Emergence and Consequences of Division of Labor in Associations of Normally Solitary Sweat Bees

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Abstract

Division of labor is a pervasive feature of animal societies, but little is known about the causes or consequences of division of labor in non-eusocial cooperative groups. We tested whether division of labor self-organizes in an incipient social system: artificially induced nesting associations of the normally solitary sweat bee *Lasioglossum* (*Ctenonomia*) NDA-1 (Hymenoptera: Halictidae). We quantified task performance and construction output by females nesting either alone or with a conspecific. Within pairs, a division of labor repeatedly arose in which one individual specialized on excavation and pushing/tamping while her nestmate guarded the nest entrance. Task specialization could not be attributed to variation in overall activity, and the degree of behavioral differentiation was greater than would be expected due to random variation, indicating that division of labor was an emergent phenomenon generated in part by social dynamics. Excavation specialists did not incur a survival cost, in contrast to previous findings for ant foundress associations. Paired individuals performed more per capita guarding, and pairs collectively excavated deeper nests than single bees – potential early advantages of social nesting in halictine bees.

Introduction

Each of the major evolutionary transitions in biological organization, including multiple independent origins of animal societies, has been characterized by division of labor (Maynard Smith & Szathmáry 1995). In social systems, division of labor is a group-level pattern whereby different individuals specialize on different tasks (Michener 1974). Division of labor has been studied intensively in eusocial insects, for both reproductive and non-reproductive functions (Wilson 1971; Oster & Wilson 1978; Seeley 1982; Hölldobler & Wilson 1990; Robinson 1992; Beshers & Fewell 2001). However, the causes and consequences of division of labor in non-eusocial cooperative groups, which occur broadly across taxa, remain largely unknown (Bednarz 1988; Stander 1992; Underwood & Shapiro 1999; Costa & Ross 2003; Arnold et al. 2005; Gazda et al. 2005; Jeanson et al. 2005; Costa 2006). Recent theory suggests that division of labor can self-organize from local interactions among group members and their environment that generate behavioral differentiation, and may thus emerge spontaneously at the origins of sociality before becoming a target of natural selection (Page 1997; Fewell & Page 1999; Beshers & Fewell 2001; Camazine et al. 2001). We empirically tested whether division of labor is an emergent property of group living in artificially induced nesting associations of normally solitary sweat bees.

A prominent hypothesis for the self-organization of division of labor is the response threshold model,

which postulates that an individual performs a given task when the external stimulus level it encounters exceeds an intrinsic response threshold (Robinson & Page 1989; Bonabeau et al. 1996, 1998; Page & Mitchell 1998; Beshers & Fewell 2001). When an individual with a low threshold for a task performs it, the stimulus for that task may decline, reducing the probability that others in the group will also perform it. That individual becomes the task specialist, and if different individuals perform different tasks, division of labor emerges. According to the general variance-based model, this feedback between task performance and stimulus intensity can amplify initially slight differences among individuals. Response thresholds may also be self-reinforced by experience: individuals who perform a task are more likely to continue performing it, and vice versa (Deneubourg et al. 1987; Plowright & Plowright 1988; Theraulaz et al. 1998). Alternatively, division of labor can be produced via behavioral dominance, if more dominant individuals force others to perform tasks (Hogeweg & Hesper 1983), and/or by spatial dynamics (Franks & Tofts 1994; Jeanson et al. 2005). These models, which are not mutually exclusive, have largely been developed for, and supported by, eusocial insects (e.g. Detrain & Pasteels 1991; Robinson 1992; O'Donnell 1998, 2001; Fewell & Bertram 1999; Powell & Tschinkel 1999; Fewell & Page 2000; O'Donnell & Foster 2001; Jones et al. 2004). However, they can also be applied to simpler, non-eusocial groups, and the same mechanisms could lead to the emergence of basic forms of division of labor early in social evolution (Page 1997; Fewell & Page 1999; Costa & Ross 2003; Helms Cahan & Fewell 2004; Jeanson et al. 2005, 2008; Jeanson & Fewell 2008).

