

UCLA

UCLA Previously Published Works

Title

Age-related division of labor occurs in ants at the earliest stages of colony initiation

Permalink

<https://escholarship.org/uc/item/37w2d1mh>

Journal

Behavioral Ecology and Sociobiology, 75(2)

ISSN

0340-5443

Authors

Enzmann, Brittany L

Nonacs, Peter

Publication Date

2021-02-01

DOI

10.1007/s00265-021-02974-w

Peer reviewed



Age-related division of labor occurs in ants at the earliest stages of colony initiation

Brittany L Enzmann¹ · Peter Nonacs²

Received: 21 October 2020 / Revised: 31 December 2020 / Accepted: 8 January 2021
© Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Mature colonies of many social insect species exhibit division of labor (DOL) where individual workers specialize in doing only a subset of the multiple tasks needed to maintain homeostasis. In newly initiated ant colonies, however, the first workers (called nanitics) are few in number and much smaller in size than those in mature colonies. This limited workforce must perform most of the tasks of mature colonies, but it is unknown if they also exhibit DOL. In this study, we tracked several inside-nest and outside-nest behaviors of nanitics in incipient *Pogonomyrmex rugosus* colonies. DOL arises in these colonies, whereby the relatively oldest workers (even if only by a few hours) are biased towards foraging, while younger nanitics concentrate on brood care. The addition of new nanitics shifts behavior in the oldest individual away from brood care but does not immediately increase its foraging. Conversely, nanitics left alone due to mortality of nest-mates forage more, but do not reduce brood care. The results suggest *P. rugosus* nanitics follow an age-related task specialization pattern that is broadly similar to mature colonies. The nanitic life stage may be, however, unique for ants in how fine-grained the DOL is in terms of absolute age differences and flexibility for task switching.

Significance statement

The ecological success of ants is thought to be facilitated by workers dividing their labor across tasks. Commonplace in mature colonies is that individuals will perform safer, within-nest tasks such as brood care when young, and shift as they age towards riskier, outside-nest tasks such as foraging. Because many do the same task, the death of any single worker has minimal effect. We show, for the first time, a similar age-related, task specialization pattern also occurs in newly founded colonies. In this earliest life, history stage workers are small and few in number, precluding the massive task redundancy that characterizes mature colonies. Nevertheless, a division of labor correlating with relative age differences arises even when workers differ in age by only a few hours. This supports the hypothesis that a similar developmental pathway for task allocation in worker behavior occurs at all stages in colony life history.

Keywords *Pogonomyrmex* · Harvester ant · Nanitic · Age polyethism

Introduction

A hallmark of many social insect species is a well-defined division of labor (DOL), in which subsets of workers focus

primarily on one or a limited range of tasks (honey bees, Robinson 1992; Seeley 1982; ants, Sorensen et al. 1984; Hölldobler and Wilson 1990; Thomas and Elgar 2003; Seid and Traniello 2006; Muscedere et al. 2009; wasps, Jeanne 1991; Shorter and Tibbetts 2009; and termites, Crosland et al. 1997). Dividing and performing tasks redundantly increases efficiency in large colonies (Jeanne 1986), and enhances colony fitness (Oster and Wilson 1978; Heinrich 1979).

In establishing a DOL, many species of social insects also exhibit age polyethism, whereby workers participate in interior-nest tasks (e.g., brood care) when they are young and transition to more dangerous exterior-nest tasks (e.g., patrolling, foraging, and colony defense) as they grow older (Wilson 1971; Robinson et al. 1994). There are differing hypotheses on the proximate mechanisms of how age becomes

Communicated by L. Keller

✉ Peter Nonacs
pnonacs@biology.ucla.edu

Brittany L Enzmann
benzmann@gmail.com

¹ School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

² Department of Ecology and Evolutionary Biology, University of California, 621 Young Dr. S., Los Angeles, CA 90095, USA

correlative and predictive of DOL (reviewed by Beshers and Fewell 2001). On an ultimate, evolutionary level having older and closer-to-senescence workers preferentially doing the riskiest work is thought to maximize the lifetime benefit that, on average, individuals can provide to their colony (Oster and Wilson 1978; Porter and Jorgensen 1981).

DOL has been extensively investigated in juvenile or mature ant colonies that often contain hundreds to thousands of individuals. In many independently founding ant species, however, the colony initiation stage is distinctively different. Newly mated females (foundresses) dig nests and subsequently produce a first brood of workers either from stored reserves, by foraging for food, or both. Due to the limited resource supply, these workers, called nanitics, are fewer in number and much smaller relative to those of mature colonies (Porter and Tschinkel 1986; Hölldobler and Wilson 1990; Peeters and Ito 2001; Johnson 2002, 2006). The nanitic caste occurs predominantly in higher ant subfamilies as a derived trait, suggesting significant positive selection (Hölldobler and Wilson 1990). Their presence, nevertheless, is only temporary. As a colony grows, workers in subsequent cohorts get larger and eventually reach the size characteristic of mature colonies (Oster and Wilson 1978; Wood and Tschinkel 1981).

