



Task partitioning in ants lacking discrete morphological worker subcastes

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Abstract

Task partitioning allows for efficient coordination of behavior in social insect colonies. Many task allocation studies focus on social insect species with discrete morphological worker subcastes, such as those possessing major and minor workers with strongly differentiated body plans. Much less is known about task partitioning among size-variable workers lacking discrete morphological subcastes. We investigated task fidelity and its correlation with worker size in *Formica* species with differing degrees of body size variation. During a mark-recapture study that focused on three worker tasks (honeydew collection, nest building, and protein foraging) across 2 days, 98.6% of 3570 recaptured workers exhibited task fidelity. In species with high levels of worker size variation, worker size is strongly correlated with task performance. This size-task correlation is weaker, but still present, in species with less variably sized workers. Our results suggest that *Formica* use size-based task partitioning, a form of morphological polyethism. We expect social insects with and without discrete morphological worker subcastes to differ in ontogeny, evolutionary history, and degree of behavioral flexibility. Identifying the scope of variation in task partitioning mechanisms will facilitate comparative studies, thereby elucidating evolutionary histories and outcomes of alternative strategies.

Significance statement

Division of labor is thought to increase the efficiency and success of animal societies by allowing the performance of multiple tasks in parallel, rather than sequentially. We investigated the task partitioning strategy employed by an ecologically dominant ant genus characterized by continuous worker size variation but lacking discrete morphological worker subcastes. We show that several species employ a form of morphological polyethism, wherein individuals specialize in tasks according to body size. Size-mediated morphological polyethism in the absence of discrete morphological worker subcastes has been demonstrated in a few other social insects. However, this task allocation strategy is likely more common than previously recognized, as most insect societies display natural worker size variation. Further, we argue that it is important to distinguish between size- and subcaste-based morphological polyethism. Alternative task partitioning strategies are likely to impact animal societies' resilience to environmental perturbations, which are becoming increasingly common in the face of global change.

Keywords Body size · Division of labor · Eusociality · Polyethism · Task allocation

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Introduction

In animal societies, cooperation between individuals confers benefits such as increased survival, reproduction, access to shared resources, and success of kin (reviewed in Clutton-Brock 2002). Cooperative individuals may benefit from division of labor, enabling the performance of multiple tasks in parallel. Division of labor can be either reproductive or non-reproductive. In reproductive division of labor, some individuals forego reproduction and instead aid other group members in raising their offspring (e.g., Jarvis 1981; Walters et al. 1988). For example, in many species of cooperatively

breeding birds, reproductively mature individuals act as “helpers,” providing alloparental care prior to inheriting breeding status (Walters et al. 1988). In non-reproductive division of labor, individuals often specialize in a single or a few similar tasks, such as resource collection or defense. In many cases, non-reproductive division of labor is accomplished without any central control directing the behavior of individuals. In such cases, task specialization is mediated by a combination of internal and environmental cues (Gordon 1996). Task specialization increases the functional efficiency of societies by enabling individuals to effectively learn skills associated with a small suite of tasks, transfer skills when performing similar tasks, and avoid costs associated with switching tasks (Oster and Wilson 1979; Chittka and Muller 2009).

In line with the idea that task specialization increases efficiency, the ecological success of social insects is often attributed to division of labor (Oster and Wilson 1979). Eusocial insects are incredibly successful. Ants and termites alone, though representing only 2% of insect species, comprise more than half of all insect biomass worldwide and approximately one-third of all animal biomass in tropical systems (Hölldobler and Wilson 1990; Wilson and Hölldobler 2005a). Eusocial insects live in groups of closely related individuals and are characterized by cooperative brood care, overlapping generations, and reproductive division of labor (Wilson and Hölldobler 2005b). All eusocial insects use some form of reproductive division of labor, in which one or more egg-laying queens focus primarily on reproduction, while workers carry out all other tasks within the colony, including nest maintenance, brood care, and foraging (Wilson 1971). These and other non-reproductive tasks are divided among workers in most insect societies. Natural variation among workers enables them to specialize in one or a few tasks effectively based upon their individual characteristics (Wilson 1968; Hasegawa 1997).

One form of non-reproductive division of labor, morphological polyethism, relies on morphological variation among workers. In a broad sense, morphological polyethism is defined as task specialization on the basis of variation in the size and/or shape of workers (reviewed in Beshers and Fewell 2001; Robinson 1992). Within eusocial Hymenoptera, morphological polyethism has been identified in at least 15% of ants (Oster and Wilson 1979) and in some stingless bees (Grüter et al. 2012; Grüter et al. 2017). A kind of morphological polyethism is also present in most termites, but the fundamental differences in polyethism that arise from their hemimetabolous development, such as specialization based on developmental stage, are beyond the scope of this paper (Noirot and Pasteels 1987). Morphological polyethism has been studied primarily in ants with non-linear allometric scaling among workers, wherein the log-log allometric regression is broken into two or more linear associations with different slopes

(Wilson 1953). In these species, workers that perform different tasks not only differ in overall size but also differ from each other in the relative proportions or scaling of their body plan. For example, workers of many *Pheidole* species are split into a major (or soldier) subcaste, which specialize in colony defense, and a minor subcaste, which performs brood care and foraging (Mertl and Traniello 2009). Throughout this manuscript, we refer to these species as those possessing “discrete morphological worker subcastes.” However, many hymenopteran social insect species lack discrete morphological worker subcastes (Wilson 1953; Oster and Wilson 1979; Harvell 1994) but still exhibit substantial variation in body size. Much less is known about how these species partition tasks.

