or carrying egg, larva, or pupa; feeding larva.

Food processing: antennating, manipulating, or carrying seed or fly in nest.

Foraging: antennating, manipulating, or carrying seed or fly in foraging arena.

Waste management: antennating, manipulating, or carrying refuse or dead worker.

Other behaviors were scored as undifferentiated activity (could not be assigned to a specific task; e.g., walking, antennating adult nest mate) or inactivity (including self-grooming and receiving allogrooming). Foraging and waste management were likely underestimated because our definitions conservatively excluded workers that were walking in the foraging arena but not contacting food or waste. Following observation, all queens, workers, and brood were removed from the nest, counted, and weighed by caste/developmental stage. Colonies were housed in long-term maintenance nests between observation periods.

### Between-colony comparison at 1 year

To test for effects of colony size, independent of colony age, we utilized natural size variation among 21 unmanipulated, 1-year-old colonies that differed in net growth rate. Ten of the colonies were founded in 2007; 11 were founded in 2008. Seven of the latter were those also observed at 3 months. We followed the same protocol as above, except we performed 60 scan samples per colony across 2 days (30 samples per

day; at least 50 total observations per worker). Fruit flies were provided at the beginning of each day.

In addition, to determine whether the rate of encounter between nest mates varied as a function of colony size, we video-recorded colonies for 1 h between 12:00 and 14:00 h on the first day of observation. A Canon GL2 digital video camcorder was focused on the entire brood chamber. During playback, we randomly selected 20 focal workers per colony by imposing a grid on a still image and using a random number generator; 5 workers each were selected at 0, 15, 30, and 45 min to control for temporal variation in activity. Each individual was observed continuously for 2 min. An encounter was scored when the focal worker came within one antenna-length of another worker. Encounter rate ( $\text{min}^{-1}$ ) was averaged across workers in each of 20 colonies (one recording was accidentally erased). We also used the still images to estimate local density, defined as the number of workers in the brood chamber divided by the number of  $1\text{-cm}^2$  squares occupied (of 121), averaged across the 4 images per colony.

### Data analysis

Division of labor was quantified using the  $\text{DOL}_{\text{indiv-tasks}}$  index, which represents the extent to which individuals specialize on a subset of tasks, or in information theory terms, the degree to which knowing the identity of an individual predicts the task it performs (Gorelick et al. 2004; for an earlier information theory analysis of task specialization, see also Kolmes 1985). When there are more individuals than tasks,  $\text{DOL}_{\text{indiv-tasks}}$  can range from 0 (no division of labor) to 1 (maximal division of labor) and is insensitive to changes in the number of individuals, thus permitting statistical comparison across groups of varying size (Gorelick et al. 2004; Jeanson et al. 2007; Jeanson and Fewell 2008; Dornhaus et al. 2009). For each colony, we generated an individual  $\times$  task data matrix, using the proportions of observations during which each individual performed each of the 5 tasks: allogrooming, brood care, food processing, foraging, or waste management. Next, we normalized the data matrix so that the sum of all entries equaled 1. From the normalized matrix, we calculated Shannon's diversity index or marginal entropy of tasks ( $H_{\text{tasks}}$ ):

$$H_{\text{tasks}} = - \sum_{j=1}^m p_j \log p_j,$$

where  $p_j$  is the probability that any individual performed the  $j$ th task. We then calculated mutual entropy between individuals and tasks ( $I_{\text{indiv,tasks}}$ ), given by

$$I_{\text{indiv,tasks}} = \sum_{i=1}^n \sum_{j=1}^m p_{ij} \log \left( \frac{p_{ij}}{p_i p_j} \right),$$

where  $p_i$  is the probability that the  $i$ th individual performed any task, and  $p_{ij}$  is the joint probability that the  $i$ th individual performed the  $j$ th task. Finally,  $\text{DOL}_{\text{indiv-tasks}}$  is defined as

$$\text{DOL}_{\text{indiv-tasks}} = \frac{I_{\text{indiv,tasks}}}{H_{\text{tasks}}}.$$

For the full derivation, see Gorelick et al. (2004), but note that the definitions of  $\text{DOL}_{\text{indiv-tasks}}$  and  $\text{DOL}_{\text{tasks-indiv}}$  are switched (Dornhaus et al. 2009).

