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Journal

Insectes Sociaux, 63(1)

ISSN

0020-1812

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Publication Date

2016-02-01

DOI

10.1007/s00040-015-0454-y

Peer reviewed

Ontogeny of division of labor in a facultatively eusocial sweat bee *Megalopta genalis*

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Received: 28 July 2015 / Revised: 7 November 2015 / Accepted: 16 November 2015 / Published online: 11 December 2015
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Abstract In eusocial nests, colony tasks are divided among queens and workers, but how this division of labor develops is unknown for most species. We compared division of labor and aggressive behavior among queens and workers in the facultatively eusocial bee, *Megalopta genalis*, using nests with established queen-worker pairs and nests in which the incipient worker had recently emerged. We find that the majority of aggression is directed from queens toward workers in both incipient and established relationships. Established workers forage and perform trophallaxis as donors more frequently than queens, but both queens and workers perform trophallaxis as donors when workers are young. Queens spend significantly more time nest guarding than incipient and established workers, perhaps because older workers spend more time foraging and incipient workers spend significantly more time in cells than do queens. Our results show that the development of worker behavior involves dynamic temporal changes in task performance among queens and workers during the 10 days after worker emergence. During this establishment period, queens engage in maternal care by feeding their daughters,

but are also aggressive toward them. This may be a mechanism by which queens coerce their daughters into becoming non-reproductive workers.

Keywords Dominance behavior · *Megalopta genalis* · Behavioral ontogeny · Division of labor · Eusociality

Introduction

Division of labor is one of the defining features of eusociality (Batra 1966; Michener 1990). Eusocial queens specialize in egg-laying and non-reproductive workers forage, defend the nest, and care for the developing brood. In most social insect colonies, nest foundresses pass through a solitary phase before their workers emerge and they become queens. During this time, foundresses perform all tasks associated with reproduction and maternal care, including those that later are performed primarily by workers. One hypothesis for how division of labor develops as foundresses transition to the role of queen is that aggression directed from the foundress to her daughters is a causative factor leading to worker-like behavior (Michener and Brothers 1974). Indeed, prior laboratory studies of a eusocial halictid bee, *Lasioglossum zephyrum*, have demonstrated the role of intraspecific interactions in shaping division of labor (reviewed in Michener 1990). Multivariate behavioral analysis of small artificial *L. zephyrum* colonies maintained in the laboratory yielded discrete clusters of queens, foragers and guards, with the queens being the most distinct. In a similar study, bees that became queens exhibited a sharp increase in their rates of aggression toward other bees, and workers that were agonistic toward queens received increased aggression (Buckle 1982a). Simulated aggression and disturbance has been shown to suppress

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ovary development in young bees (Michener and Brothers 1974), and workers actively avoid queens who position themselves in locations where they are able to influence worker behavior (Buckle 1982b). Furthermore, relative to other castes, the queens tend to be highly active (Breed and Gamboa 1977), and workers that are not primary guards nor primary foragers spend more time being inactive (Kukuk 1980). The causative factors leading to division of labor is thus well understood for the obligately eusocial *L. zephyrum*, but whether these patterns can be generalized to other species, particularly those with facultative eusociality, is unknown. The ontogeny of social differentiation is critical as it can have a substantial impact on colony productivity and the queen's ability to control worker reproduction (Kukuk and May 1991).

We studied the development of a division of labor in a facultatively eusocial bee, *Megalopta genalis*. Solitary and eusocial nests coexist throughout the tropical dry season within the same population (Smith et al. 2003; Wcislo et al. 2004). Most solitary nests are the result of a foundress strategy to produce all sons in the first brood, and thereby forego the option of having daughters as workers (Kapheim et al. 2013). In those nests where foundresses produce daughters in the first brood, at least one daughter typically stays in the nest as a non-reproductive worker. In some cases, daughters supersede their mothers (12.4 % of all nests) or disappear without working (6.2 % of all nests) (Kapheim et al. 2013). In eusocial nests, workers do not mate or lay eggs (Kapheim et al. 2013), and they perform most of the foraging and feed their queens through trophallaxis (Wcislo and Gonzalez 2006). Previous research has shown that workers in eusocial nests do not gain enough indirect benefits to make up for the direct fitness costs of working (Kapheim et al. 2013; Kapheim et al. 2015). This finding suggests that workers are being coerced into working, but the mechanism by which this occurs is not known. Workers are significantly smaller than queens (Kapheim et al. 2012), and daughters that supersede their queens are relatively closer in size to their queens than are daughters who become workers (Kapheim et al. 2013). Furthermore, workers have smaller ovaries and lower juvenile hormone levels when in the presence of the queen (Kapheim et al. 2012; Smith et al. 2013), but mate and become reproductively active when the queen is removed (Smith et al. 2009).