In some size-variable social insects lacking discrete morphological worker subcastes that have been investigated, an association between task specialization and worker size is noticeable. In some cases, close examination has revealed subtle changes in body shape associated with body size, as in some stingless bees (Grüter et al. 2012; Grüter et al. 2017) and some fire ants (Tschinkel et al. 2003; Tschinkel 2013). Allometric scaling relationships among workers of these species are primarily linear, meaning that the same allometric scaling relationships exist across all body sizes. Worker size variation is also often associated with differences in timing of task performance and task repertoire. Within bumble bees (Richards 1946; Brian 1952) and a few *Vespula* and *Polybia* wasp species (Spradbery 1972; O'Donnell and Jeanne 1995), for example, large workers tend to perform exterior tasks earlier or more frequently than small workers, but task specialization is weak overall (Jandt et al. 2009). As size variation among workers is likely present in most insect societies, it is possible that size-based task allocation systems are relatively common, even though they are relatively understudied. In order to understand how widespread size-based task partitioning is, it is important to understand how the degree of size variation among nestmate workers impacts this strategy.

The ant genus *Formica* is widespread throughout North America, Europe, and Asia (Bondroit 1918; Dlussky 1965; Bernard 1968; Francoeur 1973). Species of this genus lack discrete morphological worker subcastes, and workers within colonies are continuously variable in size (e.g., Bernstein 1976; Billick 2002; Schwander et al. 2005; Fig. S4; Fig. S5). Comparison of body measurements in some species has revealed linear allometric (and some isometric) scaling relationships associated with body size (Tawdros, MW, and JP, submitted). Previous studies suggest that *Formica* exhibits morphological polyethism, such that size variation among workers is associated with task allocation (Herbers 1979; Bernstein 1976; Batchelor et al. 2012; Parmentier et al. 2015; Véle and Modlinger 2019). Additionally, Billick and Carter (2007) found that lab colonies with natural worker size variation were better able to maintain colony biomass (i.e., worker survival) than those with only small or only large

workers. However, little is known about task fidelity in *Formica*, which is important for understanding the strength of the association between morphology and behavior in this system. Across *Formica* colonies and species, the magnitude of variation in worker size can vary drastically, allowing us to ask how much size variation is needed to yield this task allocation strategy and whether task switching is more common in colonies with less size variance. Few studies have investigated task allocation strategies in closely related species that differ in the degree of size variation or polymorphism (but see Wilson 1978).

Formica provides an opportunity to investigate the factors contributing to task allocation in social insects with high levels of natural worker size variation and enables us to make direct comparisons between related species that differ in the degree of this size variation. The main goals of this study were to determine whether (1) individual *Formica* workers specialize in single tasks over short periods, (2) there is an association between worker size and task across diverse species in this genus, and (3) within-colony size variation impacts the strength of the size-task association. We conducted a multi-species mark-recapture study, investigating behavioral fidelity and worker size associated with individual task performance.

Materials and methods

In June–August of 2017, we conducted behavioral observations on and collected specimens from 51 *Formica* ant colonies. We observed colonies of ten species at ten localities distributed throughout southern Alberta, Canada (Table 1). It

was not possible to collect data blindly, as our study involved focal ant workers in the field.

Mark-recapture

We observed each colony over 2 days, for a total of 4 h per colony. We split each day into four half-hour observation periods, spread throughout the day in order to capture each colony's active period and to minimize any temporal biases. Due to weather constraints, we observed three colonies for three or three and a half hours.

We focused on three tasks: honeydew collecting (HC), nest building (NB), and protein foraging (PF). Honeydew collectors tended to aphids or departed an aphid-infested plant with fully engorged abdomens. Nest builders carried nest materials (e.g., pine needles, wood chips, dirt, pebbles) on or adjacent to the nest mound or entrance. Protein foragers carried prey (a variety of insects and spiders) toward the nest entrance. We chose these three tasks because they consistently had a large proportion of the workforce allocated to them across colonies, and observations did not require nest destruction. It was critical for the success of our mark-recapture study to maintain the integrity and normal activity of the observation nests. While one researcher observed and paint-marked nest builders and protein foragers at the nest, the other observed and paint-marked honeydew collectors at a nearby aphid-infested plant.