In large colonies with DOL, the death of one worker is buffered by redundancy in task performance by others. However, in incipient colonies lacking redundancy, the death of a single specialist could have significant colony-wide ergonomic consequences. Therefore, selection could favor different optimal patterns of task allocation across the stages of colony ontogeny (Jeanson et al. 2007). Significant advantages of worker task flexibility include the ability to adjust to fluctuations in colony size or demography (Winston and Fergusson 1985), changing demands for particular tasks (Gordon 1989; O'Donnell and Jeanne 1990; Tripet and Nonacs 2004; Robinson et al. 2009), or varying environments (Oster and Wilson 1978). Indeed, in a variety of social insect species, workers in small colonies are behaviorally less specialized and more flexible than those in large colonies (István and Wenzel 1998; Thomas and Elgar 2003; Holbrook et al. 2011).

No study to date has explicitly observed how a nanitic worker cohort determines its task allocation patterns. Given that task distribution can vary across species in larger or mature ant colonies, there are no obvious a priori expectations for how a few nanitic workers allocate tasks among themselves. The possible outcomes could range from no DOL with all nanitics doing all tasks at approximately equal frequencies to a DOL across individuals that might reflect their immediate experiences or genetically biased proclivities, or to a DOL that correlates to nanitic age differences. To explore these possibilities, we observed how nanitic workers in the harvester ant, *Pogonomyrmex rugosus*, allocated their tasks.

Material and methods

Set-up

Pogonomyrmex rugosus harvester ants range throughout the deserts of southwestern North America and northern Mexico (Johnson 2000). The workers are monomorphic, and colonies typically contain ~7000–15,000 workers when mature (MacKay 1981; Johnson 2000; Oettler and Johnson 2009). Foundresses form new colonies independently (without workers) and are fully claustral (i.e., they rear nanitics from stored body reserves and do not forage).

Foundresses were collected following nuptial flights on West McCartney Rd and at the Scottsdale Community College, AZ on July 17 and 22, 2013, respectively. Within a couple of days, each individual was placed into a glass tube that was partially filled with water and plugged with cotton. The tubes were placed in a darkened incubator at 30 °C. Because *P. rugosus* is fully claustral, no food was provided. The tubes were observed daily for the presence of eggs. After foundresses began to oviposit, the foundress and eggs were each transferred to a nest enclosure consisting of two 100 × 15-mm petri dishes connected by ~5 cm of plastic tubing. A Labstone base (Darby Dental Supply LLC, NY) was added to one petri dish in order to retain moisture and thus resemble a nest interior. The base of this dish was moistened, and a 1.5-ml microcentrifuge tube provided water ad libitum. The other petri dish was left open (with sides covered in Fluon to prevent any escape) to resemble a nest exterior. All nests were kept in a room at a constant 28 °C temperature with a 12-h dark/12-h light photoperiod. Once the first nanitic eclosed from the pupal state, five Kentucky bluegrass seeds (*Poa pratensis*) and an artificial ant diet (Bhatkar and Whitcomb 1970) were provided in the foraging arena and replenished as needed. The term “nanitic” often refers to only the first brood of workers in incipient colonies. Here, we refer to all workers that eclosed during the study period as nanitics because all individuals were much smaller than workers in mature colonies. However, worker size did gradually increase across this period, as occurs in natural colonies.

Recording mass and marking

The lifespan and wet mass (at eclosion) of each nanitic were recorded. Because the nanitics are fragile on the day of eclosion (the exoskeleton is soft), the mass of each nanitic was recorded 2–3 days post-eclosion and marked on the abdomen with a unique color using Testors enamel paint (Vernon Hills, IL). Marking ants in this way is common and is not associated with increased mortality. The number of nanitics in each nest and their relative ages were recorded daily.

Behavioral observations

Three observers used an ethogram that coded for the following commonly observed behaviors:

1. Nursing (brood care): interacting with eggs, larvae, or pupae
2. Walking inside nest or tube
3. Sitting stationary inside the nest or tube
4. Grooming either self, another nanitic, or the foundress
5. Foraging as present in the foraging arena or carrying food into the nest interior

Prior to any recordings, all observers compared test observations to ensure consistency in scoring. Point behavioral observations of each nanitic were taken at no less than 30-min intervals, between 10:00 and 17:00 h. The number of observations of each colony ranged from 1 to 12 per day and were taken between August 23 and December 13, 2013. The number of observations varied across individuals due to mortality. In total, there were 13,107 recorded scan samples of the activities of 101 nanitics in 37 nests.

Statistical analyses

The eclosion rate of nanitics and their survival varied across colonies. Therefore, at various times, nanitics could either be alone or with others. When several nanitics were simultaneously present, they were ranked based on their eclosion order into categories that represent their relative age. The oldest one present for any given observation was designated as Rank 1 (highest rank), the next oldest was Rank 2, and so on. Individual colonies produced up to seven nanitics in total over the course of the study. Rarely, however, were more than three nanitics alive at the same time. Therefore, for analytical purposes, Rank 4 and higher nanitics were combined with Rank 3 nanitics. In two cases, a fifth nanitic eclosed when four others were already present, and the oldest nanitic was removed to limit the maximum number. Nanitics that lived less than 4 days were excluded from analyses of activity patterns. The numbers of each activity observed (e.g., forage and nurse) were calculated as a frequency relative to the total number of scan samples (arcsine-square root transformed for statistical tests).