To understand the role of aggression in queen-worker relationships, and more generally, how division of labor develops in colonies with simple forms of eusociality, we compared queen and worker task allocation in nests with naïve, young workers and nests with experienced, older workers.

Materials and methods

Videotaping

We videotaped behavior inside 18 *M. genalis* observation nests on Barro Colorado Island, Panama during two consecutive dry seasons (2008–2009). Half ($n = 9$) of these nests had established queen-worker pairs, defined as a worker that is at least 10 days old (median age = 19 d, mean age = 26 d, range = 10–55). Previous research with this species has revealed that queen-worker dominance relationships are established within 10 d after worker emergence. All observed supersedures occur prior to 10 d, and after 10 d workers do not lay eggs and do the majority of the foraging for the nest (Wcislo and Gonzalez 2006; Kapheim et al. 2013). The other half ($n = 9$) had incipient queen-worker pairs, with workers less than 10 days old (median age = 5 d, mean age = 4.5 d, range = 0–9 d; age 0 indicates the worker emerged that day). *Megalopta genalis* workers begin foraging within 10 days of emergence (Kapheim et al. 2013). *M. genalis* nest in dead sticks suspended in tangled vegetation above the forest floor. We constructed observation nests by sandwiching a thin piece of balsa wood between two panes of clear acrylic and covering these with black fabric or plastic (for additional detail, see Kapheim et al. 2012). Observation nests mimic natural nests and allow the resident bees to freely fly in their natural habitat, while standardizing nest size and quality, local environmental conditions, and early foundress experience. We avoided disturbing the bees prior to, during, and after videotaping by constructing a camera box that housed a camcorder and fit flush to the viewing portion of the nest. This allowed the inside of the nest to be filmed, but prevented light from coming into the nest, which has a dark interior except for light at the entrance. We activated recording remotely or on a timer, without disturbance to the bees. We concentrated videotaping around *M. genalis* foraging time, which is approximately 1 h before sunrise and 1 h after sunset (Wcislo et al. 2004), on consecutive days.

Behavioral scoring and statistical analysis

We scored 324.6 h of video covering a total of 98 nest-days. We used focal animal surveys, based on a standard ethogram (Table 1) to score behaviors (Altmann 1974). The ethogram was based on previous descriptions of *M. genalis* behavior (Arneson and Wcislo 2003; Wcislo and Gonzalez 2006). While the reliability of using a priori categorization of behaviors as agonistic or cooperative has been questioned for some alldapine bees (Dew et al. 2014), the behaviors we classify avoid these problems because they are based on a long history of reliable results using circle tube