On the first day of observation, we paint-marked individuals observed doing one of the previously described tasks with a task-associated color. We randomized color-task associations for each colony through blindly choosing paints from a collection of 12 Testors® enamel paints. Using a toothpick, we painted a small dot on the gaster of each individual. If we

Table 1 A list of the localities in Alberta, Canada where we conducted observations and collected samples. The number of colonies observed per species is indicated in parentheses after each species name

Locality	Latitude (°N)	Longitude (°W)	Number of colonies	Species
Barrier Lake Day Use Area	51.03	−115.04	5	<i>F. obscuriventris</i> (3), <i>F. neoclara</i> (2)
Castle Provincial Park	49.38	−114.35	2	<i>F. aserva</i> (1), <i>F. rufa</i> sp. #1 (1)
Exshaw	51.08	−115.12	3	<i>F. dakotensis</i> (2), <i>F. neoclara</i> (1)
Grassi Lakes Day Use Area	51.08	−115.4	2	<i>F. neoclara</i> (1), <i>F. rufa</i> sp. #2 (1)
Nose Hill Park	51.11	−114.1	3	<i>F. glacialis</i> (1), <i>F. neoclara</i> (1), <i>F. obscuriventris</i> (1)
Peter Lougheed Provincial Park	50.69	−115.13	3	<i>F. neoclara</i> (1), <i>F. neorufibaris</i> (1), <i>F. podzolica</i>
Sibbald Lake Provincial Campground	51.05	−114.86	2	<i>F. aserva</i> (1), <i>F. ulkei</i> (1)
Sylvan Lake Provincial Park	52.35	−114.08	15	<i>F. glacialis</i> (6), <i>F. podzolica</i> (4), <i>F. aserva</i> (3), <i>F. neoclara</i> (1), <i>F. ulkei</i> (1)
University of Calgary Biogeosciences Research Station	51.03	−115.03	14	<i>F. obscuriventris</i> (7), <i>F. podzolica</i> (4), <i>F. neoclara</i> (3)
Wasootch Creek Day Use Area	50.97	−115.09	2	<i>F. obscuriventris</i> (1), <i>F. podzolica</i> (1)

observed a previously painted worker switching tasks, we added another dot of paint of a different color. We used manual counters to keep track of the number of individuals painted for each task during each observation period and noted any workers observed switching tasks.

On the second day of observation, which was usually the following day ($N = 45$ nests; 3 days later, $N = 3$ nests; 4 days later, $N = 3$ nests), we recaptured painted individuals observed doing the same or a different task into a $26.7 \times 20.3 \times 15.2$ cm plastic bin, lined with fluton to prevent escape. We used manual counters to keep track of the number of workers recaptured doing the same task. We also noted any workers recaptured doing a different task. From the recapture bins, we haphazardly collected up to 15 of the recaptured workers performing the same task and all workers observed switching tasks for head-width measurements. Hereafter, we refer to these as “consistent workers” and “task-switchers,” respectively. We stored consistent workers (by task) and task-switchers separately in 100% ethanol. Additionally, we collected up to 15 unmarked nest builders, protein foragers, and honeydew collectors from each colony into 100% ethanol when feasible.

Head measurements

We used a Leica S8AP0 microscope with a Leica DMC2900 camera attached and Leica imaging software to photograph the head of each specimen at $25\times$ magnification. We then used the Leica imaging software to measure the head width of each specimen to one-thousandth of a millimeter, measuring the widest point across the eyes (Fig. S1). We chose to measure head width because it is a good proxy for overall body size in *Formica selysi* (Schwander et al. 2005) and other ants (e.g., Kaspari 1996; Fournier et al. 2008).

Species identification

We used genetic sequencing (RADseq) to verify field identification of species collected for this study. Please see the supplementary material for a full description of relevant methods and a neighbor-joining tree showing relationships between sampled nests (Fig. S6). In total, we observed ten *Formica* species during our mark-recapture study (Table 1). We were unable to identify two species in the *F. rufa* group. These are denoted as “*F. rufa* sp. #1” and “*F. rufa* sp. #2” in Table 1.

For the purposes of this study, we separated the species into two groups: mound-building and subterranean species. The distinction between these two groups is based primarily on phylogeny (Fig. S6). However, it is important to note that the two groups generally differ in the degree of worker size variation and many aspects of their life histories. For example, the mound-building species included in this study are facultative social parasites, while the subterranean species are common hosts (e.g., Savolainen and Deslippe 2001). The use of

the “mound-building” and “subterranean” descriptors throughout this manuscript refers to the external view of nests built by each species; mound-building species typically build thatch mounds with conifer needles and bark or dried grasses atop their underground nests (e.g., Scherba 1961), while subterranean species’ nests are either entirely underground or include an aboveground dirt mound (e.g., Sankovitz et al. 2019).

Statistical analyses

We performed all statistical analyses in R version 3.5.2 (R Core Team 2017). In order to compare recapture rates and task dynamics across species and task groups, we performed a series of Fisher’s exact tests using the *fisher.test* function.

In the primary size-task association analyses, we included the species for which we had more than one colony and five or more workers per task (36 of 51 colonies, six of ten species). The 36 colonies included in the size-task association analyses are members of three mound-building species, with generally high worker size variance (*F. aserva*, *F. dakotensis*, and *F. obscuriventris*) and three subterranean species, with low worker size variance (*F. glacialis*, *F. neoclara*, and *F. podzolica*). We used the *lmer* function from the *lme4* package, with the *lmerTest* modification (Bates et al. 2014; Kuznetsova et al. 2015) to build six linear mixed-effects models (one for each species) in order to compare the head widths of individuals that performed different tasks. In these models, head width was the response variable, task was the fixed effect, and colony was the random effect. As a post hoc analysis, we performed Tukey’s range tests in order to compare average head widths across all task categories for each species using the *multcomp* package (Hothorn et al. 2017). In addition to these primary analyses, we carried out analyses on the remaining four species but note that we had lower statistical power due to small sample sizes (Supplementary Methods; Fig. S3; Table S1).