New eclosions or deaths meant that individual nanitics could spend significant periods of time in more than one state (i.e., Alone or in one of the three ranks). To be included as a case in the analysis, at least 96 consecutive hours had to be spent in a given state. This resulted in 101 behavioral series across 77 observed nanitics. A multiple discriminant analysis (MDA, using JMP™) incorporating all five observed activity states elucidated if Alone or Ranks 1–3 states produced significantly different behavioral repertoire clusters. A series of one-way ANOVAs, with nanitic Ranks 1–3 as the independent variable, tested for differences in the frequencies of the

individual behaviors. In cases where an individual nanitic experienced a change in state, Wilcoxon signed-rank tests tested for significant changes in before and after activity patterns. Note that mortality could only move nanitics up in rank and never down. Nanitics could, however, move back and forth between Rank 1 and Alone states.

We tracked the longevity of each nanitic by recording the eclosion and mortality dates of each individual. For nanitics that died during the experimental observation period, we ran a one-way ANOVA of lifespan (range = 1 to 90 days) with relative birth order. We also regressed lifespan against wet mass (mg) measured soon after eclosion ($n = 64$, mean = 3.4 mg, range 2.1–5.7 mg, normally distributed). Effects on nanitic lifespan were also examined by multiple regression against individual activity rates.

Results

Overall, the results strongly support a pattern of DOL with an interior-to-exterior task bias that positively correlates with age (an age-related system, *sensu* Tripet and Nonacs (2004), where relative age determines task allocation). Two lines of data show that older workers, even when only a day older, gravitated to be the foragers and younger workers cared for brood. The first is the MDA analysis where the 95% confidence ellipse for the mean of the Rank 1 nanitic cluster significantly separates from those for Ranks 2, 3, or Alone (Fig. 1; detailed analysis outputs are provided in Supplement). Alone and Rank 3 means are also significantly different. Rank 2, however, overlaps with both Alone and Rank 3. The model correctly identifies Alone behavioral state in 23 out of 34 (68%) cases; Rank 1, 15 out of 24 (62%); Rank 2, 10 out of 27 (37%); and Rank 3, 14 out of 16 (88%). If, however, the Alone and Rank 1 states are combined into the “forager” role, then the analysis correctly identifies 49 out of 58 cases (84%) as being the forager. Similarly, if Ranks 2 and 3 are combined into the “nurse” role, then the analysis correctly places 28 out of 43 cases (65%) as being the brood tender. Second, when multiple nanitics are simultaneously present, one-way ANOVAs show that Rank 1 nanitics significantly walk ($F_{2,64} = 9.56$, $p = 0.0002$) and forage ($F_{2,64} = 7.12$, $p = 0.0016$) more often, and nurse less often ($F_{2,64} = 20.99$, $p < 0.0001$) than lower ranked nanitics (Fig. 2).

There were several behavioral shifts associated with directional changes in state. In 9 cases, a solitary nanitic was joined by newly eclosed nanitics such that it became a Rank 1 (designated as “First”). In 10 cases, mortality reduced the workforce to a solitary nanitic (“solo”: in 9 of the cases, a Rank 2 individual was left as the sole worker). In 4 cases, nestmate mortality promoted a nanitic in rank from 3 to 2 or 2 to 1 (designated as “Gain”). Wilcoxon signed-rank tests of activity rates before and after these state changes found that walking significantly

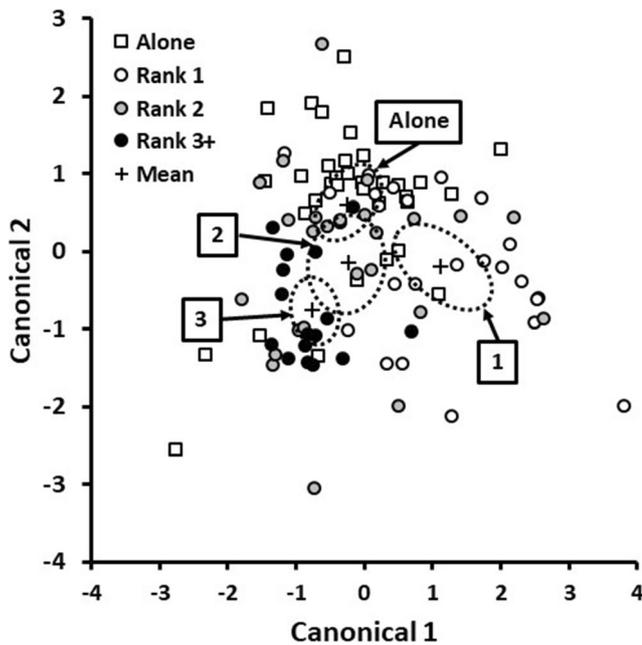


Fig. 1 Clustering of nanitic states and their 95% confidence intervals by multiple discriminant analysis. Data categories correspond to states where nanitics are Alone (the only worker present); Rank 1 (the oldest living worker in a group); Rank 2 (the second oldest); or younger than the Rank 2 worker (all such nanitics are categorized as Rank 3). Crosses are the canonical means for each state, and ellipses are the 95% confidence intervals. The MDA analysis (using a quadratic method) included the frequencies at which nanitics were observed sitting, walking, grooming, nursing brood, or foraging (arcsine-square root transformed)

increased for Solo and First changes, nursing significantly decreased for the First change (nursing marginally decreased with rank Gain, but with only 4 comparisons the power of the test is very low), and foraging significantly increased when nanitics found themselves newly Solo (Table 1). Across changes in state, the before values were subtracted from the after values for