Table 1 Behaviors scored for each focal animal

Behavior	Description
Foraging	Individual leaves nest; duration ends when bee returns to nest
Guarding	Individual positioned within one body length of the entrance collar of the nest; may simultaneously be grooming; blocks nest tunnel completely
Trophallaxis	The transfer of liquid food from one individual to another within the nest. 1 = The transfer of liquid droplet is clearly observed 2 = A liquid droplet can be seen, but transfer of liquid from one individual to another is uncertain 3 = Individuals are (i) with mandibles in contact, at a suitable angle; and (ii) for a minimum time period (3 s); and (iii) one has returned from a foraging trip within a minute, but no droplet was visible 4 = A combination of two of these three criteria from #3 were observed
Cell activity includes the following behaviors:	
Investigating cell(s)	An individual is present and touching the area of a cell entrance with antennae 1 = Individual puts head inside cell, remaining outside 2 = Individual remains outside the cell
Entering cell(s)	An individual's entire body enters a cell 1 = Individual enters cell, no part of body is visible, and no activity can be seen 2 = Individual enters cell, with moving legs or antennae visible, or small movements into and out of the cell
Provisioning	Depositing nectar/pollen inside cell 1 = Possible provisioning when individual has returned from foraging within the last 20 min 2 = Probable provisioning when individual has returned from foraging within the last minute
Aggression includes the following behaviors:	
Nudging	Use of head, often angled downwards, to push against head or body of another individual
Biting	Mandibles of one (or both) individual(s) are open, and contact/close around part of the body of another individual
Lunging	Sharp and fast, 'jerky' movement forward by one individual, in the direction of another individual, starting from no contact between the two individuals
C-posture	The abdomen of one individual is curled under, such that the posterior end is presented towards another individual

experiments in other halictine bees (McConnell-Garner and Kukuk 1997; Pabalan et al. 2000; Boesi et al. 2009), and we do not attempt to distinguish between cooperative and aggressive behaviors (Table 1). Observers scoring the videos were blind to the caste and identity of each bee, which were identified by white paint marks on their thoraces. Each video was scored by a single observer, but consecutive videos from within a single nest were randomly distributed among observers so that any variation that existed among observers was distributed within and across nests. Appropriate measures, such as thorough training and comparisons of the same video scored by all observers, were taken to ensure consistency across observers.

Behaviors related to foraging, cell activity, and nest guarding were scored as state behaviors, and all other behaviors were scored as events. For trophallaxis and aggressive events, we calculated the proportion of each event directed from workers to queens, queens to workers, and all other directional interactions among nestmates as a function of the number of total events of each type observed in each nest. Cell activity, foraging, and nest guarding behaviors were standardized by the amount of time all individuals could be accounted for in each nest. We used

non-parametric statistics to compare the normalized rate of each behavior within each nest type among queens and workers. All statistical analyses were performed in Stata (v. 9.2).

Results

The length of recorded behavioral observations and number of days observed per nest were not significantly different between nests with incipient and established caste relationships (observation length: Wilcoxon rank-sum $Z = -0.49$, $p = 0.63$; days per nest: Wilcoxon rank-sum $Z = -1.62$, $p = 0.10$).

We found clear differences in the division of labor between incipient and established queen-worker relationships. Consistent with previous research based on workers of known relative age, but unknown absolute age (Wcislo and Gonzalez 2006), our results showed that workers in established nests spent significantly more time foraging than did queens (Wilcoxon signed-rank $Z = -2.55$, $p = 0.01$, $n = 9$ matched pairs; Table 2). In contrast, we found no significant difference between queen and worker foraging

Table 2 Mean proportion \pm one standard deviation of each behavior initiated by workers and queens in nests with incipient and established relationships ($n = 9$ in each cell)

Behavior	Incipient nests			Established nests		
	Workers	Queens		Workers	Queens	
Foraging	0.06 \pm 0.06	0.10 \pm 0.08	n.s.	0.15 \pm 0.08	0.04 \pm 0.05	*
Trophallaxis	0.35 \pm 0.42	0.65 \pm 0.42	n.s.	0.78 \pm 0.22	0.22 \pm 0.22	*
Nest guarding	0.08 \pm 0.07	0.42 \pm 0.27	*	0.23 \pm 0.10	0.43 \pm 0.14	*
Overall cell activity	0.37 \pm 0.28	0.06 \pm 0.07	*	0.18 \pm 0.12	0.13 \pm 0.16	n.s.
Entering cell	0.30 \pm 0.23	0.04 \pm 0.06	*	0.12 \pm 0.11	0.08 \pm 0.10	n.s.
Investigating cell	0.03 \pm 0.05	0.02 \pm 0.02	n.s.	0.03 \pm 0.03	0.05 \pm 0.01	n.s.
Provisioning cell	0.04 \pm 0.06	0.01 \pm 0.01	n.s.	0.02 \pm 0.02	0.02 \pm 0.05	n.s.
Overall aggression	0.38 \pm 0.17	0.62 \pm 0.17	*	0.34 \pm 0.25	0.66 \pm 0.25	n.s.
Nudging	0.49 \pm 0.33	0.51 \pm 0.33	n.s.	0.44 \pm 0.26	0.56 \pm 0.26	n.s.
Biting	0.29 \pm 0.27	0.71 \pm 0.27	n.s.	0.34 \pm 0.46	0.66 \pm 0.46	n.s.
Lunging	0.29 \pm 0.23	0.71 \pm 0.23	*	0.10 \pm 0.13	0.90 \pm 0.13	*
C-posture	1.00 \pm 0.00	0.00 \pm 0.00	*	–	–	–