To assess the impact of within-colony worker size variance on the strength of size-task associations, we carried out a phylogenetic independent contrast (PIC) for each task comparison (NB-HC, HC-PF, and PF-NB). We carried out the PICs using a total of 48 colonies for which we had sufficient genomic, behavioral, and morphological data. We excluded two colonies for which we lacked head-width measurements for at least two workers per task from at least two of the three focal tasks and one colony for which we lacked genomic data. As such, we included a variable number of colonies in each PIC: 47 colonies when comparing honeydew collectors to nest builders, 46 colonies when comparing nest builders to protein foragers, and 45 colonies when comparing honeydew collectors to protein foragers. We calculated the effect size (Cohen’s d) of each task comparison per colony using the *cohen.d* function from the *effsize* package (Torchiano and Torchiano 2018) and within-colony head-width variance and then log-

transformed the data. We generated neighbor-joining trees based on genomic data from one worker per colony (see supplementary material for detailed genomic methods). We chose to carry out these analyses across colonies, since our conspecific samples were collected from different populations (Table 1), and we observed substantial intraspecific variation in some species (Fig. S2; Fig. S6). We used PLINK (Purcell et al. 2007) to calculate genetic distance matrices for the colonies associated with each PIC. We then generated neighbor-joining trees in the Newick format using the web-based platform T-REX (Boc et al. 2012). The trees were not dichotomous so we rerooted them using the *midpoint.root* function in the phytools package (Revell 2012). Phylogenetic comparative methods appear to be robust to tree misspecification, so it is unlikely that rerooting the trees significantly impacted the results of the PICs (Stone 2011). We then examined the correlation between within-colony size variance and effect size for each task comparison while correcting for phylogeny using the *pic* function from the ape package (Paradis and Schliep 2019). Within-colony variance in head width was the fixed effect and Cohen's *d* was the response variable.

Results

Mark-recapture

During our mark-recapture study, we marked 8831 ant workers (HC, $N = 6074$; NB, $N = 1689$; PF, $N = 1068$). On subsequent observation days, we recaptured 3570 (40.4%) marked ants (HC, $N = 3276$; NB, $N = 241$; PF, $N = 53$). We carried out several Fisher's exact tests to compare recapture and task fidelity rate across species and focal tasks. Across all species, the honeydew collectors were more likely to be recaptured than the nest builders ($p < 0.0001$) and protein foragers ($p < 0.0001$), and the protein foragers were less likely to be recaptured than the nest builders ($p < 0.0001$). Of those recaptured, 3520 (98.6%) were consistent workers (HC, $N = 3260$; NB, $N = 222$; PF, $N = 38$), and 50 (1.4%) were task-switchers (HC, $N = 16$; NB, $N = 19$; PF, $N = 15$) (Fig. 1). Overall, recaptured workers from the subterranean species were more likely to switch tasks than those from the mound-building species ($p = 0.008$). Of the 1792 recaptured subterranean workers, 34 (1.9%) switched tasks (Fig. 1b), while only 16 out of 1778 (0.9%) recaptured workers from the mound-building species switched tasks (Fig. 1a). Within the mound-building species, the honeydew collectors were more likely to maintain task fidelity than the nest builders ($p = 0.002$) and protein foragers ($p < 0.0001$), and the protein foragers were more likely to switch tasks than the nest builders ($p < 0.0001$; Fig. 1a). Within the subterranean species, the honeydew collectors were also more likely to maintain task

fidelity than the nest builders ($p < 0.0001$) and protein foragers ($p < 0.0001$), but the nest builders and protein foragers were equally likely to switch tasks ($p = 0.419$; Fig. 1b). Additionally, two subterranean workers that collected honeydew on the first day of observation were observed performing a non-focal task on the second day of observation—one was removing a dead worker from the colony and the other was observed carrying an aphid.

We revisited two colonies about 1 month after initial markings. We observed approximately 15 painted honeydew collectors tending to aphids in both cases. This observation suggests that workers consistently perform this task for at least 1 month. We did not observe previously painted nest builders or protein foragers carrying out any focal tasks.

Size and task partitioning

We find a consistent pattern when considering associations between worker size and task in the mound-building species (*F. obscuriventris*, *F. aserva*, and *F. dakotensis*). For these species, honeydew collectors are significantly smaller than both nest builders and protein foragers, which are not significantly different in size from each other (Fig. 2: a, $F_{2,189} = 144.6$, $p < 0.0001$; b, $F_{2,67} = 30.53$, $p < 0.0001$; c, $F_{2,43} = 9.76$, $p = 0.0003$). These trends are consistent when considering workers within colonies of each mound-building species (Fig. S2A). We find slightly different patterns when considering the association between size and task in the subterranean species (*F. podzolica*, *F. glacialis*, and *F. neoclara*). For all three species, honeydew collectors are small, but the differences between nest builders and protein foragers vary (Fig. 2: d, $F_{2,196} = 4.26$, $p = 0.015$; e, $F_{2,159} = 5.18$, $p = 0.007$; f, $F_{2,155} = 3.67$, $p = 0.028$). Overall, there is a weaker relationship between worker size and task in the subterranean *Formica* included in our study. In contrast with the mound-building species, the relationship between worker size and task differs among subterranean colonies of the same species (Fig. S2B). The presence of intraspecific body size variation across colonies within the subterranean species likely contributes to weaker associations between size and task overall (Fig. S6). Size-task associations for the four additional species are provided in the supplementary material (Fig. S3).