We used paired  $t$ -tests to analyze within-colony differences (3 months vs. 1 year) in  $\text{DOL}_{\text{indiv-tasks}}$ , proportional task allocation (proportions of colony observations during which workers were engaged in each of the 5 tasks, and their sum), and per capita activity (total task performance plus undifferentiated activity). Across 1-year-old colonies, we used simple linear regression to test for effects of colony size (number of workers) on the

same response variables, plus per capita encounter rate. Proportions were arcsine transformed to improve normality. Individuals that died or lost their paint marks were excluded. Within each series of multiple tests, we controlled the false discovery rate using the Benjamini-Yekutieli method (adjusted  $\alpha = 0.018$ ), which is more powerful than Bonferroni corrections for family-wise error rate and does not assume that tests are independent (Benjamini and Yekutieli 2001; Nakagawa 2004; Narum 2006). Analyses were performed using STATISTICA (StatSoft, Inc., Tulsa, OK). Means ( $\bar{X}$ ) are reported  $\pm 1$  standard error.

## RESULTS

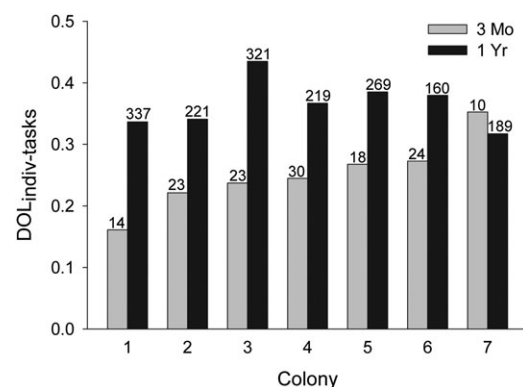
### Longitudinal study: 3 months versus 1 year

Colonies increased in size from 10–30 workers at 3 months to 160–337 workers at 1 year of age. Worker age structure did not change over time (paired  $t$ -test:  $t_6 = 0.95$ ,  $P = 0.38$ ;  $\bar{X}_{3\text{ months}} = 7.6 \pm 4.6\%$  callows,  $\bar{X}_{1\text{ year}} = 3.0 \pm 0.7\%$  callows), but the brood-to-worker ratio was higher in 1-year-old colonies ( $t_6 = 4.52$ ,  $P = 0.004$ ;  $\bar{X}_{3\text{ months}} = 0.6 \pm 0.1\text{mg/worker}$ ,  $\bar{X}_{1\text{ year}} = 1.1 \pm 0.1\text{mg/worker}$ ). Average worker body size was larger at 1 year ( $t_6 = 5.58$ ,  $P = 0.001$ ; grand means:  $\bar{X}_{3\text{ months}} = 2.1 \pm 0.1\text{mg}$ ,  $\bar{X}_{1\text{ year}} = 2.8 \pm 0.1\text{mg}$ ); however, colony age did not affect the coefficient of variation of body size ( $t_6 = 0.02$ ,  $P = 0.99$ ).

Division of labor ( $\text{DOL}_{\text{indiv-tasks}}$ ) was higher at 1 year than at 3 months in 6 of 7 colonies, a significant effect (paired  $t$ -test:  $t_6 = 4.08$ ,  $P = 0.006$ ;  $\bar{X}_{3\text{ months}} = 0.25 \pm 0.02$ ,  $\bar{X}_{1\text{ year}} = 0.37 \pm 0.01$ ; Figure 1). Colony-level task allocation also shifted; older, larger colonies performed relatively less brood care, but colony age did not significantly affect proportional allocation to the other tasks, total task performance, or per capita activity (Table 1). Intracolony distributions of individual activity were left skewed, with over 90% of workers active during at least half of observations; neither skewness ( $t_6 = 0.69$ ,  $P = 0.51$ ) nor the coefficient of variation ( $t_6 = 1.19$ ,  $P = 0.28$ ) differed between 3 months and 1 year.