For trophallaxis and aggression, values indicate the proportion of total interactions between the queen and worker attributed to either the queen or worker. *Asterisk* indicate statistical significance ($p < 0.05$) in a paired Wilcoxon signed-rank test. n.s., $p > 0.05$

rates within nests characterized by incipient queen-worker relationships (Wilcoxon signed-rank $Z = 1.24$, $p = 0.21$, $n = 9$ matched pairs; Table 2). Workers in incipient relationships foraged at a significantly lower rate than workers in established relationships (Wilcoxon rank-sum $Z = 2.43$, $p = 0.02$, $n = 18$). Queens in incipient relationships foraged significantly more than queens with established workers (Wilcoxon rank-sum $Z = -2.08$, $p = 0.04$, $n = 18$).

We observed a similar pattern for trophallaxis. Qualitatively similar patterns were observed for different characterizations of trophallaxis (Table 1) when analyzed independently, so we combined them into a single category. In established nests, workers were significantly more likely to feed the queen through trophallaxis than vice versa (Wilcoxon sign-rank $Z = 2.57$, $p = 0.01$, $n = 9$ matched pairs; Table 2). In incipient nests, however, there was no significant difference in the direction of trophallaxis (Wilcoxon sign-rank $Z = -1.10$, $p = 0.27$, $n = 9$ matched pairs; Table 2). The proportion of all trophallaxis events with workers as donors was significantly higher among nests with established relationships than in incipient relationships (Wilcoxon rank-sum $Z = 2.86$, $p = 0.004$, $n = 18$). The proportion of trophallaxis events with queens as donors was not statistically different for the two kinds of social relationships (Wilcoxon rank-sum $Z = -1.53$, $p = 0.13$, $n = 18$). In established nests, the majority of trophallaxis events are from workers to queens (74.64%), but these workers also feed other workers (2.02%) and males (1.06%). Queens feeding workers (21.75%) and males (0.53%) contributed a substantial proportion of the trophallaxis events, even in established nests (Fig. 1a).

Workers in established relationships guarded the nest entrance at a significantly higher rate than workers in incipient relationships (Wilcoxon rank-sum $Z = 2.78$, $p = 0.005$, $n = 18$), but guarding rates by queens did not differ significantly between relationship types (Wilcoxon rank-sum $Z = 0.49$, $p = 0.63$, $n = 18$). Despite this increase in the guarding time of workers in established relationships, queens had a higher rate of guarding than workers in both incipient and established relationships (incipient: Wilcoxon signed-rank $Z = 2.67$, $p = 0.008$, $n = 9$ matched pairs; established: Wilcoxon signed-rank $Z = 2.31$, $p = 0.02$, $n = 9$ matched pairs; Table 2). This is probably due to the fact that established workers were more likely to be out foraging, leaving the queen to guard the nest.