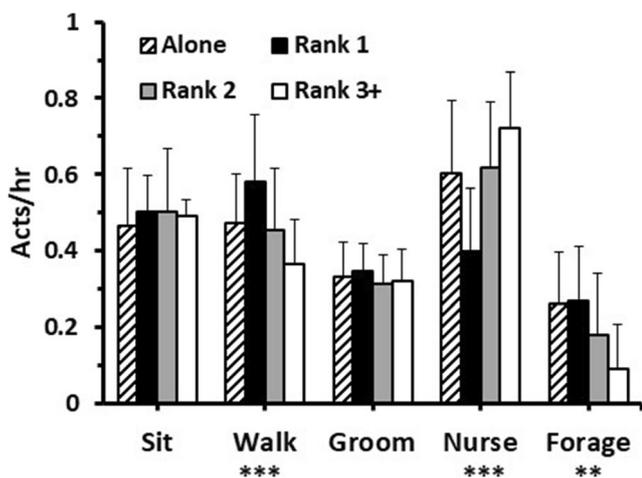


Fig. 2 Mean observed activity frequencies (+SD) of nanitics in various states. Rank reflects relative age from oldest (Rank 1) to youngest (Ranks 2 and 3+). A one-way ANOVA (data arcsine-square root transformed) compared activities across individuals of Ranks 1–3 in multi-nanitic groups: ** = $p < 0.01$; *** = $p < 0.001$

nursing and foraging and then regressed against the age of the nanitic at the time of the change (ranging from 6 to 95 days old). Neither magnitude of the change in behavior was significantly affected by the age at which it happened (nursing, $F_{1,21} = 0.040$, $p = 0.8434$; foraging, $F_{1,21} = 1.466$, $p = 0.240$). Older nanitics did not exhibit significantly greater changes in their behavior in response to a state change.

When a solo nanitic was joined by a newly eclosed worker, their chronological age difference had no effect on the magnitude of the division of labor that arose (Fig. 3). Pairs of nanitics that differed in 0–7 days of age divided tasks similarly to pairs that differed in 27–99 days of age, with the older of the pair doing more of the foraging and the younger doing more of the brood care.

Nanitic lifespans were highly variable, ranging from dying on the day they eclosed to surviving the length of the study (114 days). A multiple regression across the deceased found that nanitic lifespan (ln transformed for normality) was strongly correlated with an individual’s likelihood to walk ($t = 5.650$; $p < 0.0001$). Contrary to a prediction that doing more physical activity would wear out a nanitic and lead to a reduced lifespan, the effect is positive. A higher rate of walking correlates with a longer life. The only other activity with a statistically significant effect was grooming rate. Grooming more often is associated with a significant decline in lifespan ($t = -2.380$; $p = 0.0232$). Nanitic weight at eclosion had a negative effect on lifespan, but the effect was not significant ($F_{1,63} = 3.355$, $p = 0.072$, $R^2 = 0.051$). There was no significant effect of maturation order (categorized as 1st, 2nd, or 3rd+ to eclose) on lifespan ($F_{2,62} = 0.471$, $p = 0.627$).

To further examine the effects of chronological age (as opposed to relative age), we created a subsample of nanitic point observations restricted to those of individuals with a minimum known age of 15 days and either by themselves (Alone, 4824 observations) or in groups of two (Rank 1, 1386 observations or Rank 2, 1007 observations). From these three groups, we randomly drew (without replacement so that no single point observation would be multiply counted) 100 individual observations. For each observation, we recorded the age of the scanned nanitic (in days) and the observed behavior of the individual. Such random draws were replicated 1000 times, and the proportion of times nursing or foraging events were observed was recorded relative to age day. Regressing the proportions against chronological age (Fig. 4) found no significant effect on the likelihood of individuals foraging outside the brood chamber (Alone, $F_{1,77} = 0.839$, $p = 0.362$; Rank 1, $F_{1,47} = 1.938$, $p = 0.170$; Rank 2, $F_{1,34} = 0.423$, $p = 0.520$). Similarly, age did not affect nursing in the nest for Alone and Rank 1’s ($F_{1,77} = 0.177$, $p = 0.675$; $F_{1,47} = 0.446$, $p = 0.508$, respectively). For Rank 2’s, however, the propensity to nurse did significantly decrease with their chronological age ($F_{1,34} = 21.68$, $p < 0.0001$). This, however, did not indicate a task switch as foraging rates did not

Table 1 Wilcoxon signed-rank tests for the effect of changing state on nanitic behaviors

Activity	A-B	Solo Z	p	A-B	First Z	p	A-B	Gain Z	p
Sit	-0.011	-0.153	0.878	0.035	-0.770	0.441	0.113	-1.095	0.273
Walk	0.123	-2.599	0.009	0.217	-2.666	0.008	0.135	-1.095	0.273
Groom	-0.008	-0.357	0.721	0.007	-1.244	0.214	-0.010	-0.000	0.999
Nurse	-0.116	-1.274	0.203	-0.309	-2.073	0.038	-0.282	-1.826	0.068
Forage	0.146	-2.803	0.005	-0.014	-0.178	0.859	0.136	-1.606	0.109

The tests (Z scores and significance levels) compare the after (A) frequencies of behavior to frequencies before (B) the change. The three categories of change in state are Solo, nanitic becomes sole worker due to mortality ($n = 10$ occurrences); First, solitary nanitic is joined by newly-enclosed worker ($n = 9$); and Gain, 2nd or 3rd ranked nanitic promotes to 1st or 2nd Rank due to mortality ($n = 4$). Significant changes are shown in bold

significantly increase. Instead, the significant decrease in nursing was matched with a significant increase in the rate at which Rank 2 individuals were observed being inactive (sitting: $F_{1,34} = 5.598, p = 0.0238$). Grooming and walking rates did not significantly change.