### Between-colony comparison at 1 year

Colony size ranged from 30 to 390 workers and was not affected by the year of colony founding ( $t$ -test:  $t_{19} = 0.98$ ,  $P = 0.34$ ) or the number of queens (analysis of variance [ANOVA]:  $F_{2,18} = 0.98$ ,  $P = 0.39$ ); colonies were pooled for further analysis. Variation in colony size was not associated with the proportion of callow workers (linear regression:  $F_{1,19} = 0.04$ ,  $P = 0.85$ ,



**Figure 1**

Division of labor in *Pogonomyrmex californicus* colonies at 3 months versus 1 year of age.  $\text{DOL}_{\text{indiv-tasks}}$  represents the degree to which individuals specialize on a subset of tasks. Values above bars are numbers of workers in each colony at time of observation.

Table 1

Proportional task allocation and per capita activity in *Pogonomyrmex californicus* colonies at 3 months (10–30 workers) versus 1 year of age (160–337 workers)

Task	Proportion of observations		$t_6$	$P$
	3 months	1 year		
Allogrooming	0.044 ± 0.003	0.036 ± 0.006	1.06	0.33
Brood care	0.118 ± 0.014	0.062 ± 0.011	3.80	0.009*
Food processing	0.218 ± 0.024	0.235 ± 0.022	0.54	0.61
Foraging	0.007 ± 0.001	0.019 ± 0.007	1.93	0.10
Waste management	0.025 ± 0.008	0.062 ± 0.008	2.55	0.04
Total task performance	0.411 ± 0.025	0.414 ± 0.023	0.11	0.92
Total activity	0.746 ± 0.023	0.828 ± 0.019	2.27	0.06

Proportion of observations is mean ± standard error proportion of colony observations during which workers performed tasks or were active. Total task performance is sum of 5 tasks. Total activity is total task performance plus undifferentiated activity.  $t$  is from paired  $t$ -test. Benjamini-Yekutieli adjusted  $\alpha = 0.018$  (\*denotes significance).

$R^2 = 0.002$ ) or the brood-to-worker ratio ( $F_{1,19} = 0.10$ ,  $P = 0.75$ ,  $R^2 = 0.005$ ). There was a nonsignificant trend of increasing worker body size with colony size ( $F_{1,19} = 4.06$ ,  $P = 0.06$ ,  $R^2 = 0.18$ ), but no effect of colony size on the coefficient of variation of body size ( $F_{1,19} = 0.14$ ,  $P = 0.71$ ,  $R^2 = 0.007$ ).

Division of labor ( $DOL_{\text{indiv-tasks}}$ ) increased with colony size across 1-year-old colonies (linear regression:  $DOL_{\text{indiv-tasks}} = 0.23 + 2.9 \times 10^{-4}$  worker number;  $F_{1,19} = 11.25$ ,  $P = 0.003$ ,  $R^2 = 0.37$ ; Figure 2). There was no effect of queen number on  $DOL_{\text{indiv-tasks}}$  (ANOVA:  $F_{2,18} = 0.53$ ,  $P = 0.60$ ). Colony size did not affect the proportional allocation of workers to tasks, total task performance, or per capita activity (Table 2). Intracolony activity distributions were not related to colony size (skewness:  $F_{1,19} = 0.99$ ,  $P = 0.33$ ,  $R^2 = 0.05$ ; coefficient of variation:  $F_{1,19} = 0.03$ ,  $P = 0.86$ ,  $R^2 = 0.002$ ).