Effect of degree of within-colony size variation on the association between size and task

The 48 colonies included in our phylogenetic independent contrast exhibited a range of worker size variance (0.002–0.117 mm). As intracolony worker size variation increased, the association between worker size and task strengthened, when comparing certain tasks (Fig. 3). This pattern was

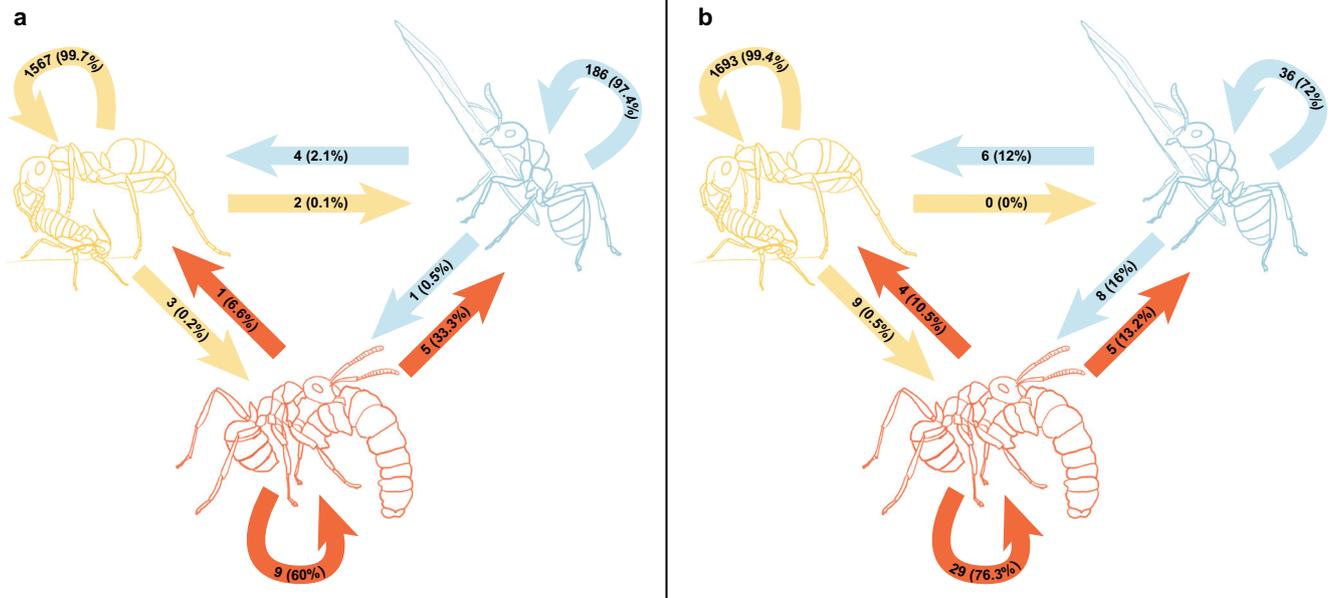


Fig. 1 Diagram depicting the number of workers that were recaptured collecting honeydew (HC, yellow), nest building (NB, blue), and protein foraging (PF, orange) for mound-building (a) and subterranean (b) species. For each arrow, the blunt end indicates the task observed when workers were initially marked, and the point indicates the task observed

when workers were recaptured. As such, curved arrows represent consistent workers and straight arrows between tasks represent task-switchers. Raw numbers are followed by the percentages of recaptured honeydew collectors, nest builders, or protein foragers that were observed performing the tasks indicated by the direction of the arrow

particularly strong when comparing honeydew collectors to nest builders ($R^2 = 0.24, p < 0.0001$) and protein foragers ($R^2 = 0.33, p < 0.0001$) (Fig. 3a, b). However, an increase in

worker size variation did not affect the strength of the size-task association when comparing nest builders and protein foragers ($R^2 = 0.050, p = 0.074$) (Fig. 3c).