Discussion

A eusocial life history requires complex behavioral repertoires to maintain nests, care for and defend cohorts of dependent

offspring, and procure enough food to sustain a large group of individuals (Hölldobler and Wilson 1990). This is often accomplished by dividing the labor such that individuals

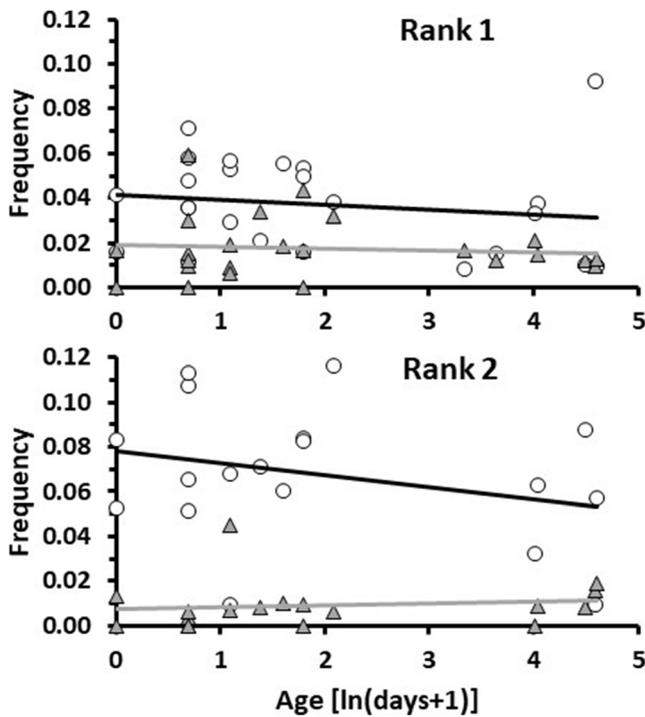


Fig. 3 The effect of chronological age difference (in days, ln-transformed) on the division of labor between older and younger nanitics. There was no significant effect of age differences on the rate that older Rank 1 nanitics either forage (shaded triangles; $F_{1,22} = 0.145, p = 0.7073, R^2 < 0.001$) or nurse brood (open circles; $F_{1,22} = 0.490, p = 0.4914, R^2 < 0.001$). Similarly, there was no significant age effect on younger Rank 2 nanitics (foraging, $F_{1,16} = 0.284, p = 0.6017, R^2 < 0.001$; nursing, $F_{1,16} = 1.478, p = 0.2417, R^2 = 0.027$)

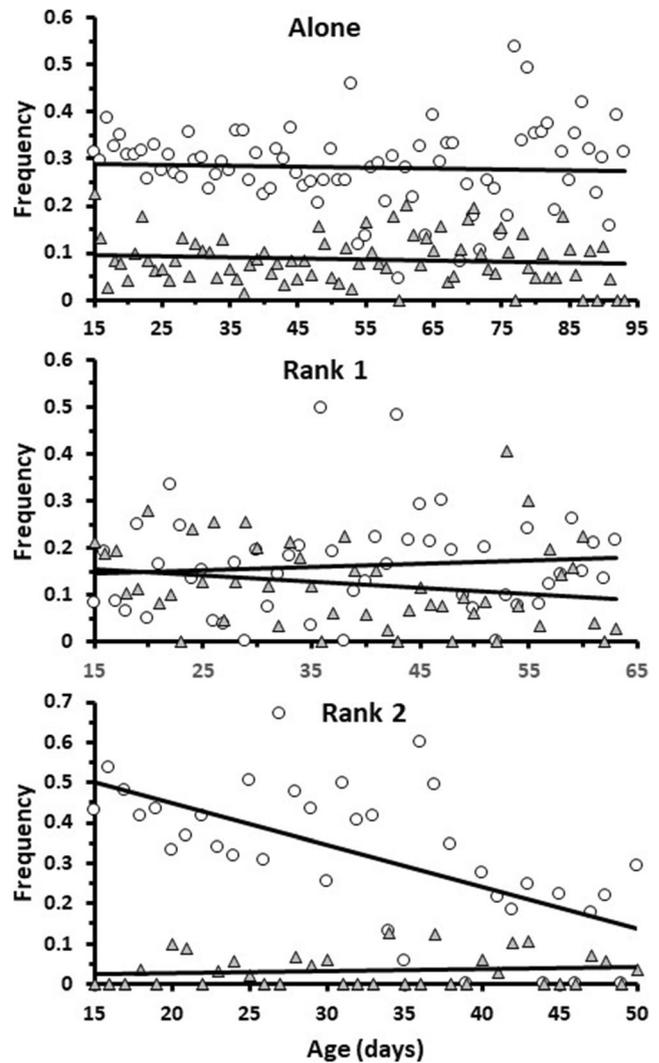


Fig. 4 The effect of chronological age on the frequencies of nursing brood (open circles) and foraging (shaded triangles). The data points are means of multiple resamples (see text) of nanitics that were in states of being Alone or Ranks 1 or 2 within a multi-nanitic group

specialize in executing only one or a limited series of tasks (Wilson 1971; Jeanne 1986). In many species, however, individuals experience a series of task specializations as they transition from brood-associated work within the nest, to food and defense-associated work outside the nest (Robinson 1992; Robinson et al. 1994). A pattern of transitional specialization is hypothesized to be a major factor in the success and dominance of eusocial insects within terrestrial ecosystems (Wilson 1990; Traniello and Rosengaus 1997).

