ORIGINAL PAPER

Survival and productivity benefits to social nesting in the sweat bee *Megalopta genalis* (Hymenoptera: Halictidae)

Adam R. Smith · William T. Wcislo · Sean O'Donnell

Abstract Facultatively solitary and eusocial species allow for direct tests of the benefits of group living. We used the facultatively social sweat bee *Megalopta genalis* to test several benefits of group living. We surveyed natural nests modified for observation in the field weekly for 5 weeks in 2003. First, we demonstrate that social and solitary nesting are alternative behaviors, rather than different points on one developmental trajectory. Next, we show that solitary nests suffered significantly higher rates of nest failure than did social nests. Nest failure apparently resulted from solitary foundress mortality and subsequent brood orphanage. Social nests had significantly higher productivity, measured as new brood cells provisioned during the study, than did solitary nests. After accounting for nest failures, per capita productivity did not change with group size. Our results support key predictions of Assured Fitness Return models, suggesting such indirect fitness benefits favor eusocial nesting in *M. genalis*. We compared field collections of natural nests to our observation nest data to show that without accounting for nest failures, *M. genalis* appear to suffer a per capita productivity decrease with increasing group size. Calculating per capita productivity from collected nests without accounting for the differential probabilities of survival across group sizes leads to an overestimate of solitary nest productivity.

R. F. A. Moritz

S. O'Donnell
Animal Behavior Area, Department of Psychology,
University of Washington,
Seattle, WA 98195, USA

A. R. Smith (✉) · W. T. Wcislo
Smithsonian Tropical Research Institute,
Unit 0948,
APO, AA 34002, USA
e-mail: smithad@si.edu

Introduction

Species where individuals choose between solitary or eusocial nesting are valuable for testing the selection pressures favoring the evolution of eusociality. Facultatively eusocial species permit direct examination of the switch from solitary to group living (Schwarz et al. 1997, 1998; Wcislo 1997, 2000; Field et al. 2000; Hogendoorn et al. 2001; Smith et al. 2003). Understanding the transition from solitary to social behavior requires understanding the selective advantage to individuals living in groups relative to solitary nesters (Maynard Smith and Szathmáry 1995).

One such advantage can arise when an offspring depends on parental care throughout development. Assured fitness returns, or "insurance-based" models (hereafter AFR models), argue that in such cases adults will be favored to remain at their natal nest as helpers because they may die before successfully raising an offspring (Queller 1989, 1994, 1996; Strassmann and Queller 1989; Gadagkar 1990, 1991; Bull and Schwarz 2001). A solitary individual will lose all parental effort if she dies before offspring independence. In contrast, a helper who remains at her natal nest can accrue indirect fitness by helping raise related offspring. If a helper dies before the offspring reaches maturity, her parental effort will be protected by surviving nestmates. AFR models predict that the combined ecological pressures of extended parental care and adult mortality will favor eusociality via kin selection. AFR models have been supported by studies of species that must provision offspring throughout larval development (progressive provisioners),

which is unsurprising because immatures would starve without adult provisioning (Queller 1989; Gadagkar 1990; Bull and Schwarz 1996, 1997; Schwarz et al. 1997, 1998; Field et al. 2000; Hogendoorn et al. 2001; Shreeves et al. 2003).

Offspring may still depend on adult presence for protection, however, even if they do not need to be fed, as is true for mass provisioning species in which adults fully provision each brood cell before laying an egg (Queller 1994; Eickwort et al. 1996; Kukuk et al. 1998; Forbes et al. 2002; Smith et al. 2003). Extending AFR models beyond progressive provisioners offers the chance to focus on the role of offspring defense in favoring the evolution of sociality (Lin and Michener 1972). In mass provisioning species, adults fully provision each brood cell before laying an egg, but they often remain at and defend their nests (Queller 1994; Eickwort et al. 1996; Kukuk et al. 1998; Forbes et al. 2002; Smith et al. 2003). The mass-provisioning bee family Halictidae is a key taxon for understanding social evolution. Halictids exhibit multiple evolutionary origins and losses of eusociality, communality, brood parasitism, and solitary nesting (Michener 1974, 1990; Danforth and Eickwort 1997; Wcislo and Danforth 1997; Wcislo 1997, 2000; Danforth 2002; Soucy and Danforth 2002; Coelho 2002; Richards et al. 2003; Danforth et al. 2004). In fact, AFR may be greater in mass provisioners. In progressive provisioners, the amount of fitness returns that can be "assured" after a female's death is limited, and sometimes completely erased, by the requirement that remaining foragers increase their foraging workload to compensate for their departed nestmate(s) (Field et al. 2000; Hogendoorn and Zammit 2001; Tibbets and Reeve 2003). Mass provisioners suffer no such constraint because the food for all developing offspring has already been provided.

Nest defense and other benefits that increase with group size have often been considered insufficient to favor eusociality because per capita productivity decreases with increasing colony size across many species of social insects (Michener 1964; Wenzel and Pickering 1991; Karsai and Wenzel 1998). However, many facultatively and/or primitively social species show an increase in per capita productivity when moving from solitary to social groups (Schwarz 1994; Tierney et al. 1997, 2000, 2002; Schwarz et al. 1998; Field et al. 1999, 2000; Hogendoorn and Zammit 2001; Coelho 2002; Joyce and Schwarz 2006; Thompson and Schwarz 2006), and even in larger-colony species, the negative relationship may not be universal (Bouwma et al. 2005, 2006). Studies of per capita productivity that are based on nest collections may overestimate productivity of small groups by ignoring failed nests (Clouse 2001). Moreover, comparing average per capita productivity between solitary and social nesters may not even be

relevant if those females with relatively low reproductive ability choose to help while those with greater ability nest solitarily (West-Eberhard 1975, 1978).