Task specialization and division of labor have been observed in forced associations of normally solitary animals, including *Ceratina* carpenter bees (Sakagami & Maeta 1987), *Lasioglossum* sweat bees (Jeanson et al. 2005, 2008), and *Pogonomyrmex* seed-harvester ant queens that typically initiate colonies alone (Fewell & Page 1999; Helms Cahan & Fewell 2004; Jeanson & Fewell 2008). Evidence suggests that behavioral differentiation in these incipient groups can be achieved through a combination of response threshold variation and spatial dynamics (Fewell & Page 1999; Helms Cahan & Fewell 2004; Jeanson et al. 2005). Unlike previous studies, however, we quantified the performance of multiple tasks in concurrent solitary and social conditions; this design allowed task specialization to be dissociated from variation in overall activity and provided a controlled test for the emergence of division of labor via underlying changes in individual behavior, without confounding effects of prior social experience.

Surprisingly, induced pairs of solitary *Lasioglossum* and *Pogonomyrmex* species have repeatedly exhibited higher levels of task specialization and division of labor than communal or quasisocial congeners in which small groups of unrelated, reproductively active females nest together (Fewell & Page 1999; Helms Cahan & Fewell 2004; Jeanson et al. 2005; but see Jeanson & Fewell 2008). Division of labor can generate fitness disparities within *Pogonomyrmex* foundress associations; excavation specialists are more likely to die than non-specialists (Fewell & Page 1999; Helms Cahan & Fewell 2004), possibly reflecting increased energy expenditure and/or desiccation due to cuticular abrasion (Johnson 2000). The maintenance of stable, non-kin, cooperative groups may thus require the sharing of costly tasks, equalizing fitness but reducing division of labor (Fewell & Page 1999; Helms Cahan & Fewell 2004). Here, we asked whether differentiation for excavation performance in incipient *Lasioglossum* societies could also have survival consequences that in turn shape the evolution of division of labor. In ground-nesting bees and wasps, excavation may impose costs in time, energy, body wear, and water loss, potentially favoring both social nesting and task generalization (Abrams & Eickwort 1981; Evans & Hook 1986; McCorquodale 1989; Danforth 1991).

We examined the emergence and consequences of division of labor during nest construction in artificially established associations of the normally solitary halictine bee *Lasioglossum* (*Ctenonomia*) NDA-1 (Hymenoptera: Halictidae). *Lasioglossum* is a cosmopolitan genus of ground-dwelling sweat bees that includes solitary, communal, and eusocial species, making it an ideal system for studying changes in division of labor during social evolution (Michener 1974; Wcislo 1997a; Schwarz et al. 2007). We measured task performance and nest construction output by bees nesting alone vs. in forced pairs to determine (1) whether division of labor emerges in incipient groups, (2) how the transition from solitary to social nesting affects individual behavior and total construction output, and (3) whether excavation specialization reduces survival.

Methods

Collections

We collected adult females of *L*. NDA-1 in the Cobboboonee State Forest, southwestern Victoria,

Australia (38.217°S, 141.558°E; 62 m elev) on Dec. 14, 16, and 18, 2006. This population exhibits an annual, univoltine life cycle that begins in late spring, when overwintered, mated females construct new nests in exposed soil. Females are predominantly solitary; 17 of 19 excavated nests contained only one female, while two nests contained two females each (McConnell-Garner & Kukuk 1997). Low frequencies of two-female nests occur in many 'solitary' bees and wasps (Wcislo et al. 1993; Wcislo 1997a; Wcislo & Tierney 2009). Nests consist of vertical tunnels with lateral, wax-lined brood cells, which are mass provisioned with pollen and nectar.

We netted above nest aggregations between 10:00 h and 13:00 h, when bees were foraging, and individually transferred each female to a vial kept in a cooler on ice. Upon return to the laboratory, each bee was marked on the thorax and abdomen with an enamel paint pen and held individually in a Petri dish provisioned with moistened filter paper and a 1:1 mixture of honey and water. Bees were maintained at ambient temperature overnight.