A key element to the ergonomic efficiency of DOL may be the size of the group (Oster and Wilson 1978; Jeanne 1986; Jeanson et al. 2007). DOL has been found to become more pronounced as colonies get larger with more workers (Jeanne 1986; Thomas and Elgar 2003; Holbrook et al. 2011). However, a critical and unstudied life history phase in many independently founding ant species is when mated females produce their first worker cohort in the form of a few small nanitics. In a first test for DOL in such incipient ant colonies, we find that task allocation in *P. rugosus* is significantly age-related. Relatively older nanitics do more foraging and younger ones do more brood care. This pattern with 2–4 nanitics is similar to relative age distributions across tasks in mature colonies comprising hundreds to thousands of workers (Wilson 1971; Beshers and Fewell 2001).

In incipient colonies overall, foraging effort appears to be minimized. Given that the loss of any individual can significantly impact colony survival, the bulk of the most dangerous task is delegated to the one oldest worker. Thus, rather than maximizing input from outside food sources, colonies appear to still rely on stored resources (e.g., trophic eggs from the foundress). They have not completely switched from a capital to an income economy (Johnson 2006).

Foremost about DOL in the nanitic phase of colony life history is the role that relative age plays within incipient nests. If a nanitic is the sole worker in the nest, it has a relatively balanced portfolio of tasks (Figs. 1 and 2). As other nanitics mature, the previously alone and now oldest worker shifts in behavior to become more biased towards foraging, while the younger ones primarily exhibit within-nest behaviors. Of particular note is that this DOL can arise even when absolute age differences are as small as a single day or a few hours. Moreover, the actual age differences between pairs of nanitics also had no significant effect on the degree to which they partitioned the foraging and nursing tasks (Fig. 3). An effect on task choice with such a minimal age difference has been observed within cohorts of age-controlled honey bee workers (Page Jr et al. 1992). This is the first report of such an effect among ant workers, and a question remains as to whether or not this is a unique feature of incipient colonies.

In comparison to relative age differences, actual chronological age seems to have a smaller influence on task allocation. The propensity to forage does not increase with chronological age (Fig. 4). Furthermore, although a change in the state of the

nanitic significantly affects nursing and foraging frequencies (Table 1), how large those changes are in terms of absolute frequencies is not significantly correlated with the age of the nanitic. These results support neither physiological aging, per se, shifting behavioral proclivities towards more dangerous work, nor older workers having had more opportunities to encounter the foraging task and thus drift into doing it. Similarly in *P. badius*, the effects of chronological age are also more attuned to colony needs and life history. Cohorts of workers that eclose at different times of the year routinely vary by more than 150 days in age before they begin to forage (Kwapich and Tschinkel 2013).

Rank 2 individuals do reduce brood care as they age. The shift, however, seems to be towards doing less work altogether. What might account for such an effect is that overall brood needs are declining (which, by design, were not measured), or possibly that increasingly inactive nanitics are shifting into a pool of reserve labor; this is available for emergency needs (Charbonneau et al. 2017).

The results also reveal an interesting pattern in how task performance adjusts to changes in the number of workers present. When a solitary nanitic is joined by newly eclosed nanitics, this results in a significant drop in its frequency of nursing (Table 1: “First” columns). The presence of younger nursing biased nestmates “pushes” the older nanitic away from nursing, but it does not immediately significantly increase its foraging frequency. This type of shift is similar to behavior in *Camponotus floridanus* when the entire forager retinue is removed. The oldest brood-tenders reduce that behavior (Tripet and Nonacs 2004). In contrast, when mortality leaves a nanitic as the solitary worker (in 9 out of 10 cases, it happened to a Rank 2), foraging frequencies significantly increase (Table 1: “Solo” columns). However, the nanitic is not “pulled” away from nursing, which continues without a significant decline in frequency. This is similar to *Pheidole dentata* minor workers with respect to age (without the social environment being manipulated). They add outside nest tasks to their behavioral repertoires without dropping inside nest tasks as they get older (Seid and Traniello 2006). These patterns differ, however, from those observed by Kwapich and Tschinkel (2016) in manipulating forager longevity in mature *P. badius* colonies. Increased longevity decreased the addition of new foragers (i.e., continued maturation of new workers did not push excess brood-care workers into becoming foragers). Decreasing forager longevity also did not pull larger numbers of nest workers into becoming replacement foragers. Thus, both mature *P. badius* (Kwapich and Tschinkel 2013, 2016) and incipient *P. rugosus* colonies show that some task transitions are less behaviorally flexible than others. It remains to be determined if the differential distribution of behavioral flexibility is a species-level or life-history stage effect. Overall, *P. rugosus* nanitic colonies are consistent with previous observations that flexibility of task allocation in DOL is the

greatest with fewer workers (István and Wenzel 1998; Thomas and Elgar 2003; Holbrook et al. 2011). The behavior of each focal nanitic appears to track a combination of relative age rank and the numbers of nestmates.