We previously demonstrated that immature offspring of the facultatively social halictid bee *Megalopta genalis* require adults to repel predatory ants by showing that experimentally orphaned offspring were consumed by ants (Smith et al. 2003). Thus, AFR may favor group living in *M. genalis* by ensuring that at least one adult will remain at the nest throughout brood development. Because orphaned brood are likely to be consumed by ants, social nesting should be selected for to the extent that it minimizes brood orphanage.

To demonstrate benefits to social nesting via AFR, several further questions must be addressed in *M. genalis*. First, are social and solitary nesting really alternative behavioral choices by bees or just different points on the same developmental trajectory? Many obligately eusocial insect species pass through a solitary foundress stage before the emergence of the first workers (Michener 1974), so the mix of social and solitary nests found in *M. genalis* populations may simply be a mix of pre- and postemergence developmental stages. The goal of this study is to determine whether solitary and social nesting are different behaviors and then test three predictions of AFR models. (1) *Social nests should have a survival advantage over solitary ones.* If social nesting in *Megalopta* decreases the chance of brood orphanage by protecting against ant predation, then multi-female nests will be less likely to fail than single-female nests. (2) *Adult mortality must be high enough that solitary-nesting females suffer a substantial risk of leaving their brood orphaned.* If most solitary adults survive until brood emergence, protection against brood orphaning is unlikely to be an important selective force because brood would rarely be orphaned. (3) *Total group productivity should increase in multi-female nests relative to solitary ones, and social females should not suffer a per capita productivity cost.* The efforts of nonreproductive bees must increase colony fitness; that is, there must be an incremental investment to protect upon their death, and it should be substantial enough to offset the direct fitness benefits that these bees would have sacrificed by staying to help.

To test these predictions, we monitored adult female number, brood production, and nest survivorship in natural *M. genalis* nests in the field for 5 weeks, which is the approximate egg to adult development time for this species (Wcislo et al. 2004; Wcislo and Gonzalez 2006). These observations allowed us to detect changes in female number over time, to compare survival between solitary and social nests, and to correlate female number with productivity. For additional tests of the effect of group size on productivity, we analyzed data from glass-topped observation nests and natural nests collected from the field.

Materials and methods

Synopsis of natural history

M. genalis is a mass provisioner. Both solitary and multi-female nests are found throughout the tropical dry and early wet seasons (Wcislo et al. 2004). During this time, approximately one-third to one-half of nests are multi-female, each typically containing two to four adult females. Subordinate bees are offsprings that have remained at their natal nests, and thus, are presumably daughters or sisters of the queen. Multi-female nests usually show strong division of labor: in glass-topped observation nests, one bee monopolizes reproduction, while the other female(s) perform >90% of the foraging trips and feed the queen via trophallaxis (Wcislo and Gonzalez 2006). *M. genalis* forages nocturnally approximately 45 min after sunset and 90 min before sunrise (Kelber et al. 2006; for further details of *Megalopta* behavior see Smith et al. 2003; Arneson and Wcislo 2003; Wcislo et al. 2004; Warrant et al. 2004).

Study sites

All studies except for the La Selva collections were conducted on Barro Colorado Island (BCI; 9°09′ N, 79°51′ W), Republic of Panamá. BCI is a lowland tropical semi-deciduous moist forest (Rau 1933, Leigh 1999). Nests in the La Selva collections were collected at La Selva Biological Station (10°26′ N, 83°59′ W), Costa Rica. La Selva is a lowland tropical wet forest (McDade et al. 1994).

Natural observation nests

For the focal nests in the study, we modified 29 naturally occurring nests in the field for observation. *Megalopta* excavate tunnel nests in dry, rotting sticks (dead branches or lianas) suspended in vegetation or otherwise raised above the ground (Smith et al. 2003; Wcislo et al. 2004). To enable observations, we cut away part of the side of the stick that formed the tunnel wall. We covered the exposed tunnel with flexible, transparent acetate secured with rubber bands, creating a window. The window was then covered with black plastic and secured with rubber bands or wire twist-ties to block light and water from entering the nest. These nests were left in their natural locations in the field for 5 weeks, between February 23 and March 30, 2003. We checked the nests weekly for number of females, number of males, and number and status of brood cells. These inspections were the only times the plastic cover was removed. Only nests containing brood were included.

Glass-topped observation nests

Young bees do not forage or disperse until about 1 week of adult age (Wcislo and Gonzalez 2006). Thus, counting all females other than the queen as foragers may overestimate forager number when young bees are included. To quantify this overestimate, we used data gathered from bees of known ages from eight glass-topped observation nests placed in the forest on BCI (Wcislo and Gonzalez 2006). Glass-topped observation nests consisted of a piece of balsa wood (~15×20 cm) with a tunnel, sandwiched between two panes of glass or transparent acrylic that were covered with a ~7-mm thick piece of opaque styrofoam (removed during observations) and held together with binder clips (Wcislo and Gonzalez 2006). Pupae allowed to eclose inside these nests used them as adults. All females were uniquely marked on the thorax with quick-drying Decocolor® paint markers, and nests were censused daily between February 7 and June 1, 2001.

Other nest collections

Nests were collected from the field during the middle of the day when all adults were inside by plugging the nest entrance with cotton and placing the stick containing the nest into a freezer. The nests in each dataset were collected during the following dates: La Selva 2003: April 13–May 23; BCI 2003: May 12–June 16; BCI 2004: March 13–March 23.