Experimental Design

General activity

To determine whether differences in task performance during nest construction are associated with variation in general activity, we assayed individual activity levels and speed in circular, transparent plastic tubes (circumference = 20 cm, internal diameter = 4 mm) before introducing bees to nests (Breed et al. 1978; Jeanson et al. 2005). Trials were conducted 24 h after bees were collected, between 10:00 h and 13:00 h on day 1 of the experiment (Dec. 15, 17, or 19, depending on date of collection), in homogeneously-lit arenas maintained at 27.0 ± 1.0°C. Each bee was individually loaded into a tube, allowed to acclimate for 2 min, and then observed for 5 min. We recorded amount of time spent active (walking forward or backward, or turning) vs. inactive (immobile or grooming), and calculated speed by timing bees as they moved unidirectionally through an arc length of 10 cm. We obtained up to three speed measurements per individual when possible. Immediately following each activity trial, the test bee was returned to her individual Petri dish. Each section of tubing was used for only one trial per day and was washed with ethanol and water between days to remove any persistent odors.

Task performance during nest construction

At 18:00 h on day 1, 5 h after the conclusion of activity trials, we introduced bees into vertical observation nests (12 cm wide × 15 cm deep × 3 mm thick) filled with moistened, sifted soil from the bees' nesting area. Each nest had a central, upper entrance connected by a 5-cm long plastic tube to a glass vial (diameter = 2 cm, height = 4 cm) provisioned with a 1:1 honey–water solution. A vertical indentation of 1 cm was formed in the soil directly below the entrance to encourage the construction of a single tunnel. Nests were maintained at 30.0 ± 2.0°C under a photoperiod of 15 h light to 9 h dark (beginning at 19:00 h). We watered nests and replenished honey water *ad libitum*.

We randomly assigned individuals to one of two social contexts: 'single', in which bees nested alone (n = 39 individuals), or 'paired', in which nests were cohabited by two conspecifics (n = 74 individuals; 37 pairs). Members of each pair were introduced into nests simultaneously. We did not account for potential differences in age or body wear when pairing bees, but variation was assumed to be minimal because all individuals belonged to the same generation and were collected at the same time relatively early in the season, soon after nests were established. Behavior was sampled through a total of 90 scan surveys per individual distributed as follows: 30 scans from 19:00 h to 21:30 h on day 1, 30 scans from 8:00 h to 10:30 h on day 2, and 10 scans each from 16:00 h to 16:50 h on days 3, 4, and 5. Scans were performed every 5 min within each observation period. We sampled most intensively during the first 24 h because preliminary observations indicated that excavation declines thereafter, but we continued to observe behavior through day 5 to quantify temporal changes in activity. For each bee, we recorded performances of the following tasks:

1. Excavating – excavating soil with mandibles at distal end of tunnel.

2. Pushing – pushing loose soil with legs toward nest entrance or into vial.

3. Tamping – packing loose soil with abdomen into tunnel side walls.

4. Guarding – sitting in tube connecting nest and vial.

5. Foraging – extending proboscis into honey water solution in vial.

Bees that were not performing one of these specific tasks were classified as walking, self-grooming, or inactive (i.e. idle). Guarding is widely recognized in halictine bees as an individual sitting just inside

the nest entrance and responding aggressively toward intruders (Michener 1974). Although natural enemies were absent from the laboratory, guards blocked the nest entrance with a defensive C-posture when disturbed by a toothpick.

Nest construction output

To estimate the amount of excavated soil, we digitally photographed nests following each observation period. Tunnel length and area were measured using Image J (National Institutes of Health: http://rsb.info.nih.gov/ij). We considered tunnel area to be directly proportional to tunnel volume, because all tunnels were as thick as the nests (3 mm).

Survival

We monitored individual survival daily through day 17. Dead bees were removed immediately upon detection.