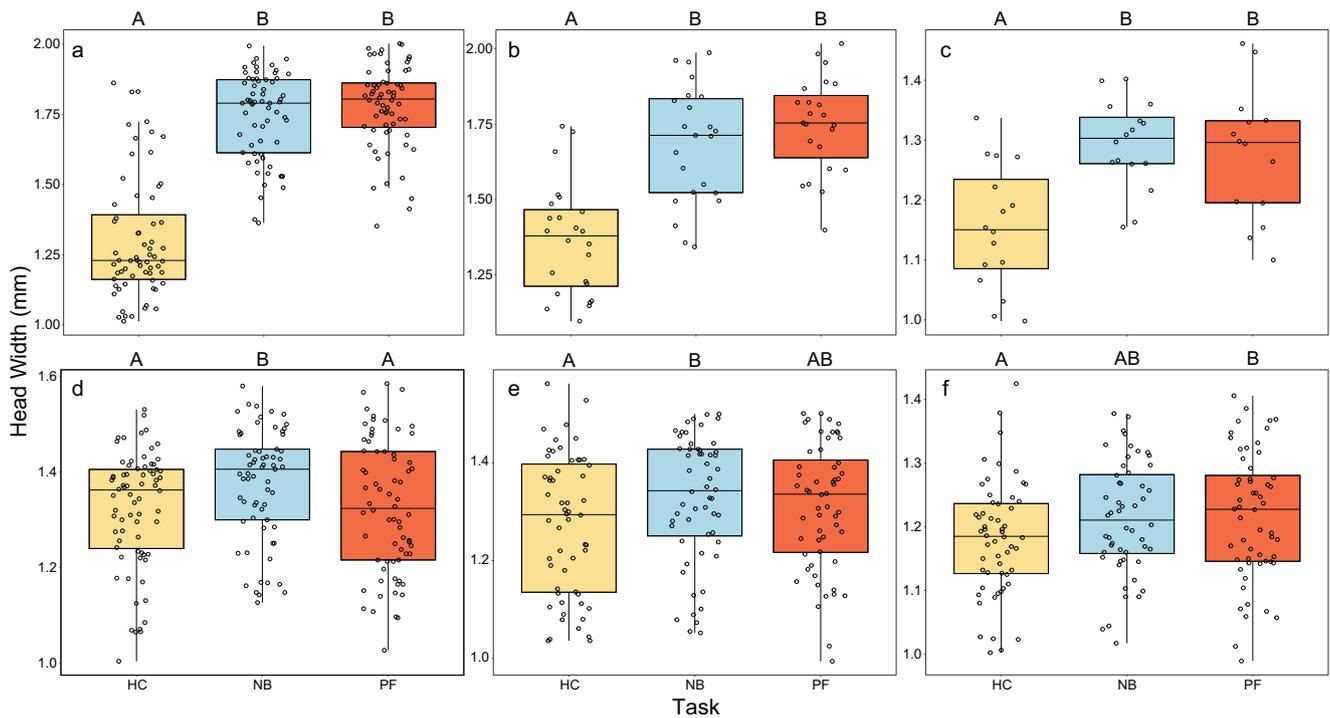


Fig. 2 Boxplots depicting the association between task (HC = honeydew collecting, NB = nest building, and PF = protein foraging) and head width for each of three mound-building *Formica* species: *F. obscuriventris* (a), *F. aserva* (b), *F. dakotensis* (c) and three subterranean *Formica* species:

F. podzolica (d), *F. glacialis* (e), and *F. neoclara* (f). Letters are placed above each box to signify whether there is a significant difference between the head widths of workers from each task based on Tukey’s range post hoc test