The per capita rate of encounter between nest mates increased with colony size (linear regression: encounters/min =  $4.27 + 0.014$  worker number;  $F_{1,18} = 16.02$ ,  $P = 0.001$ ,  $R^2 = 0.47$ ; Figure 3). Although nest size was held constant, local density within the brood chamber increased more slowly than colony size ( $\log_{10}\text{workers}/\text{cm}^2 = 0.03 + 0.14 \log_{10}\text{worker number}$ ; slope vs. 1:  $t_{18} = 22.81$ ,  $P < 0.0001$ ,  $R^2 = 0.45$ ); in other words, a 10-fold increase in colony size resulted in just a 1.4-fold increase in local density. This allometry was caused by aggregation of workers in small colonies rather than an

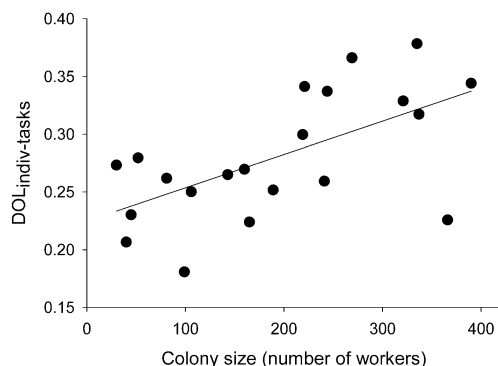


Figure 2

Division of labor as a function of colony size in 1-year-old *Pogonomyrmex californicus* colonies.  $DOL_{\text{indiv-tasks}}$  represents the degree to which individuals specialize on a subset of tasks. Ordinary least squares regression line is shown ( $Y = 0.23 + 2.9 \times 10^{-4}X$ ;  $R^2 = 0.37$ ).

Table 2

Proportional task allocation and per capita activity regressed against colony size in 1-year-old *Pogonomyrmex californicus* colonies (30–390 workers)

Task	Regression versus colony size		
	$R^2$	$F_{1,19}$	$P$
Allogrooming	<0.001	0.004	0.95
Brood care	0.08	1.63	0.22
Food processing	0.006	0.11	0.75
Foraging	0.02	0.32	0.58
Waste management	0.09	1.99	0.17
Total task performance	0.01	0.21	0.65
Total activity	0.01	0.21	0.65

For each response variable, results are from simple linear regression of arcsine-transformed proportion of colony observations on number of workers. Total task performance is sum of 5 tasks. Total activity is total task performance plus undifferentiated activity. Benjamini-Yekutieli adjusted  $\alpha = 0.018$ .

inverse relationship between colony size and the proportion of workers residing inside the nest ( $F_{1,18} = 3.27$ ,  $P = 0.09$ ,  $R^2 = 0.15$ ). As a consequence, variation in encounter rate was not explained by variation in local density ( $F_{1,18} = 0.63$ ,  $P = 0.43$ ,  $R^2 = 0.03$ ).

## DISCUSSION

The extension of biological scaling beyond organisms implies that the size of a social group can affect the structure, function, and ecology of its individual members and of the group as a whole (Bonner 2004; Yip et al. 2008). Social scaling relations potentially occur in groups of all forms, but size seems to be especially important for the organization of highly integrated eusocial colonies (Tschinkel 1993; Bourke 1999; Anderson and McShea 2001; Jeanne 2003; Hou et al. 2010; Waters et al. 2010). Here, we show that division of labor, a fundamental colony-level phenotype, scales positively with colony size in the harvester ant *Pog. californicus*; individual workers in larger (and older) colonies specialize on narrower subsets of tasks. This relationship is found in 2 different contexts: 1) during early colony ontogeny or sociogenesis, as a colony grows from tens to hundreds of workers and 2) across colonies that vary in size, independently of age.

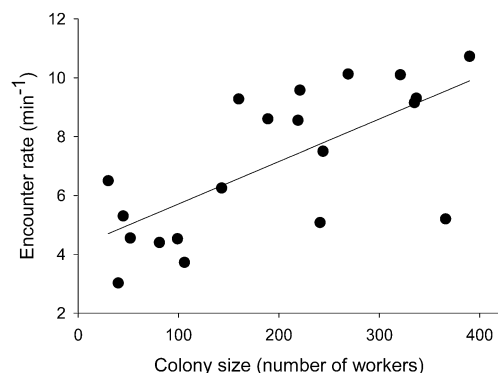


Figure 3

Colony size versus per capita rate of encounter between nest mates in 1-year-old *Pogonomyrmex californicus* colonies. Encounter rate ( $\text{min}^{-1}$ ) is average of 20 focal workers per colony. Ordinary least squares regression line is shown ( $Y = 4.27 + 0.014X$ ;  $R^2 = 0.47$ ).