Productivity calculations

For the natural observation nests, the number of new cells provisioned during the 5-week study period was used as a measure of productivity. This includes newly constructed cells and cells reused after brood emergence. Per capita productivity was calculated as the number of cells provisioned in the nest divided by the mean number of females in the nest per census during the 5-week study period. Failed nests were scored as zero with respect to productivity (no adults eclosed before failure). Newly opened cells (those that were closed with brood inside during the previous week) were counted as adult emergences. Emergence of a brood parasite would be counted as an emergence using this method, but because only ~2% of *Megalopta* cells are parasitized, this is unlikely to bias our data (Wcislo et al. 2004). Glass-topped observation nest data suggest that this method is likely to count most emergences before the cell is reused and closed again (mean time from emergence of an adult to closing a reused cell is 16.6 days, with only one of 24 emergences resealed in <6 days).

For the glass-topped observation nests, we included only data collected between Feburary 1 and June 1 to avoid

biasing analyses with data from the relatively unproductive late wet season (late July–early December; Wcislo et al. 2004) because none of our other groups contained data from this period. Productivity was measured as the number of new cells per week because there was no predetermined observation period as in the natural observation nests. To test for the effect of young, non-foraging bees on productivity, we calculated per capita productivity of postemergence nests (at least one offspring had emerged as an adult) using both the total number of females present and again including only the females older than 10 days of age (*Megalopta* females begin foraging at about 1 week of age; Wcislo and Gonzalez 2006).

For the collected nests, the number of provisioned cells was used as the measure of productivity. Only nests with either late stage brood (pupae) and/or at least one adult emergence were included to avoid biasing the results with newly initiated nests still under construction. Previous adult emergence can be detected in a collected nest by either the presence of larval feces in an open cell or adjacent cells in which the brood cells are not arranged in order of age.

Statistical analyses

All statistics were performed in SPSS 10.0 or Microsoft Excel. All means are presented ±SD, and all *P* values are two-tailed. All correlations are Pearson product-moment correlations. To compare the number of females in nests that began our census with one female to those that began with multiple females, we used a repeated measures GLM in SPSS with "start solitary" or "start multi-female" as a between-subjects factor to account for the nonindependence of weekly samples of the same nest.

Results

Are social and solitary nesting behaviors different behaviors?

Of those nests that survived the census, nests that began with a single female were more likely to end the census with a single female, and nests that started with multiple females were more likely to remain multi-female ($n=23$ surviving nests, Pearson's $XP^{2P}=7.08$, $df=1$ $P=0.008$; Table 1). Nests that started single-female finished with fewer females ($\bar{x}=1.40\pm0.70$) than those that started multi-female (3.08 ± 1.26; $t=4.06$, $P<0.001$).

There was weekly within-nest variation in female numbers due to new emergences, adult mortality, and/or bees leaving their nest. Five nests were solitary for the entire census, while all others showed some variation in female number, including seven nests that were exclusively

Table 1 Nests that survived the 5-week census are sorted by the number of females that were present at the beginning and end of the study

		End study:	
		1 ♀	>1 ♀
Begin study:	1 ♀	7	3
	>1 ♀	2	11

Nests were significantly more likely to stay in the same category than to change ($XP^{2P}=9.7$, $P<0.01$).

multi-female. Despite variation in female number, those nests that began the census with a single female had significantly fewer females throughout the census period than did those nests that began with multiple females (average weekly number of adult females for nests that began single-female: 1.28 ± 0.61; for those that began multi-female: 2.65 ± 1.00; repeated measures GLM $F=25.81$, $df=1$, $P<0.001$). Thus, solitary and social nests tended to maintain differences in female number throughout the census.

It is unlikely that the differences we observed were due to the inclusion of nests that were too young to have adult offspring. This study lasted 5 weeks, approximately the egg to adult development time for *M. genalis* (Wcislo et al. 2004). Thus, if emerging bees were going to stay as helpers, we should have seen this in our study. Nests founded immediately before the census may not have had time for bees to emerge and potentially stay to help, but most nests were discovered before the census began, and all nests had provisioned cells upon discovery, implying that none were discovered just as they were being initiated. The mean time from discovery to the end of the 35-day census was 49.5 ± 10 days (range: 35–65). Also, all but one nest had at least one adult emergence, although not necessarily a female, during the study ($\bar{x}$ for all nests=3.3 ± 2.2 emergences). The one nest without an emergence was at least 59 days old at the conclusion of the study and averaged 2.5 adult females during the census. The two nests discovered immediately before the census both had multiple emergences (at least 36 days old and 2 emergences, and 35 and 6, respectively). The 36-day-old nest was exclusively solitary, while the 35-day one averaged 1.83 females. These observations support the hypothesis that social and solitary nesting represent different behaviors, rather than different points along the same developmental trajectory.

1) Do social nests have a survival advantage over solitary nests?

Given that social and solitary nesting apparently represent behavioral choices, we can test hypotheses for benefits to social nesting. Only 5 of 28 nests used for the study failed (82% survival), which is one of the highest survival

rates seen in this species (Smith et al. 2003; Wcislo et al. 2004; AR Smith, unpublished data). In one case, no adult was present for the second week's census, but the brood cells were intact. This nest was left in the field, and the next week contained an adult that presumably had emerged from a newly open brood cell before the nest was discovered by ants; this nest was counted as surviving. All other nests without adults contained brood being consumed by ants and/or signs of predation such as pierced cell caps or ragged-edged cell openings, presumably caused by ants, and were counted as dead (see Smith et al. 2003).

Single-female nests are more likely to suffer brood predation. All five nest failures occurred in singleton nests. Moreover, none of these nests had more than one female between the start of the census and their demise. Treating the mean number of females in a nest per week as a continuous variable in a logistic regression model shows a significant effect of group size on survival ($X_P^{2P}=10.33$, $df=1$, $P=0.001$).