Statistical Analyses

Because individual performance can covary across tasks, we initially performed a repeated-measures MANOVA to test for overall effects of social context (single vs. paired) and time (days 1–5) on four response variables combined: per capita proportion of observations spent excavating, pushing/tamping (which generally co-occurred in space and time), guarding, and inactive. Foraging was not analyzed due to infrequent occurrence (<1% of observations). Here, we used proportion of observations because the total number of scan samples per day decreased from 30/d on days 1–2 to 10/d on days 3–5. We treated each nest as an experimental unit and analyzed per capita task performance and inactivity (averaged within pairs) to statistically control for non-independence between nestmates. When Wilks' lambda values for overall effects on the combined response variables were significant (p < 0.05), we performed separate univariate repeated-measures ANOVAS on each response variable (Zar 1999). For within-subject effects (i.e. time), we employed the Greenhouse–Geisser adjustment for deviations from the assumption of sphericity; corrected p-values are reported (Geisser & Greenhouse 1958; von Ende 1993). Two single bees and three pairs were excluded because an individual failed to perform any tasks throughout the experiment. Nests in which a bee died before day 5 were excluded from subsequent behavioral analyses; thus, sample sizes declined from 37 single individuals and 34 pairs on day 1 to 31 single individuals and 18 pairs on day 5.

Division of labor within each pair was quantified following the derivation of Shannon's diversity index (1948) by Gorelick et al. (2004; see for details). Calculations were based on the number of times each individual was observed excavating, pushing/tamping, or guarding. $DOL_{tasks \rightarrow indiv}$ (division of tasks across individuals) indicates the degree to which each task is performed by a subset of group members and ranges from 0 (no division of labor) to 1 (complete division of labor) when there at least as many tasks as individuals. Because we were interested in the expression of division of labor when there was an opportunity for it to occur (i.e. multiple individuals performing multiple tasks), we excluded pairs in which one individual failed to perform any tasks or both nestmates performed only one of the focal tasks. We did not calculate the complementary index $DOL_{indiv \rightarrow tasks}$ (division of individuals into tasks) because individual specialization is restricted when there are more tasks than individuals, as in this study (Gorelick et al. 2004).

To further analyze behavioral differentiation and its survival consequences, we identified specialization on a potentially costly task – excavation. We designated a higher-frequency excavator (HFE) and a lower-frequency excavator (LFE) within each pair based on the nestmates' relative frequency of performance across days 1–2. Four pairs were excluded: two in which an individual died before day 2, one in which both members performed the same frequency of excavation, and one in which neither bee was observed excavating. Because the behaviors of nestmates were not independent, we tested for differences in task performance and inactivity between HFE and LFE bees and between HFE/LFE and single individuals using paired and 2-sample t-tests respectively, with a sequential Bonferroni correction (Rice 1989) applied to each set of comparisons (adjusted p-values are reported).

We used a Monte Carlo simulation resampling procedure to determine whether behavioral differentiation within pairs was greater than would be expected due to random variation alone (Sokal & Rohlf 1995; Spessa et al. 2000). First, we calculated the mean ratio of observed excavation frequency between paired individuals (LFE/HFE, plus one pair with a ratio of 1; n = 31 pairs). Next, 10 000 iterations of 31 pairs each were sampled randomly with replacement from the single bees (n = 37), and the mean excavation frequency ratios (LFE/HFE as above) were used to generate a null distribution. We

then calculated the proportion of expected excavation ratios that were lower (i.e. higher differentiation) than the observed ratio.

We conducted log-rank tests for effects of social context and excavation specialization on individual survival distributions across 17 d. Two single bees and two pairs were excluded because they escaped from their nests before the end of the experiment.

Data were arcsine- or ln-transformed to achieve normality and/or equal variance when necessary. All statistical tests were two-tailed and performed with STATISTICA (v. 7.1, StatSoft, Inc., Tulsa, OK). Unspecified values are mean ± 1 SE.