About half (55.19%) of all cell-related activities performed by incipient workers targeted the cell from which they recently emerged. Established workers spent significantly less time in cells (Table 1: entering cell level 1 or 2) than incipient workers (Wilcoxon rank-sum $Z = -1.99$, $p = 0.05$, $n = 18$), but a similar change in behavior was not seen between queens in incipient and established relationships (Wilcoxon rank-sum $Z = 1.63$, $p = 0.10$, $n = 18$). Workers in incipient relationships entered cells at significantly higher rates than their queens, but there was no significant difference in the rate of cell entrance between established queens and workers (incipient: Wilcoxon signed-rank $Z = -2.19$, $p = 0.03$, $n = 9$ matched pairs; established: Wilcoxon signed-rank $Z = -1.123$, $p = 0.26$, $n = 9$ matched pairs; Table 2). There were no significant differences observed between incipient and established nests for the proportion of time spent investigating and provisioning cells for either queens or workers

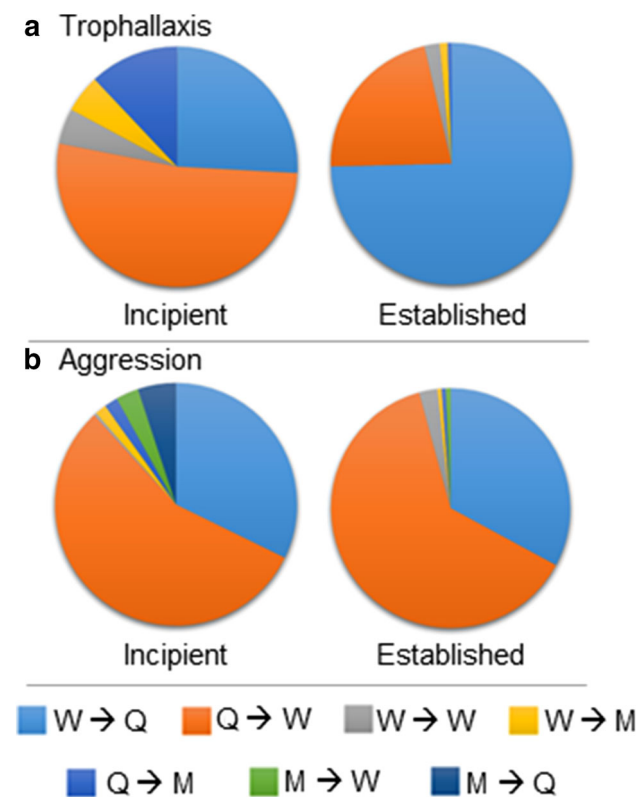


Fig. 1 Distribution of interacting partners for all **a** trophallaxis and **b** aggression within nests with incipient and established queen-worker relationships. *W* workers, *Q* queens, *M* males

(investigating, workers: Wilcoxon rank-sum $Z = 0.57$, $p = 0.57$, $n = 18$; investigating, queens: Wilcoxon rank-sum $Z = 1.81$, $p = 0.07$, $n = 18$; provisioning, workers: Wilcoxon rank-sum $Z = 1.33$, $p = 0.89$, $n = 18$; provisioning, queens: Wilcoxon rank-sum $Z = -0.39$, $p = 0.70$, $n = 18$). There were no significant differences in the rate of cell investigating or cell provisioning between queens and workers in incipient or established nests (incipient, investigating: Wilcoxon signed-rank $Z = -0.65$, $p = 0.51$, $n = 9$ matched pairs; established, investigating: Wilcoxon signed-rank $Z = -0.06$, $p = 0.95$, $n = 9$ matched pairs; incipient, provisioning: Wilcoxon signed-rank $Z = -1.32$, $p = 0.19$, $n = 9$ matched pairs; established, provisioning: Wilcoxon signed-rank $Z = -1.60$, $p = 0.12$, $n = 9$ matched pairs). Overall, workers spent significantly more time interacting with cells than queens in incipient relationships, but not in established relationships (incipient: Wilcoxon signed-rank $Z = -2.31$, $p = 0.02$, $n = 9$ matched pairs; established: Wilcoxon signed-rank $Z = -1.24$, $p = 0.21$, $n = 9$ matched pairs). This result is likely driven by the amount of time young workers spent in their natal cells.