2) Estimating adult mortality

Estimating adult mortality in socially flexible species is difficult because it is impossible to know whether a female that disappears from a nest has died or left the nest to found her own. If we assume, however, that a solitary foundress provisioning a nest is not likely to abandon it, we can estimate the mortality for solitary foundresses from single-female nest survival (Mueller 1996), using nests with an average of ≤ 1.5 females as "solitary" (this is necessary because newly eclosed females stay in the nest for approximately 7 days before foraging or dispersing [Wcislo and Gonzalez 2006]). Under this assumption, female mortality is 38.5% over 5 weeks (5 nest failures out of 13 presumptive solitary nests) or 9.3% per week. This estimate should be taken as an approximation given that (1) it is based on only a single sample, (2) not all solitary nests were solitary every week, and (3) some social nests were occasionally solitary.

3) Do social nests have a productivity advantage over solitary nests?

The number of females in the nest shows a strong, positive correlation with number of new cells, our measure of productivity ($n=28$, $r=0.72$ $P<0.001$; Fig. 1a, Table 2). When productivity is calculated per female, the correlation with mean number of females is positive but not significant ($r=0.24$ $P=0.22$; Fig. 1b, Table 2). Generally solitary nests had significantly lower mean productivity than multi-female nests (1.47 ± 1.68 vs 3.77 ± 2.20 new cells; $t=3.13$, $P=0.004$), but similar per capita productivity (1.16 ± 1.28 vs 1.33 ± 0.66 new cells per capita; NS).

These results incorporate survival data, (see section on "Do social nests have a survival advantage...", above) using values of zero for numbers of new cells from nests that failed. Including only the nests that survived, the entire
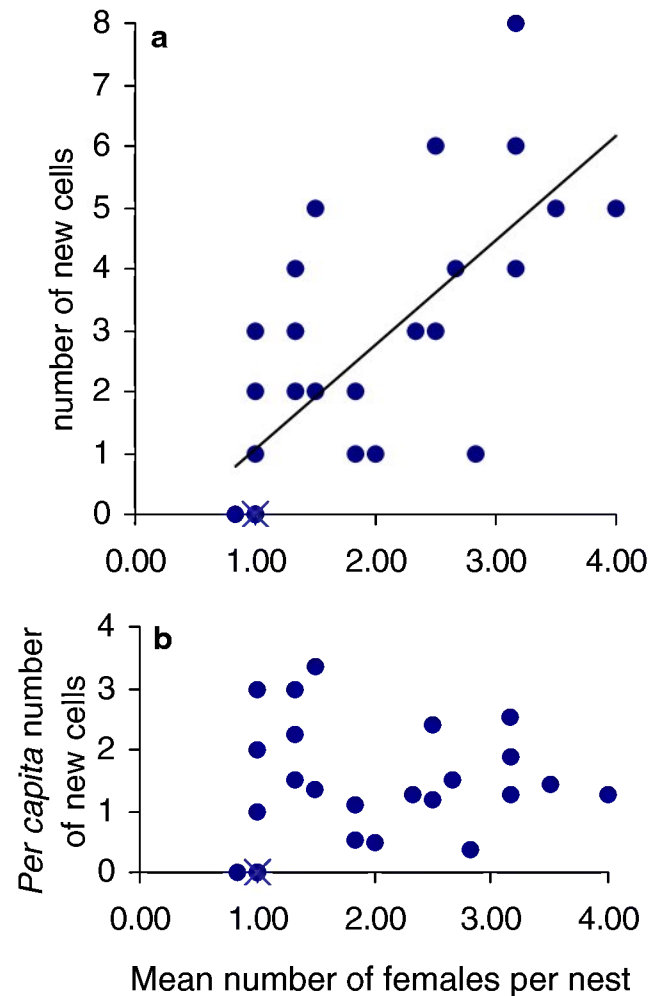

Fig. 1 **a** Nest productivity measured as the number of new cells provisioned in each nest plotted against the mean number of females in each nest for the 5-week census. **b** Per capita nest productivity plotted against mean number of females in each nest. A linear regression line is shown for (**a**), which is significant ($r_P^{2P}=0.49$, $P<0.01$), but not for (**b**), which is not significant ($r_P^{2P}=0.06$, $P=0.22$). In both plots, there are five points at 1, 0

census gave similar results, but with weaker correlations (overall productivity: $n=23$, $r=0.64$, $P=0.01$; per capita productivity: $r=-0.02$, $P=0.94$). Likewise, the difference in average productivity between generally solitary and multi-female nests is diminished (2.20 ± 1.62 vs 3.77 ± 2.20 new cells; $t=1.89$, $P=0.07$). Among the survivors, multi-female groups added more cells to their nests during the census ($\bar{x}=1.31\pm1.03$ vs 0.30 ± 0.48; $t=2.84$, $P=0.03$) and had more than twice as many brood cells in their nests than did generally solitary nesters ($\bar{x}=9.46\pm2.60$ vs 4.50 ± 2.50; $t=4.61$, $P<0.001$).