Does this consistent scaling pattern have adaptive significance? Division of labor is generally thought to enhance colony “efficiency” and thus fitness; benefits may include individual learning gains, reduction of task switching costs, and the evolution of specialized morphological or physiological “machinery” (Smith 1776/1976; Oster and Wilson 1978; Dornhaus 2008; Chittka and Müller 2009). Actual advantages have rarely been verified, with most tests focusing on the rate or speed of individual performance, not the ultimate conversion of labor and resources into sexual offspring (Wilson 1980; Porter and Tschinkel 1985; Tschinkel 1993; Dukas and Visscher 1994; Chittka and Thomson 1997; Trumbo and Robinson 1997; Julian and Cahan 1999; Dornhaus 2008). Assuming colony-level benefits exist, they may be more important to larger colonies, if increased size imposes physical or ecological constraints (Jun et al. 2003; Bonner 2004). Division of labor may also confer costs that outweigh its benefits in smaller colonies; for instance, the need for specific tasks to be performed may be too low and/or variable to keep task specialists employed (Bell and Mooers 1997; Karsai and Wenzel 1998), or individual specialization may reduce system reliability when worker redundancy is low (Oster and Wilson 1978; Herbers 1981). Alternatively, the scaling of division of labor could be an emergent epiphenomenon with little, if any, adaptive value (Gautrais et al. 2002; Merkle and Middendorf 2004; Jeanson et al. 2007).

Our study did not directly address those hypotheses, but it does provide relevant insights. First, if the scaling relationship is driven by functional limitations or costs in small colonies, then division of labor might be expected to stabilize once a critical colony size is attained; yet, it appears to increase continuously throughout the range of colony sizes we observed (Figure 2). This raises the question of how colonies respond to further increases in size, which can reach several thousand workers in full-grown colonies (Johnson 2000). Second, Waters et al. (2010) demonstrated that whole-colony metabolic rate scales with negative allometry in *Pog. californicus* (i.e., larger colonies use less energy per gram of worker). Perhaps higher division of labor enables larger colonies to operate more efficiently, reducing their relative energy requirements. Or, metabolic scaling may arise from energetic constraints imposed by increased colony size, which could simultaneously favor or even necessitate increased division of labor (Bonner 2004).

The scaling of division of labor could possibly be mediated by underlying changes in worker body size. Body size is correlated with task performance in ants with polymorphic workers (Oster and Wilson 1978; Hölldobler and Wilson 1990), and to a lesser extent, in some social insects lacking distinct physical worker subcastes (Schwander et al. 2005; Jandt and Dornhaus 2009). Moreover, in polymorphic ants, the range of worker sizes can expand during colony ontogeny, potentially facilitating division of labor (Wilson 1983; Tschinkel 1988, 1993). Although workers of *Pog. californicus* are monomorphic (i.e., body size is normally distributed), average body size increased between 3 months and 1 year of colony age, and there was a weak trend of increasing body size with colony size among same-aged colonies. Worker size variability, however, was not related to colony age or size.

### Colony-size effects on task allocation and activity

Colony needs or priorities may covary with colony size, causing size-related changes in the allocation of workers across tasks (Gordon 1996; Mailleux et al. 2003; Thomas and Elgar 2003; Tschinkel 2006). For example, smaller colonies may invest relatively more effort in tasks promoting colony

growth, such as brood care and foraging (Kolmes and Winston 1988; Schmid-Hempel et al. 1993; Thomas and Elgar 2003; Tschinkel 2006). In our longitudinal comparison, younger and smaller *Pog. californicus* colonies performed proportionally more brood care, even though they contained less brood mass per worker. In contrast, task allocation did not shift with colony size among 1-year-old colonies. This discrepancy indicates that ontogenetic changes in the organization of work can differ from effects of colony size alone and highlights the importance of distinguishing within- versus between-colony scaling relations.