Results

Effects of Social Context and Time

Social context had a significant overall effect on per capita task performance and inactivity combined (rmMANOVA: $F_{4,44} = 4.35$, p = 0.005; Fig. 1). Subsequent univariate analyses revealed a significant difference only in guarding, which paired individuals performed approximately twice as frequently as sin-

Table 1: Mean ± SE per capita number of observed task performances by single and paired bees across days 1–5

	Single bees	Paired bees	$F_{1,47}$	p
Excavating	9.5 ± 1.6	7.9 ± 1.7	0.11	0.7
Pushing/tamping	11.7 ± 1.8	8.3 ± 1.3	0.29	0.6
Guarding	9.5 ± 1.7	18.8 ± 2.8	16.47	<0.001
Inactive	47.7 ± 3.7	41.5 ± 3.3	1.14	0.3

Effects of social context were analyzed using repeated measures ANOVA.

gle bees across days 1–5 (Table 1). Excavation, pushing/tamping, and inactivity did not differ between bees nesting alone vs. in pairs.

Individual behavior also changed over time (rmMANOVA: $F_{16,32} = 6.74$, p < 0.0001; Fig. 1). Across days 1–5, there were declines in per capita excavation (rmANOVA: $F_{4,188} = 10.21$, p < 0.0001), pushing/tamping ($F_{4,188} = 13.39$, p < 0.0001), and guarding ($F_{4,188} = 8.22$, p < 0.001). Concordantly, bees were less active during days 3–5 than on days 1 and 2 ($F_{4,188} = 20.21$, p < 0.0001; Tukey's pairwise comparisons: p < 0.0001). There were no significant interaction effects between social context and time (0.1 < p < 0.9).
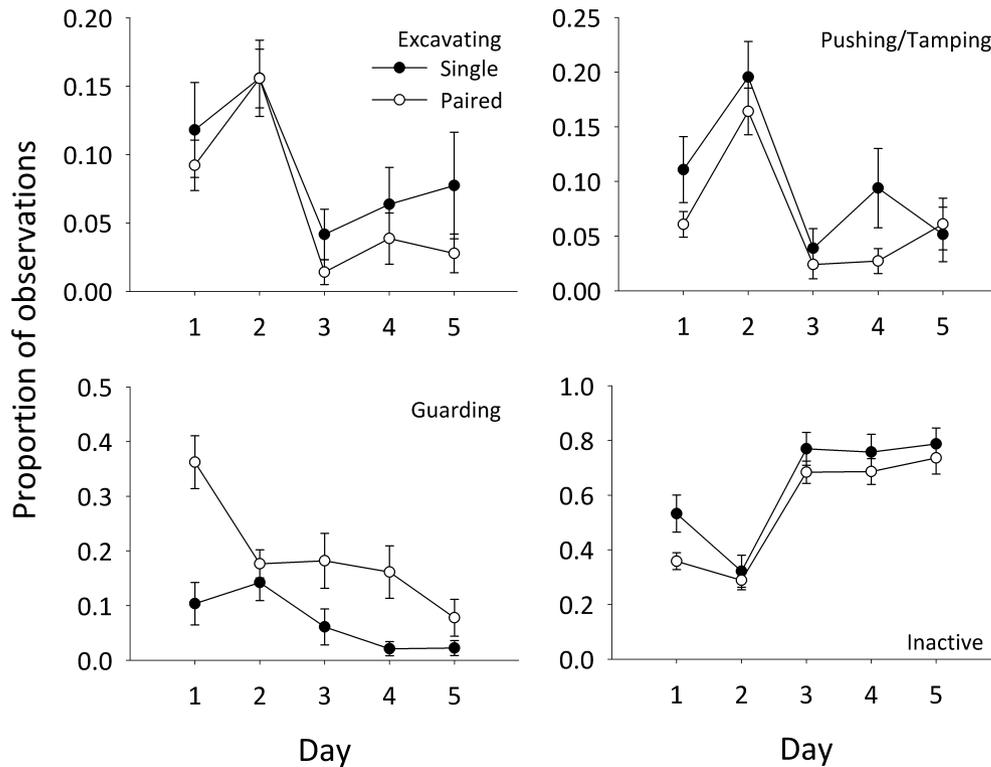

Fig. 1: Per capita task performance by bees nesting alone vs. in artificially established pairs. Values are mean (± SE) proportion of observations per scan survey (30 surveys per bee per day on days 1–2, 10 surveys per bee per day on days 3–5). Due to mortality, sample sizes declined from 37 single individuals and 34 pairs on day 1 to 31 single individuals and 18 pairs on day 5.