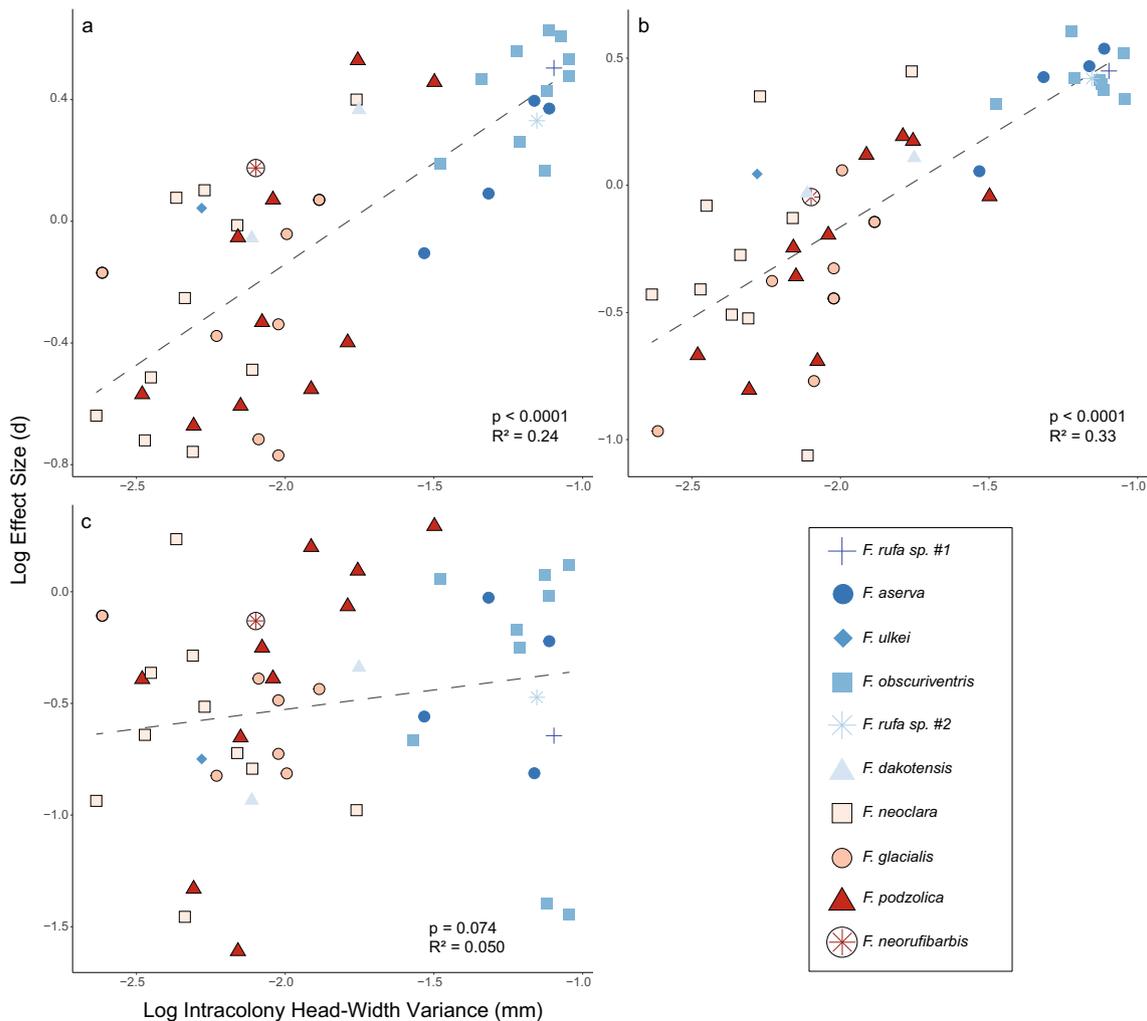


Fig. 3 The relationship between effect size of the size-task association within each colony (Cohen's d , log-transformed) and intracolony worker size variance (log-transformed) for each task comparison: honeydew collectors compared to nest builders (**a**), honeydew collectors compared to protein foragers (**b**), and nest builders compared to protein foragers (**c**).

Regression lines are shown for each task comparison (dashed lines). Colonies from subterranean species are represented by red shapes (outlined in black) and colonies from mound-building species are represented by blue shapes (no outline). Within each plot, the p and R^2 values are based on results from phylogenetic independent contrasts

Discussion

We provide strong support for a form of morphological polyethism operating in *Formica* ants. In addition to exhibiting high task fidelity, *Formica* ants partition non-reproductive tasks on the basis of worker size. Other social insects that lack discrete morphological worker subcastes utilize variation in size among workers in their task partitioning strategies (stingless bees: Grüter et al. 2012; Grüter et al. 2017; fire ants: Tschinkel et al. 2003; Tschinkel 2013; Wilson 1978; bumble bees: Richards 1946; Cumber 1949; Brian 1952; Jandt and Dornhaus 2009; sweat bees: Spradbery 1972; Breed et al. 1978; wasps: O'Donnell and Jeanne 1995). Researchers often assume that insect societies lacking discrete morphological worker subcastes utilize temporal polyethism, a task partitioning strategy wherein individuals switch tasks as they age (reviewed in Robinson 1992; Goldsby et al. 2012).

We provide evidence to suggest that morphological polyethism is potentially much more common in these insect societies than previously expected, whether alongside or in the absence of temporal polyethism.

Though we suspect that temporal polyethism is not shaping the allocation of the external tasks we observed in *Formica*, we cannot rule it out. We conducted our observations over brief periods, and task switching may occur over longer time-scales as workers age. Temporal and morphological polyethism operate alongside each other in some species (e.g., Seid and Traniello 2006; Camargo et al. 2007; Muscedere et al. 2009), and it is possible that a similar strategy exists in *Formica*. For example, for tasks where there is no observable difference in size, age might contribute to task fidelity. In mound-building *Formica*, for example, large workers may specialize in nest building and protein foraging at different ages. Additionally, we have not investigated

within-nest tasks in the present study, because the necessary destructive sampling would have undermined our mark-recapture approach. However, small stingless bee workers stay within the nest longer than their larger sisters (Hammel et al. 2016) and, in many ant species, workers change from within-nest tasks to external tasks as they age (e.g., Retana and Cerdá 1990; Vieira et al. 2010). *Formica* workers may have a similar task trajectory. Although we observed continuing task fidelity in two colonies up to a month after our initial markings, a longer-term study is needed to determine whether temporal polyethism operates alongside morphological polyethism in *Formica*.

Finding high levels of task fidelity reveals that *Formica* colonies employ a successful task allocation system. Our comparison of task allocation across species and colonies that differ in the magnitude of worker size variance suggests that there may be two alternative strategies operating within *Formica*. When size variance is high, workers are more likely to carry out tasks according to their size (Fig. 3). However, size is not the only factor operating in this system, since we find task fidelity, but no size difference, among nest building and protein foraging workers (Figs. 2a–c, 3c). When there is very little size variance, workers still carry out tasks according to their size, but there is far less consistency between colonies (Fig. 2d–f; Fig. S2). This indicates the possibility that their body size and, potentially, associated shape may predispose ants to take on different tasks, but that the reaction norms may vary according to other factors (e.g., genetics, social or abiotic environment). Thus, we see two extremes: high task fidelity and size differences distinguishing honeydew collectors from nest builders and protein foragers consistently in species with large worker size variance, and high task fidelity with less distinct and inconsistent size differences in colonies with low worker size variance.