Social insect workers spend much of their time either inactive or engaged in undifferentiated activity not associated with a specific task (Lindauer 1961; Cole 1986; Schmid-Hempel 1990). Does activity or workload vary predictably with colony size? If economies of scale reduce relative task demand (Jeanson et al. 2007) and/or energy expenditure in larger colonies (Hou et al. 2010; Waters et al. 2010), then the average individual workload is expected to decrease with increasing colony size. Yet, neither of our measures of per capita activity—based strictly on task performance or including all activity—changed with colony size. A previous study that quantified locomotory activity in *Pog. californicus* likewise found no colony-size effect on average worker speed, although larger colonies exhibited a greater disparity between fast and slow individuals (Waters et al. 2010). Colony size has an opposite effect in *T. albipennis*; intracolony distributions of workload during nest emigration are more skewed in smaller colonies (Dornhaus et al. 2008). We did not detect any relationship between colony size and the distribution of activity across workers.

### Size-dependency of encounter rate

In functionally integrated eusocial insect colonies, workers communicate task needs and opportunities through dense networks of social interaction (Wilson and Hölldobler 1988; Seeley 1995; Gordon 1996; Fewell 2003; Hölldobler and Wilson 2009). Size-dependent changes in the rate of encounter between nest mates could thus modulate information flow and the organization of work (Gordon 1996; Pacala et al. 1996). Encounter rate may also provide a cue of colony size or density that influences workers’ task decisions (Pratt 2005). In our study, per capita encounter rate scaled positively with colony size. Although nest size was held constant, the aggregation of workers in small colonies caused worker density to increase more slowly than colony size; as a result, variation in encounter rate was not explained by variation in density alone. This pattern is consistent with previous findings in other ants. Workers of *Lasius fuliginosus* cluster together when global density is low, elevating their local rate of encounter (Gordon et al. 1993). Encounter rate also increases with colony size (and task specialization), independently of density, in *R. metallica* (Thomas and Elgar 2003). It remains unclear, however, whether encounter rate and division of labor are functionally linked or respond separately to changes in colony size.

Most laboratory studies, including our own, employ simplified nest designs that may reduce spatial segregation between workers and/or between tasks. Spatial task-encounter models (Tofts and Franks 1992) and empirical evidence of worker spatial fidelity within nests (Sendova-Franks and Franks 1994; Tschinkel 2004) suggest that nest architecture can contribute to patterns of social interaction and task organization. Spatial constraints are implicated in many biological scaling phenomena (Brown and West 2000; Yip et al. 2008); potential interactions between colony size, spatial structure, and division of labor merit further research.

## CONCLUSIONS

Changes in size have broad implications for the form and function of biological entities, across levels of organization (Peters 1983; Schmidt-Nielsen 1984; Tschinkel 1993; Brown and West 2000; Bonner 2004; Yip et al. 2008). The observed relationship between size and division of labor in social insect colonies parallels the scaling of physiological division of labor with body size in multicellular organisms, which, like colonies, are collectives of lower level subunits (Bell and Mooers 1997; Bonner 2004). Task specialization increases with population size in many human organizations as well (Smith 1776/1976; Young 1928; Changizi et al. 2002; Bonner 2004). These patterns are undoubtedly generated by different mechanisms, but their convergence may reflect common selective pressures (natural or economic) and/or self-organizing processes.

Although division of labor has been evolutionarily elaborated in eusocial insects, it remains a basic attribute of sociality that is expressed by groups of varying size, composition, and complexity (Michener 1974; Fetherston et al. 1990; Stander 1992; Lacey and Sherman 1997; Underwood and Shapiro 1999; Clutton-Brock et al. 2003; Arnold et al. 2005; Gazda et al. 2005; Ridley and Raihani 2008; Fewell et al. 2009; Holbrook et al. 2009; Bruinjtjes and Taborsky 2010). Size increase can promote task specialization in smaller, less integrated social groups, such as cooperative colony-founding associations of ant queens (Jeanson and Fewell 2008). We advocate further investigations of social scaling, of division of labor and other traits, within and among diverse systems. The aim of this pursuit is 2-fold: to gain novel insights into the social organization, evolution, and ecology of specific taxa, and to determine whether sociobiology is governed by, or gives rise to, general scaling principles.

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