A greater proportion of aggressive behavior was directed toward workers by queens, but this result was only marginally significant in established relationships (incipient:

Wilcoxon signed-rank $Z = -1.96$, $p = 0.05$, $n = 9$ matched pairs; established: Wilcoxon signed-rank $Z = -1.84$, $p = 0.07$, $n = 9$ matched pairs; Table 2). This difference was driven primarily by the relative frequency of lunging behavior, which was significantly different between queens and workers in both incipient and established relationships (incipient: Wilcoxon signed-rank $Z = -1.955$, $p = 0.05$, $n = 9$ matched pairs; established: Wilcoxon signed-rank $Z = -2.53$, $p = 0.01$, $n = 9$ matched pairs). C-posturing was only observed in nests with incipient relationships, and this behavior was always performed by the worker, directed toward the queen (Wilcoxon signed-rank $Z = 2.00$, $p = 0.05$, $n = 4$ matched pairs). Queens and workers in both types of relationships directed nudging and biting toward each other with similar frequency (incipient, nudging: Wilcoxon signed-rank $Z = -0.06$, $p = 0.95$, $n = 9$ pairs; incipient, biting: Wilcoxon signed-rank $Z = -1.68$, $p = 0.09$, $n = 8$ pairs; established, nudging: Wilcoxon signed-rank $Z = -0.60$, $p = 0.55$, $n = 9$ pairs; established, biting: Wilcoxon signed-rank $Z = -0.70$, $p = 0.48$, $n = 7$ pairs). (Variation in samples sizes is reflective of the fact that some behaviors were never observed in certain pairs.) The relative amount of aggression between queens and workers was not significantly different between incipient and established queen-worker pairs (aggressive interactions normalized to time all individuals were in sight; Wilcoxon rank-sum $Z = 0.04$, $p = 0.96$, $n = 18$). Most aggressive interactions in each nest were between workers and queens (88 and 96 % in incipient and established relationships, respectively), but aggression among workers and between workers and males, and queens and males also occurred (Fig. 1b).

Discussion

In species with simple forms of eusociality, such as sweat bees in the family Halictidae, interactions among adults are expected to play a major role in caste determination. Our results reveal that, in *M. genalis*, this process occurs over a period of 10 days, during which the frequencies of behaviors expressed by queens and workers can shift.

Consistent with what is known for other halictid bees (Batra 1968), queens were more aggressive toward workers than workers were toward queens, though the scale of this aggression varies widely among species. In *L. zephyrum* colonies, aggression is relatively low, and most of this is directed from queens to workers with the largest ovaries (Brothers and Michener 1974; Buckle 1982a). For example, Buckle (1982a) recorded 4471 aggressive nudges by queens to workers, and workers returned the nudge only 44 times, suggesting potential conflicts can be resolved without fights. In species with larger colonies (e.g., *L. versatum* and *L.*

imitatum), queens are not aggressive toward workers at all (Batra 1968). This ritualization is presumably to avoid the energetic costs associated with aggression in larger social colonies. Direct comparisons of these bees are complicated by the fact that the laboratory studies of *L. zephyrum* typically involved differentiation of replacement queens relative to workers (reviewed in Michener 1990), while studies of other species concern the developmental differentiation of foundresses and workers. Our results show that the amount of agonism between queens and workers did not diminish as the relationship became established. Fighting was also observed in established nests of *Halictus rubicundus* with only 2–3 females (Batra 1968), suggesting that constant maintenance of dominance status may be more necessary in small colonies than it is in large colonies.

The fact that C-posturing was only observed among incipient relationships, and was only performed by the worker, suggests that the C-posture may be a submissive behavior or used for self-defense in *M. genalis*. C-posturing has been reported as an aggressive presentation of the sting (Wcislo 1997; Arneson and Wcislo 2003), and has been assumed to be such in many studies of halictine agonistic behavior (see references in Packer 2005), but seemed to be used in self-defense in *L. zephyrum* as well (Buckle 1982a). *M. genalis* also used the C-posture to defend the nest against experimentally introduced ants (Smith et al. 2003). Self-defense may be a more specific type of aggressive behavior, and it is possible that the C-posture can be used in this specific way. We had very few observations of this behavior, so further testing is required to deduce the meaning of the C-posture in *M. genalis*.