One potentially confounding factor with our data is that young bees do not begin foraging until about a week after emergence, although they might help the colony before then by guarding the nest entrance. Thus, if some of the bees counted as helpers in our analysis, they are, in fact,

Table 2 Correlations between number of females and number of brood in postemergence *M. genalis* nests

Dataset	Productivity				Per capita productivity		
	n	x̄±SD	r	P	x̄±SD	r	P
Natural observation nests	28	0.51±0.45	0.72	<0.001	0.25±0.21	0.24	0.22
Glass-topped observation nests	8	0.65±0.35	0.73	0.04	0.42±0.14	0.18	0.66
La Selva 2003	49	3.12±1.96	0.69	<0.001	1.66±0.88	0.32	0.03
BCI 2004	25	6.00±2.96	0.54	0.005	3.96±1.84	−0.43	0.03
BCI 2003	53	4.27±2.96	0.77	<0.001	3.02±1.52	−0.24	0.04
This study, start: all nests	28	6.43±3.13	0.62	<0.005	3.66±1.88	−0.30	0.12
–start with dead nests as zeros	*28*	*5.86±3.17*	*0.65*	*<0.001*	*3.57±1.84*	*−0.04*	*0.84*
This study, finish: survivors only	23	7.30±3.55	0.73	<0.001	3.44±1.66	−0.45	0.03
–finish with dead nests as zeros	*28*	*6.00±4.29*	*0.77*	*<0.001*	*2.83±2.01*	*−0.02*	*0.92*

n is number of nests in each dataset, x̄±SD is the mean ± standard deviation for each sample. Note that the values for the natural and glass-topped observation nests represent number of new brood cells per week, while values of the other collections represent number of brood cells in the nest. *r* is the coefficient of correlation with number of females in the nest, and *P* is the two-sided *P* value for the correlation. Significant correlations are underscored. Data from the start and finish of this study that incorporate nest failures are in italics.

young bees that are not yet foraging, we would underestimate per capita productivity for multi-female nests by overestimating the number of potential foragers. We used the glass-topped observation nests, in which bees were marked and censused daily, to compare observed multi-female group size to group size without young bees (<10 days of age). The observed group size (n=6 nests, x̄=1.77±0.48 females) was only 5% larger than counts of group size that excluded young bees (x̄=1.69±0.44), suggesting that the presence of young bees does not strongly affect our per capita productivity calculations.

The number of females in a nest was correlated with overall productivity in the glass-topped observation nests, just as it was in the natural ones (n=8 nests, r=0.73, P=0.04), and per capita productivity showed a similar weak, nonsignificant positive correlation with group size (r=0.18, P=0.66). Thus, in the two datasets in which both productivity and number of females could be measured over time (i.e., natural observation nests in 2003 and the glass-topped observation nests in 2001), the number of females in the nest correlated significantly with productivity, but not with per capita productivity.

Other nest collections

Overall productivity (measured as the number of provisioned brood cells per female) in three additional collections of natural nests was positively correlated with the number of females in the nest just as it did in our observation nests (Table 2, upper left section). Unlike our observation nests, collected nests from all three groups show a relatively weak but significant negative correlation between per capita productivity and group size (Table 2, upper right section). This contradicts our observation nest results of no per capita productivity cost. We believe that the discrepancy is

likely due to the inability of field collections to detect nest failure and the omission of nest failure data from calculations of productivity. For instance, when we analyzed our observation nests as if they were a sample collected at either the first or last census, thus, discarding week-to-week data, they showed a negative correlation between per capita productivity and group size of similar magnitude to that of the actual collections (Table 2, lower right section). However, when we included nests that failed during the census, the negative correlation was reduced to essentially zero (Table 2, lower right section, italics). This finding suggests that the negative correlations seen in the nest collections would also be reduced if we could incorporate nest failure rates for different group sizes.

Discussion

Social vs solitary nesting behavior

Our data show that over the course of a complete brood cycle, social nests tended to remain social, and solitary nests tended to remain solitary, even though all but one nest had at least one adult emerge during the census. Social nests arise from females remaining at their natal nest to help their mothers (Wcislo et al. 2004, A.R. Smith, personal observation), so many newly initiated solitary nests do develop into social nests (Smith 2005). Although some nests switched categories during the census, our data support the hypothesis that among established nests, solitary and social nesting represent the results of different decisions by emerging females regarding whether or not to remain at the natal nest as a helper. We do not know what criteria females use to make these decisions, although

relative body size appears to play a role, with smaller females being more likely to stay than larger ones (Smith 2005).

Survival

Our census showed that single-female nests were less likely to survive than multi-female ones. Several factors, such as whole-nest predation (presumably by vertebrates such as anteaters and birds) or the inexorable rotting of wood in the tropics, destroy nests regardless of the number of females inside (Smith et al. 2003; Wcislo et al. 2004). Based on earlier results, however, singleton nests are much more likely to succumb to ant predation because the death of the lone female leaves the brood orphaned (Smith et al. 2003). An adult female can defend a nest against even sustained attack by ants such as *Camponotus*, *Crematogaster*, *Azteca*, and *Pachychondolya*, while orphaned brood are defenseless (Smith et al. 2003). Also, *Megalopta* brood are apparently ignored by army ants (Smith et al. 2003 for *Eciton hamatum*; AR Smith unpublished data for *E. burchellii* and *Labidus praedator*), which are often a colony size-independent source of mortality for other social insects (Chadab 1979; Gotwald 1995). Thus, only in single-female nests will the death of one adult lead to orphaned brood susceptible to ant predation. Protection against brood orphanage as an advantage of group living has been demonstrated for other species of both eusocial and communal halictids (Eickwort et al. 1996; Kukuk et al. 1998) and may be a widespread force favoring group living in this family.

The overall survival rate for this study (82%) was among the highest measured in six survival censuses of *Megalopta*, which range as low as 50% survival over 5 weeks (Smith et al. 2003; Wcislo et al. 2004, AR Smith unpublished data). The fact that nest survival in our study was relatively high suggests that selection for group living to avoid offspring mortality and the effects of solitary nest mortality on per capita productivity are probably generally stronger than we have documented. No other studies monitored both female number and survival simultaneously, and there were relatively few nest failures in our sample; so further work is necessary to confirm this hypothesis (Smith et al. 2003; Wcislo et al. 2004).