A preliminary comparison of tunnel length and tunnel area revealed that mean tunnel width was highly consistent across nests (2.9 ± 0.1 mm; n = 40); therefore, we used tunnel length to estimate nest construction output. Pairs dug nearly twice as far as single individuals over the course of the experiment (rmANOVA: $F_{1,47}$ = 6.65, p = 0.01; cumulative tunnel length on day 5: single = 9.8 ± 1.4 cm, pairs = 17.5 ± 2.4 cm). Five pairs and two single bees excavated to the bottom of their nests between days 2 and 3, and a total of nine pairs and seven single bees reached the bottom by day 5, partly explaining the reduction in excavation and pushing/tamping over time.

Division of Labor and Task Specialization

We calculated $DOL_{tasks \rightarrow indiv}$ – the degree to which each of the three focal tasks was performed by a single individual within each pair – using pooled task performance across days 1–2 only (60 scan surveys per individual), because bees reaching the bottom of their nests during days 3–5 experienced fewer available tasks. $DOL_{tasks \rightarrow indiv}$ averaged 0.25 ± 0.05 (n = 31 pairs).

We further analyzed task specialization by comparing higher-frequency vs. lower-frequency excavators (HFE and LFE respectively) within each pair. Designations were based on the relative frequency of excavation observed across days 1–2: HFE bees performed 79.4 ± 2.8% of the excavation within pairs (Fig. 2). To test whether asymmetry in excavation behavior was emergent, instead of reflecting general variation across the population, we performed a Monte Carlo simulation resampling procedure. The mean observed ratio of excavation performance between nestmates (0.33 ± 0.05) was lower than expected from random pairings of single bees (p = 0.006), indicating that social dynamics contributed to behavioral differentiation.

In addition, HFE bees also performed more pushing/tamping than LFE bees (HFE: 65.0 ± 6.1%; t_{29} = 3.46, Bonferroni-adjusted p = 0.006), but frequency of guarding did not differ significantly between nestmates (HFE: 42.8 ± 6.7%; t_{29} = 1.38, Bonferroni-adjusted p = 0.2; Fig. 2). Higher- and lower-frequency excavators exhibited similar overall activity in nests (t_{29} = 1.11, Bonferroni-adjusted p = 0.5; Fig. 2), pre-nesting circle tube activity (t_{29} = 0.10, p = 0.9), and speed within circle tubes (t_{10} = 0.48, p = 0.6).

Finally, we compared the task performance of HFE and LFE bees with that of bees nesting alone to
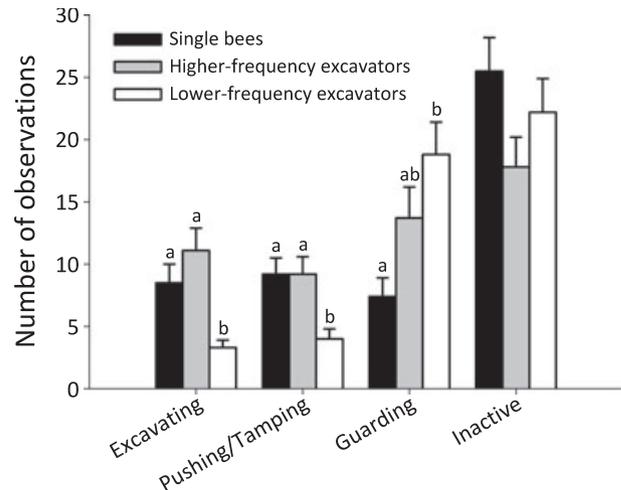

Fig. 2: Behavioral differentiation within induced pairs, relative to bees nesting alone. Each pair contained a higher-frequency excavator (HFE) and a lower-frequency excavator (LFE), classified *post hoc* using relative performance. Values are mean (± SE) number of observed task performances per individual across days 1–2 (30 scan surveys per day). For each task, different letters indicate statistical significance after sequential Bonferroni correction. n_{single} = 37, n_{HFE} = 30, n_{LFE} = 30.