Cell-related activities were not significantly different between established queens and workers of *M. genalis*, suggesting that workers are not excluded from cells. In other halictid bees, both queens and workers construct and provision cells (Batra 1964; Breed and Gamboa 1977), but queens do more nest maintenance than workers in small laboratory colonies (Brothers and Michener 1974). In *Lasioglossum*, most nest excavation was done by young females that had not yet started foraging (Batra 1968). Likewise, in our study, young workers participated in significantly more cell-related activity than queens, but this may have been resting, rather than working behavior. We did not observe tunnel excavation or cell construction in our study. In several species of diurnal bees, cell building is often completed overnight (Batra 1968). Our observation period extended for as much as 2 h before and after the active foraging period of *M. genalis*, but at least some cell construction and tunnel excavation occurs during the day (WTW, pers. obs.), when bees do not forage.

In *L. zephyrum* and *L. inconspicuum* (= *imitatum*), some individuals primarily function as guards prior to foraging

(Batra 1964; Bell et al. 1974). The scope of our analysis was on worker-queen pairs, and we thus would not have been able to detect finer divisions of worker tasks. The fact that *M. genalis* queens guarded at a significantly higher rate than workers in both incipient and established relationships suggests that workers do not specialize on guarding behavior. This may be due to the relatively small colony size of *M. genalis* (average 1.2 workers) (Kapheim et al. 2013) compared to *L. zephyrum* (average 14 workers) (Bell 1973; Breed and Gamboa 1977). If the only worker in a *M. genalis* nest is out foraging, the queen is the only bee at home to guard the nest. Previous research has demonstrated a clear advantage to nest guarding in *M. genalis* (Smith et al. 2007). Having a worker to forage means that a nest is occupied, and can thus be defended, at all times.

Our observations of foraging and trophallaxis behavior among established queen-worker relationships are consistent with previous *M. genalis* studies with workers of unknown absolute age (Wcislo and Gonzalez 2006). Our study reveals that workers have a fairly lengthy period in which they are equally likely to be the recipients of food from the queen as they are to feed the queen. Young workers also do not forage significantly more than queens until they are more than 10 days old. It is interesting that during this period, the queen is thus both caring for and behaving aggressively toward her daughter.

Trophallaxis among adults is rare in halictid bees (Wcislo and Gonzalez 2006), and this behavior may allow for the extended critical period of caste determination observed in *M. genalis*. In species without trophallaxis, daughters may need to begin foraging for the sake of sustenance soon after emergence. This hypothesis is consistent with the finding that experimentally controlled food exchange increases the survivorship of females without access to food (Wcislo and Gonzalez 2006). Requisite early departures from the natal nest could limit the opportunity for aggressive interactions between mothers and daughters, potentially changing the dynamics of caste development. Trophallaxis has also been documented in a *Lasioglossum* species with communal nest-sharing (Kukuk and Crozier 1990; see Dew et al. 2015 for a discussion of social nesting strategies), however, and intensive observations that would detect trophallaxis have been done on relatively few species. The relationship between trophallaxis and caste determination thus requires further investigation. Future studies of food supplementation for newly emerged females can test the effect this maternal care behavior has on the ontogeny of division of labor.

Overall, the results presented here demonstrate that some caste-typical behaviors have a critical period of development, and may be influenced by the stability of social interactions between queens and workers.

Acknowledgments We thank M. Lopez-Urbe, M. Reiser, R. Coscio, D. La Rosa, J. Medina Gutierrez, S. Bernal, D. Ramirez Garcia, T. Alvey for field assistance; T. Innocent for help in designing the ethogram; A. Lee, C. Sheridan, H. Denenberg, S. Dao, F. Choe, A. Bird, A. Espinosa, E. Anderson, R. Parks for help in scoring the videos; O. Acevedo, B. Jimenez, O. Arosemena, for logistical support. Research on BCI was conducted under A.N.A.M. permit # SEX/A-34-09. K.M.K was supported by funds from NSF DDIG-0808256, Smithsonian Tropical Research Institute (STRI), Smithsonian Institution, UCLA, AWIS, U.S. Dept. Ed. K.M.K and P.N. were supported by NSF grant IOS-0642085. W.T.W. and A.R.S. were supported by STRI and SENACYT grant COL-06-030.

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