Uncertainties in measuring adult mortality

Our results suggest that solitary females have about a one in three chance of dying before their offspring emerge, and thus, losing all parental effort. If female mortality is higher when constructing nests and/or nest construction substantially increases the time required to rear brood to emergence, then our calculations underestimate the probability of

solitary nest failure (Gadagkar 1991). Conversely, if females choose to abandon their nests to nest elsewhere, our calculations overestimate adult mortality. Although our estimate is approximate, it shows that independently nesting females face a substantial risk of brood loss that can be reduced by group living. This risk of solitary nest failure is at the lower end of the range reported in other studies of AFR models (Gadagkar 1991; Queller 1994; Eickwort et al. 1996; Field et al. 1998; Hogendoorn and Zammit 2001).

Productivity

Over the 5-week census period, the number of new cells provisioned increased with the number of females in the nest. Productivity also increased with additional females in the glass-topped observation nests and in three separate collections of natural nests, which suggests that nonreproductive foragers are gaining indirect fitness. Some studies of progressive provisioning wasps and bees showed that the extra offspring resulting from the effort of helpers is lost upon the helpers' death because the remaining nestmates cannot provide enough resources to sustain all of the offspring (Field et al. 2000; Hogendoorn and Zammit 2001; Tibbets and Reeve 2003). Such a loss is unlikely to be an important factor with mass-provisioning *M. genalis* because the only parental effort required of the remaining nestmates is nest defense. Nest defense takes place at the constricted nest entrance where one adult can prevent entry to the entire nest, so defending a large nest requires no more effort than defending a small one (Smith et al. 2003).

Our results from the observation nests suggest that *M. genalis* per capita productivity is independent of group size. This result is contrary to the trend first noted by Michener (1964) (see discussion in Karsai and Wenzel 1998) that per capita productivity decreases as group size increases (but see Bouwma et al. 2005, 2006). However, some other facultatively social species show no per capita productivity decrease when moving from solitary to social nesting. Increased per capita productivity in social relative to solitary nests has been shown in halictid bees (Coelho 2002), stenogastrine wasps (Field et al. 1999, 2000), and allodapine bees (Schwarz 1994; Schwarz et al. 1998; Tierney et al. 1997, 2000, 2002; Hogendoorn and Zammit 2001; Joyce and Schwarz 2006; Thompson and Schwarz 2006). Thus, while a move from solitary to social behavior may carry a per capita productivity cost as predicted by Michener (1964), enough species show the opposite result that a decrease in per capita productivity should not be viewed as generally selecting against the transition from solitary behavior to sociality (see below for the merits of per capita productivity estimates).

Our study highlights the importance of including nest survival data in calculations of productivity. Nest failures occurred disproportionately in solitary nests in our study. Consequently, any calculation of per capita productivity that does not include measurements of survival for different group sizes is biased. This finding is similar to results from various species of facultatively social allodapine bees (Apidae), in which an increase in per capita productivity from one- to two-bee nests is driven largely by the disproportionate number of solitary nests with no brood, presumably due to predation (Schwarz 1994; Schwarz et al. 1998; Tierney et al. 1997, 2000, 2002; Hogendoorn and Zammit 2001; Joyce and Schwarz 2006).

What determines whether females stay as helpers or nest independently? If the tendency of singleton nests to remain solitary represents decisions made by the resident bees, there presumably are advantages to independent nesting in some circumstances. If a nest cannot accommodate new cells due to the size of the stick it is in, or the nest already has sufficient foragers, even the most productive queen may not be able to take advantage of an additional helper's effort (ARS and WTW, personal observation). If she is unlikely to increase productivity or survival, an emerging female is unlikely to gain indirect fitness benefits by remaining at her natal nest, so she should pursue direct reproduction. In fact, some bees that were counted as helpers in this study may have been waiting before pursuing direct reproduction. In glass-topped observation nests, the youngest bees forage proportionally less as group size increases (Wcislo and Gonzalez 2006), suggesting that some "helpers" may be foraging as little as possible, biding their time before dispersing or becoming a replacement queen (Michener, 1990). Coelho (2002) showed that workers of a related sweat bee, *Augochloropsis iris*, can stop helping and leave to nest independently.

The advantages to helping vs independent reproduction are probably not equal for all bees. Wide variation in single-female reproductive output in both the observation and field-collected nests (e.g. Fig. 1) suggests that there is variation in individual reproductive ability, which is masked by average per capita calculations. Females who are relatively poor reproductives but capable foragers might gain more fitness indirectly as helpers than they could directly as reproductives, while females in better reproductive condition would gain more fitness by founding their own nest (West-Eberhard 1975, 1978). Likewise, females that are less likely to maintain social dominance over future nestmates would face a higher probability of being usurped as queen, and thus, may choose not to initiate their own nest (Michener 1990). An implicit assumption in per capita productivity analyses is that helpers could leave and potentially achieve the same reproductive success as that observed in actual solitary nesters. If subordinates do choose their helping role based on assessments of their own reproductive abilities, then, this assumption would be false. Subordinates' social contributions would have to be compared to how well they could reproduce on their own, rather than comparing them to females that choose to initiate a new nest. Our study compared social groups to those females that nested solitarily. If solitary nesters are among the relatively strongest reproductives, then our comparison was actually biased against detecting a per capita benefit to social nesting. Data from queen removal experiments show that *M. genalis* females who stay and help are smaller than their sisters (Smith 2005), perhaps limiting their reproductive and/or social dominance ability. Further experiments manipulating group size and composition will help explain how individual variation and social context interact to affect group size.