We do not yet know whether the degree of size variance is a by-product of differences in genetic background or development, or whether selection shapes the distribution of worker sizes. Notably, the three mound-building species are more closely related to each other than to any of the subterranean species (Romiguier et al. 2018; Fig. S6). However, a phylogenetic independent contrast suggests that even when correcting for phylogeny, the degree of intracolony size variation among workers significantly impacts the association between size and task across *Formica* (Fig. 3). Additionally, although the mound-building species generally possess greater worker size variance than subterranean species, there are some cases in which mound-building species possess similar (e.g., *F. dakotensis*, Fig. S4C) or lower (e.g., *F. ulkei*, Fig. S5D) worker size variance than some subterranean species. As mentioned previously, the ecology and life histories of mound-building and subterranean species differ, but the two groups often exist alongside each other within the same habitats. Clearly, there is more to learn about the factors shaping

both worker size variance and task allocation strategy in this widespread, ecologically important genus.

Within-colony task dynamics will be important to investigate in future studies in order to comprehensively understand the degree of worker flexibility and the presence or absence of temporal polyethism in this system. Although we report high task fidelity across short timescales, protein foragers are much more likely to switch tasks than either honeydew collectors or nest builders. This observation might be explained by the relative needs of *Formica* colonies. Bernstein (1976) estimated that protein comprised only about 10% of a typical *Formica* colony's diet, suggesting that protein may be in lower demand than honeydew, for example. Additionally, as Dussutour and Simpson (2008) demonstrate, ants regulate their foraging strategies based on the number of developing brood and available resources. This may cause workers to switch between protein foraging and other tasks as the needs of the colony change. Such flexibility may be beneficial to the colony during seasonal changes in protein availability. Additionally, low predictability or reliability of protein sources may lead to opportunistic protein foraging when workers encounter prey items while performing their usual tasks. Further, our ability to detect protein foraging was lower than the other tasks because it occurs over a large area and successful foraging trips are likely rare. Thus, by restricting our mark-recapture efforts to individuals that were returning to the nest after successfully collecting insect prey, our results may underestimate the effort and task fidelity of protein foragers. It is important to note that the task dynamics depicted in Fig. 1 are summed across multiple colonies of several different mound-building and subterranean *Formica* species. Even so, our results suggest that subterranean species, which tend to possess more uniformly-sized workers, have a significantly higher rate of task-switching than mound-building species.

More generally, all insect societies utilizing morphological polyethism likely share some aspects of developmental processes, evolutionary history, and limitations on worker behavioral flexibility because they all utilize body size variation (Wheeler 1991). Here, we consider some differences between species with and without discrete morphological worker subcastes that may have important implications for colony performance and species longevity. Worker size in all insect societies is shaped by developmental conditions (reviewed in Wills et al. 2018), including the temperature and nutritional quality (Parker and Johnston 2006), social environment (Purcell et al. 2012; Shpigler et al. 2013), genetics (Hughes et al. 2003; Jaffé et al. 2007; Schwander et al. 2005), and development time (Purcell and Chapuisat 2012; Shpigler et al. 2013), the latter of which may have an epigenetic basis (Alvarado et al. 2015). The production of morphological subcastes, however, relies on additional complex hormonal pathways and genetic networks that regulate differential growth patterns of individual tissues in developing workers (reviewed

in Tribble and Kronauer 2017). From an evolutionary perspective, workers of different sizes may be better at performing different tasks, such that the maintenance of size variability reinforces task specialization and enhances colony efficiency (Oster and Wilson 1979; Chittka and Müller 2009). Past studies propose that an additional evolutionary step, in which exaggerated morphologies are favored by natural selection over intermediate morphologies, led to insect societies with discrete morphological subcastes (Wilson 1953; Emlen and Nijhout 2000; reviewed in Tribble and Kronauer 2017). However, we should not infer that all social insects with size-variable workers are on an evolutionary trajectory toward the development of discrete subcastes. On the contrary, we speculate that species with continuous size variation and size-based task partitioning might achieve higher fitness than species with morphological subcastes under some conditions. Previous work, though limited, suggests that workers in insect societies with discrete morphological subcastes are less behaviorally flexible than in those without them. For example, major *Pheidole* workers are less successful at raising brood compared to minor workers (e.g., Mertl and Traniello 2009), while large *Tetragonisca angustula* workers are capable of performing all the tasks that small workers usually perform (Hammel et al. 2016). Differences in restrictions imposed by alternative task allocation strategies are important to consider, as they may impact the resilience of the species that use them in increasingly unpredictable environments (Fisher et al. 2019).

We provide strong evidence that *Formica* ant workers use a size-based task allocation strategy. Among eusocial Hymenoptera, the presence of discrete morphological worker subcastes is relatively uncommon, occurring only in 15% of ant genera (Oster and Wilson 1979). Thus, a primarily size-based form of morphological polyethism may be far more common than suggested by the literature. Morphological polyethism should not be ruled out in social insects known to use temporal polyethism, as the two strategies have been found to operate alongside each other in some species with morphological subcastes. We further identify several likely developmental, evolutionary, and behavioral distinctions between workers from species with and without morphological subcastes and argue that these should be considered in future studies. More comparative analyses will give us a better understanding of how variation within and across species impacts the robustness and flexibility of different task allocation strategies.

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