Our results also provide insight on the lifespan of *P. rugosus* nanitics. Although there is considerable variance in how long individuals live, longevity is not significantly affected by either birth order or mass at eclosion. Thus, there is no evidence that mothers differentially treat or feed individuals within the nanitic cohort in order to manipulate them into becoming task specialists. Activity, in terms of walking frequency, positively correlates with lifespan. This suggests that intrinsic robustness varies within cohorts, such that more robust individuals both move more and live longer. There is a significant negative effect of grooming rate on lifespan. Rather than suggesting this increased activity is causal, it seems more likely that a nanitic under stress from a physically deteriorating condition both grooms itself and is groomed by nestmates more often.

The evolution of social behavior in the Hymenoptera is proposed to be primarily through upregulating or downregulating gene expression from genomic pathways already present in solitary ancestral species (Amdam et al. 2004; Kapheim and Johnson 2017; Warners et al. 2019). That DOL in incipient and mature harvester ant colonies shares critical features suggests there is a basic “ground plan” for how individuals cooperate with respect to task performance (Amdam et al. 2004). What may be unique is the rapidity in terms of how quickly after eclosion DOL can arise in nanitics and how small the differences in absolute chronological ages can be.

Although other studies on ant nanitics are lacking (but see Rosengaus and Traniello (1993) for lack of DOL in incipient termite colonies), similar DOL patterns have been reported in small-group associations of ant queens. *Acromyrmex versicolor* foundresses cooperate in raising the worker broods (pleometrosis). Until the first workers mature, only one female at a time takes on the forager role (Rissing et al. 1989). Also, DOL emerges between females from a pleometrotic population of the harvester ant, *P. californicus*. Interestingly, this study also reported that foundresses from a haplometrotic population (i.e., females never cooperate in the field) developed similar DOL when foundresses were placed together in the lab (Jeanson and Fewell 2009).

Although our study offers new insights about the emergence of DOL in early colony development, evaluating the fitness consequences of such patterns is limited. Given that laboratory settings are more benign than in nature, this study could not determine the degree to which the observed DOL increases colony survival and success. We can, however, speculate to some degree about what the consequences of DOL in incipient colonies may be. For example, a disadvantage of having one foraging specialist would be increasing the day-to-day variance in foraging success and, therefore,

retarding how rapidly colonies grow out of the extremely vulnerable small size state (Wenzel and Pickering 1991). It is possible that a DOL ground plan that works well for mature colonies is not optimal for incipient colonies but is also evolutionarily difficult to escape. Thus, it would be of great interest to test how universal the pattern of *P. rugosus* nanitic behavior is across other species with a similar life history phase, and if it does indeed lead to higher colony survival than alternative patterns of task allocation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-02974-w>.

Acknowledgments We thank Robert A. Johnson and Juergen Gadau for generously supplying us with *P. rugosus* foundresses from Arizona and Jennifer Fewell for supplying the lab space to carry out observations. We extend our appreciation to Kelsey Cozzolino and Jennifer DePew who conducted many of the behavioral observations for this study.

Code availability Not applicable.

Authors' contributions BLE and PN both conceived the idea. BLE designed the experiment and collected the data. PN did the statistical analyses. BLE and PN both wrote the paper.

Data availability Data for each colony and observation will be submitted to Dryad upon manuscript acceptance. Data can be provided upon request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication BLE and PN both consent to submission and publication.

References

- Amdam GV, Norberg K, Fondrk MK, Page RE (2004) Reproductive ground plan may mediate colony-level selection effects on individual foraging behavior in honey bees. *Proc Natl Acad Sci U S A* 101: 11350–11355
- Beshers SM, Fewell JH (2001) Models of division of labor in social insects. *Annu Rev Entomol* 46:413–440
- Bhatkar A, Whitcomb WH (1970) Artificial diet for rearing various species of ants. *Fla Entomol* 53:229–232
- Charbonneau D, Sasaki T, Dornhaus A (2017) Who needs ‘lazy’ workers? Inactive workers act as a ‘reserve’ labor force replacing active workers, but inactive workers are not replaced when they are removed. *PLoS One* 12:e0184074
- Crosland MWJ, Lok CM, Wong TC, Shakarad M, Traniello JFA (1997) Division of labour in a lower termite: the majority of tasks are performed by older workers. *Anim Behav* 54:999–1012