Conclusions

We have shown that the predictions of AFR models are met in *M. genalis*: social nests have a survival advantage over solitary nests due to lower risk of brood orphanage after adult death, and adult mortality resulting in brood orphanage is the major cause of nest failure. Social nests have higher productivity than solitary ones, suggesting that females remaining at the nest as helpers gain indirect fitness through increased colony reproductive output. This increase is amplified by a survival advantage conferred by multiple females in the nest. Taken together, these data suggest that *M. genalis* helpers have ample opportunity to gain indirect fitness if they forgo reproduction. Wide variation in reproductive output suggests that variation in reproductive ability may determine which bees adopt helping roles and which reproduce. While our work demonstrates general advantages to social nesting, further manipulative studies of social groups will help explain what determines individual choice of behavioral strategy.

References

Arneson L, Wcislo WT (2003) Dominant–subordinate relationships in a facultatively social, nocturnal bee, *Megalopta genalis* (Hymenoptera: Halictidae). J Kans Entomol Soc 76:183–193

Bouwma AJ, Howard KJ, Jeanne RL (2005) Parasitism in a social wasp: effect of gregarines on foraging behavior, colony productivity, and adult mortality. Behav Ecol Sociobiol 59:222–233

Bouwma AJ, Nordheim EV, Jeanne RL (2006) Per-capita productivity in a social wasp: no evidence for an effect of colony size. Insectes Soc 53:412–419

Bull NJ, Schwarz MP (1996) The habitat saturation hypothesis and sociality in an allodapine bee: cooperative nesting is not "making the best of a bad situation". Behav Ecol Sociobiol 39:267–274

Bull NJ, Schwarz MP (1997) Rearing of non descendent offspring in an allodapine bee, *Exoneura bicolor* Smith (Hymenoptera: Apidae: Xylocopinae). Aust J Entomol 36:391–394

Bull NJ, Schwarz MP (2001) Brood insurance via protogyny: a source of female-biased sex allocation. Proc R Soc Lond B 268:1869–1874

Chadab R (1979) Army-ant predation on social wasps. PhD dissertation, University of Connecticut, Storrs, CT

Clouse R (2001) Some effects of group size on the output of beginning nests of *Mischocyttarus mexicanus* (Hymenoptera: Vespidae). Fla Entomol 84:418–425

Coelho BWT (2002) The biology of the primitively eusocial *Augochloropsis iris* (Schrottky, 1902) (Hymenoptera, Halictidae) Insectes Soc 49:181–190

Danforth BN (2002) Evolution of sociality in a primitively eusocial lineage of bees. Proc Natl Acad Sci USA 99:286–290

Danforth BN, Eickwort GC (1997) The evolution of social behavior in the augochlorine sweat bees (Hymenoptera: Halictidae) based on a phylogenetic analysis of the genera. In: Choe JC, Crespi BJ (eds) Social behavior in insects and arachnids Cambridge University Press, Cambridge, pp 270–292

Danforth BN, Brady SG, Sipes SD, Pearson A (2004) Single-copy nuclear genes recover Cretaceous-age divergences in bees. Syst Biol 53(2):309–326

Eickwort GC, Eickwort KR, Eickwort JM, Gordon JM, Eickwort A (1996) Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus*. Behav Ecol Sociobiol 38:227–233

Field J, Foster W, Shreeves G, Sumner, S (1998) Ecological constraints on independent nesting in facultatively eusocial hover wasps. Proc R Soc Lond B 265:973–977

Field J, Shreeves G, Sumner S (1999) Group size, queuing and helping decisions in facultatively eusocial hover wasps. Behav Ecol Sociobiol 45:378–385

Field J, Shreeves G, Sumner S, Casiraghi M (2000) Insurance-based advantage to helpers in a tropical hover wasp. Nature 404:869–870

Forbes SH, Adam RMM, Bitney C, Kukuk PF (2002) Extended parental care in communal social groups. J Insect Sci 2:22–28

Gadagkar R (1990) Evolution of eusociality: the advantage of assured fitness returns. Phil Trans R Soc Lond B. DOI 10.1098/rstb.1990.0146

Gadagkar R (1991) Demographic predisposition to the evolution of eusociality: a hierarchy of models. Proc Natl Acad Sci USA 88:10993–10997

Gotwald Jr WH (1995) Army ants: the biology of social predation. Cornell University Press, Ithaca

Hogendoorn K, Zammit J (2001) Benefits of cooperative breeding through increased colony survival in an allodapine bee. Insectes Soc 48:392–397

Hogendoorn K, Watiniasih NL, Schwarz MP (2001) Extended alloparental care in the almost solitary bee *Exoneurella eremophila* (Hymenoptera: Apidae). Behav Ecol Sociobiol 50:275–282

Joyce NC, Schwarz MP (2006) Sociality in the Aultralian allodapine bee *Brevineura elongate:* small colony sizes despite large benefits to group living. J Insect Behav 19:45–61

Karsai I, Wenzel JW (1998) Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. Proc Natl Acad Sci USA 95:8665–8669

Kelber A, Warrant EJ, Pfaff M, Wallén R, Theobald JC, Wcislo W, Raguso R (2006) Light intensity limits foraging activity in nocturnal and crepuscular bees. Behav Ecol 17:63–72

Kukuk PF, Ward SA, Jozwiak A (1998) Mutualistic benefits generate an unequal distribution of risky activities among unrelated group members. Naturwissenschaften 85:445–449