learn how individual behavior changed in pairs (Fig. 2). Higher-frequency excavators and single bees did not differ in frequency of excavation (t_{65} = 1.25, Bonferroni-adjusted p = 0.2), pushing/tamping (t_{65} = 0.006, Bonferroni-adjusted p = 0.996), or guarding (t_{65} = 1.63, Bonferroni-adjusted p = 0.2). In contrast, LFE bees performed less excavation (t_{65} = 2.55, Bonferroni-adjusted p = 0.03) and pushing/tamping (t_{65} = 0.238, Bonferroni-adjusted p = 0.04), and more guarding (t_{65} = 3.38, Bonferroni-adjusted p = 0.003) than single bees. Inactivity during nest construction did not differ between single individuals and either HFE (t_{65} = 2.10, Bonferroni-adjusted p = 0.12) or LFE bees (t_{65} = 0.88, Bonferroni-adjusted p = 0.4), nor was it correlated with pre-nesting circle tube activity (Pearson correlation: r_{101} = −0.12, p = 0.2) or speed within circle tubes (r_{59} = 0.05, p = 0.7).

Survival

Individual survival was not affected by social context; 26 of 37 (70%) single bees and 44 of 70 (63%) paired bees survived through day 17 (log-rank test: χ^2 = 0.92, p = 0.4). Moreover, probability of survival did not differ significantly between HFE and LFE bees; 22 of 28 (79%) HFE bees and 16 of 28 (57%) LFE bees survived (log-rank test: χ^2 = 1.71, p = 0.09). In 12 pairs, only one member died – three

were HFE and nine were LFE bees; this difference is also non-significant, although statistical power is limited (G test with Yates correction for continuity: G = 2.15, p = 0.14).

Discussion

Emergence of Division of Labor

When individuals of the normally solitary sweat bee *Lasioglossum* (*Ctenonomia*) NDA-1 were forced to establish nests with a conspecific, a division of labor repeatedly arose in which one bee specialized on nest construction tasks – excavation and pushing/tamping – while her nestmate primarily guarded the nest entrance. Higher- and lower-frequency excavators differed in their allocation of performance across different tasks; specialization could not simply be attributed to variation in overall activity, as measured before and during nest construction. Moreover, the degree of behavioral differentiation between nestmates was greater than would be expected due to random variation in task performance among independent bees, indicating that division of labor was an emergent phenomenon generated in part by social dynamics. Our findings corroborate a growing body of evidence that basic forms of division of labor can self-organize in incipient groups of normally solitary animals that are not currently under selection for task specialization (Fewell & Page 1999; Helms Cahan & Fewell 2004; Jeanson et al. 2005, 2008; Jeanson & Fewell 2008).

In theory, behavioral differentiation could result from task specialists increasing their performance relative to a solitary state and/or non-specialists decreasing the frequency at which they perform a task in a social context. The later was true for nest construction in *L.* NDA-1; lower-frequency excavators performed less excavation and pushing/tamping than both higher-frequency excavators and single bees. A similar trend has been noted for excavation by *Pogonomyrmex* foundresses nesting alone vs. in pairs (Fewell & Page 1999; Helms Cahan & Fewell 2004). This general pattern is consistent with the response threshold model: by decreasing the stimulus level associated with a given task, specialists reduce the probability that the task will be performed by other group members with higher thresholds (Robinson & Page 1989; Bonabeau et al. 1996; Beshers & Fewell 2001).

Spatial dynamics may have also contributed to the emergence of division of labor. Single and paired bees alike constructed nests typically consisting of a single, linear tunnel. Nestmates were thus prevented from excavating simultaneously, possibly channeling lower-frequency excavators toward the nest entrance, which they guarded more frequently than bees nesting alone. Moreover, the narrow confines of *Lasioglossum* nests require that individuals cooperatively rotate their bodies to pass one another (Breed et al. 1978; Kukuk 1992; McConnell-Garner & Kukuk 1997). Low tolerance to passing by *L.* NDA-1 (McConnell-Garner & Kukuk 1997) may restrict mobility throughout the nest, leading bees to encounter different tasks depending on their locations: excavation at the bottom of the nest, pushing/tamping along the length of a tunnel, and guarding at the nest entrance (Jeanson et al. 2005).