- Gordon DM (1989) Dynamics of task switching in harvester ants. *Anim Behav* 38:194–204
- Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge
- Holbrook CT, Barden PM, Fewell JH (2011) Division of labor increases with colony size in the harvester ant *Pogonomyrmex californicus*. *Behav Ecol* 22:960–966
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge
- István K, Wenzel JW (1998) Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proc Natl Acad Sci U S A* 95:8665–8669
- Jeanne RL (1986) The evolution of the organization of work in social insects. *Monit Zool Ital* 20:119–133
- Jeanne RL (1991) Polyethism. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, pp 389–425
- Jeanson R, Fewell JH (2009) Influence of the social context on division of labor in ant foundress associations. *Behav Ecol* 19:567–574
- Jeanson R, Fewell JH, Gorelick R, Bertram SM (2007) Emergence of increased division of labor as a function of group size. *Behav Ecol Sociobiol* 62:289–298
- Johnson RA (2000) Seed-harvester ants (Hymenoptera:Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology* 36:88–122
- Johnson RA (2002) Semi-claustral colony founding in the seed-harvester ant *Pogonomyrmex californicus*: a comparative analysis of colony founding strategies. *Oecol* 132:60–67
- Johnson RA (2006) Capital and income breeding and the evolution of colony founding strategies in ants. *Insect Soc* 53:316–322
- Kapheim KM, Johnson MM (2017) Support for the reproductive ground plan hypothesis in a solitary bee: links between sucrose response and reproductive status. *Proc R Soc Lond B* 284:20162406
- Kwapich CL, Tschinkel WR (2013) Demography, demand, death, and the seasonal allocation of labor in the Florida harvester ant (*Pogonomyrmex badius*). *Behav Ecol Sociobiol* 67:2011–2027
- Kwapich CL, Tschinkel WR (2016) Limited flexibility and unusual longevity shape forager allocation in the Florida harvester ant (*Pogonomyrmex badius*). *Behav Ecol Sociobiol* 70:221–235
- MacKay WP (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Psyche* 88:25–74
- Muscenedere ML, Willey TA, Traniello JFA (2009) Age and task efficiency in the ant *Pheidole dentata*: young minor workers are not specialist nurses. *Anim Behav* 77:911–918
- O'Donnell S, Jeanne RL (1990) Forager specialization and the control of nest repair in *Polybia occidentalis* Olivier (Hymenoptera: Vespidae). *Behav Ecol Sociobiol* 27:359–364
- Oettler J, Johnson RA (2009) The old ladies of the seed harvester ant *Pogonomyrmex rugosus*: foraging performed by two groups of workers. *J Insect Behav* 22:217–226
- Oster GF, Wilson EO (1978) Caste and ecology in the social insects. *Mono Pop Biol* 12:1–352
- Page RE Jr, Robinson GE, Britton DS, Fondrk MK (1992) Genotypic variability for rates of behavioral development in worker honeybees (*Apis mellifera* L.). *Behav Ecol* 3:173–180
- Peeters C, Ito F (2001) Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu Rev Entomol* 46(601): 630
- Porter SD, Jorgensen CD (1981) Foragers of the harvester ant, *Pogonomyrmex owyheeii*: a disposable caste? *Behav Ecol Sociobiol* 9:247–256
- Porter SD, Tschinkel WR (1986) Adaptive value of nanitic workers in newly founded red imported fire ant colonies (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 79:723–726
- Rissing SW, Pollock GB, Higgins MR, Hagen RH, Smith DR (1989) Foraging specialization without relatedness or dominance among co-founding ant queens. *Nature* 338:420–422
- Robinson GE (1992) Regulation of division of labor in insect societies. *Annu Rev Entomol* 37:637–665
- Robinson GE, Page RE, Huang ZY (1994) Temporal polyethism in social insects is a developmental process. *Anim Behav* 48:467–469
- Robinson EJM, Feinerman O, Franks NR (2009) Flexible task allocation and the organization of work in ants. *Proc R Soc Lond B* 276:4373–4380
- Rosengaus RB, Traniello JFA (1993) Temporal polyethism in incipient colonies of the primitive termite *Zootermopsis angusticollis*: a single multiage caste. *J Insect Behav* 6:237–252
- Seeley TD (1982) Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav Ecol Sociobiol* 11:287–293
- Seid MA, Traniello JFA (2006) Age-related repertoire expansion and division of labor in *Pheidole dentata* (Hymenoptera:Formicidae): a new perspective on temporal polyethism and behavioral plasticity in ants. *Behav Ecol Sociobiol* 60:631–644
- Shorter JR, Tibbetts EA (2009) The effect of juvenile hormone on temporal polyethism in the paper wasp *Polistes dominulus*. *Insect Soc* 56:7–13
- Sorensen AA, Busch TM, Vinson SB (1984) Behavioral flexibility of temporal subcastes in the fire ant *Solenopsis invicta* in response to food. *Psyche* 91:319–332
- Thomas ML, Elgar MA (2003) Colony size affects division of labour in the ponerine ant *Rhytidoponera metallica*. *Naturwissen* 90:88–92
- Traniello JFA, Rosengaus RB (1997) Ecology, evolution and division of labour in social insects. *Anim Behav* 53:209–213
- Tripet F, Nonacs P (2004) Foraging for work and age-based polyethism: the roles of age and previous experience in task choice in ants. *Ethology* 110:863–877
- Warners MR, Qiu L, Holmes MJ, Mikheyev AS, Linksvayer TA (2019) Convergent eusocial evolution is based on a shared reproductive groundplan plus lineage-specific plastic genes. *Nature Comm* 10: 2651
- Wenzel JW, Pickering J (1991) Cooperative foraging, productivity, and the central-limit-theorem. *Proc Natl Acad Sci U S A* 88:36–38
- Wilson EO (1971) The insect societies. Belknap/Harvard University Press, Cambridge
- Wilson EO (1990) Success and dominance in ecosystems: the case of the social insects. In: Kinne O (ed) Excellence in ecology 2, Ecological Institute, D-2124 Oldendorf/Luhe, FRG, pp 1-104
- Winston ML, Fergusson LA (1985) The effect of worker loss on temporal caste structure in colonies of the honeybee (*Apis mellifera* L.). *Can J Zool* 63:777–780
- Wood LA, Tschinkel WR (1981) Quantification and modification of worker size variation in the fire ant *Solenopsis invicta*. *Insect Soc* 28:117–128

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.