Leigh Jr EG (1999) Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, Oxford

Lin N, Michener CD (1972) Evolution and selection in social insects. Q Rev Biol 47:131–159

Maynard Smith J, Szathmáry E (1995) The major transitions in evolution. WH Freeman, New York

McDade LA, Bawa KS, Hespenheide HH, Hartshorn GS (eds) (1994) La Selva: ecology and natural history of a neotropical rain forest. Univ of Chicago Press, Chicago

Michener CD (1964) Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Soc 11:317–342

Michener CD (1974) Social behavior of the bees. Harvard University Press, Cambridge, MA

Michener CD (1990) Reproduction and castes in social halictine Bees. In: Engles W (ed) Social insects: an evolutionary approach to castes and reproduction. Springer, Berlin Heidelberg New York, pp 77–121

Mueller UG (1996) Life history and evolution of the primitively eusocial bee *Augochlorella striata* (Hymenoptera: Halictidae). J Kans Entomol Soc 69 suppl:116–138

Queller DC (1989) The evolution of eusociality: reproductive head starts of workers. Proc Natl Acad Sci USA 86:3224–3226

Queller DC (1994) Extended parental care and the origin of eusociality. Proc R Soc Lond B 256:105–111

Queller DC (1996) The origin and maintenance of eusociality: the advantage of extended parental care. In: Turillazzi S, West-Eberhard MJ (eds) Natural history and evolution of paper wasps. Oxford University Press, Oxford, pp 218–234

Rau P (1933) Jungle bees and wasps of Barro Colorado Island. Von Hoffmann, St Louis

Richards MH, von Wettberg EJ, Rutgers AC (2003) A novel social polymorphism in a primitively eusocial bee. Proc Natl Acad Sci USA 100:7175–7180

Schwarz MP (1994) Female-biased sex ratios in a facultatively social bee and their implications for social evolution. Evolution 48:1684–1697

Schwarz MP, Silberbauer LX, Hurst PS (1997) Intrinsic and extrinsic factors associated with social evolution in allodapine bees. In: Choe JC, Crespi BJ (eds) Social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 333–346

Schwarz MP, Bull NJ, Hogendoorn K (1998) Evolution of sociality in the allodapine bees: a review of sex allocation, ecology, and evolution. Insectes Soc 45:349–368

Shreeves GE, Cant MA, Bolton A, Field J (2003) Insurance-based advantages for subordinate co-foundresses in a temperate paper wasp. Proc R Soc Lond B 270:1617–1622

Smith AR (2005) The social biology of the sweat bee *Megalopta genalis*. Ph.D. dissertation, University of Washington, Seattle WA

Smith AR, WT Wcislo, S O'Donnell (2003) Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). Behav Ecol Sociobiol 54:22–29

Soucy SL, Danforth BN (2002) Phylogeography of the socially polymorphic sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Evolution 56:330–341

Strassmann JE, Queller DC (1989) Ecological determinants of social evolution. In: Breed MD, Page Jr RE (eds) The genetics of social evolution. Westview, Boulder CO

Tibbets EA, Reeve HK (2003) Benefits of foundress associations in the paper wasp *Polistes dominulus*: increased productivity and survival, but no assurance of fitness returns. Behav Ecol 14:510–514

Tierney SM, Schwarz MP, Adams M (1997) Social behaviour in an Australian allodapine bee *Exoneura (Brevineura) xanthoclypeata* (Hymenoptera: Apidae). Aust J Zool 45:385–398

Tierney SM, Cronin AL, Loussert N, Schwarz MP (2000) The biology of *Brevineura froggatti* and phylogenetic conservatism in Australian allodapine bees (Apidae, Allodapini). Insectes Soc 47:96–97

Tierney SM, Schwarz MP, Neville T, Schwarz PM (2002) Sociality in the phylogenetically basal allodapine bee genus *Macrogalea* (Apidae, Xylocopinae): implications for social evolution in the tribe Allodapini. Biol J Linn Soc 76:211–224

Thompson S, Schwarz MP (2006) Sociality and sex allocation in a tropical allodapine bee, *Macrogalea candida*. Biol J Linn Soc 89 (2): 355–364

Warrant EJ, Kelber A, Gislén A, Greiner B, Ribi W, Wcislo W (2004) Nocturnal vision and landmark orientation in a tropical sweat bee. Curr Biol 14:1309–1318

Wcislo WT (1997) Behavioral environments of sweat bees (Halictinae) in relation to variability in social organization. In: Choe JC, Crespi BJ (eds) Social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 316–332

Wcislo WT (2000) Environmental hierarchy, behavioral contexts, and social evolution in insects, pp 49–84 In: Ecologia e comportamento de insetos (RP Martins, TM Lewinsohn and MS Barbeitos, eds) Rio de Janeiro, Brasil (Oecologia Brasiliensis supplement, vol 8)

Wcislo WT, Danforth BN (1997) Secondarily solitary: the evolutionary loss of social behavior. Trends Ecol Evol 12:468–473

Wcislo WT, Arneson L, Roesch K, Gonzalez V, Smith A, Fernandez H (2004) The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitiors and enemies? Biol J Linn Soc 83:377–387

Wcislo WT, Gonzalez VH (2006) Social and ecological contexts of trophallaxis in facultatively social, nocturnal sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae). Insectes Soc 53:220–225

Wenzel JW, Pickering J (1991) Cooperative foraging, productivity, and the central limit theorem. Proc Natl Acad Sci USA 88:36–38

West-Eberhard MJ (1975) The evolution of social behavior by kin selection. Q Rev Biol 50:1–33

West-Eberhard MJ (1978) Polygyny and the evolution of social behavior in wasps. J Kans Entomol Soc 51:832–856