In some social insects, division of labor is driven by behavioral dominance, which itself can be an emergent property of group living (Hogendoorn & Schwarz 1998; O'Donnell 1998, 2001; Hogendoorn & Velthuis 1999; Powell & Tschinkel 1999; Hemelrijk 2002). However, we did not witness a single act of overt aggression (e.g. C-posture, biting, or lunging) between nestmates during many hours of observation. Furthermore, when social interactions of *L.* NDA-1 were previously assayed in circle tubes, there were no relationships among aggressive behavior, ovary condition, and/or subsequent task performance (McConnell-Garner & Kukuk 1997; Jeanson et al. 2005, 2008). These results contrast findings from forced associations of the solitary *Lasioglossum* (*Dialictus*) *figueresi*, in which bees with larger ovaries were more aggressive (Wcislo 1997b).

Survival Consequences of Specialization

Excavation specialization did not impose an individual survival cost, unlike in foundress associations of *Pogonomyrmex*, where greater mortality among excavation specialists may favor the evolution of task sharing (Fewell & Page 1999; Helms Cahan & Fewell 2004). Higher-frequency excavators actually tended to live longer than their nestmates, perhaps because individuals in poor condition were less likely to excavate, or because lower humidity near the nest entrance caused lower-frequency excavators to desiccate. In nature, within-group fitness disparities could be generated by differentiation for guarding and foraging, which are risky behaviors (Kukuk et al. 1998). The fitness consequences of these tasks, and how they are distributed across nestmates, are critical to understanding how selection shapes

division of labor during early social evolution in halictine bees.

From Solitary to Social Nesting

The artificial induction of social nesting by normally solitary bees caused spontaneous changes in task performance and nest construction output that could potentially provide selective advantages at the onset of group living, namely improved defense and shared construction costs. Paired individuals performed twice as much guarding as bees nesting alone, resulting in an approximately fourfold increase at the nest level. Guarding has been shown to protect brood from parasites and predators in other halictines, and is hypothesized to be a major benefit of group living in bees and wasps (Lin & Michener 1972; Eickwort et al. 1996; Kukuk et al. 1998; Smith et al. 2003; Wcislo & Tierney 2009). Social nesting relieves temporal constraints against guarding; one individual can guard the nest entrance while her nestmate(s) performs other tasks, including foraging. Morevover, alloparental guarding can provide assured fitness returns if a female dies before her mass-provisioned brood mature (Lin & Michener 1972; Gadagkar 1990; Queller 1993, 1994; Smith et al. 2003).

In addition, pairs collectively constructed deeper nests than single bees. Social nesting could thus reduce the individual costs of excavation (Evans & Hook 1986; McCorquodale 1989; Danforth 1991) and/or permit bees to reach soil levels with optimal water content (Abrams & Eickwort 1981). These effects may be especially important in arid regions with hard, compacted soils, such as the habitat of *L.* NDA-1.

Despite possible benefits of increased guarding and cooperative nest construction in multifemale associations, the focal population of *L.* NDA-1 is predominantly solitary. This paradox may be partly explained by avoidance of and/or aggression towards conspecifics. When compared with communal and eusocial *Lasioglossum* species, *L.* NDA-1 exhibits intermediate levels of aggression and relatively high frequencies of avoidance in circle tubes (McConnell-Garner & Kukuk 1997; Jeanson et al. 2005; see also Packer 2006). Such behavior could preclude the initial formation of groups, even though aggressive interactions are rare or non-existent when bees are forced to share nests. Furthermore, sociality may be associated with costs, including intraspecific brood parasitism and/or fitness disparities related to task specialization (Helms Cahan & Fewell 2004; Wcislo & Tierney 2009).

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