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RESEARCH ARTICLE

Survival and productivity benefits of sociality vary seasonally in the tropical, facultatively eusocial bee *Megalopta genalis*

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Abstract

Tropical habitats are characterized by strong wet and dry seasons, but the effects of seasonality on the costs and benefit of sociality are largely unknown for tropical insects. This is an important gap in our understanding of sociobiology because many social bees and wasps are in the tropics. We found evidence of seasonal effects on the costs and benefits of social and solitary behavior in the tropical sweat bee *Megalopta genalis*. Productivity, whether measured as brood cell production per nest, or brood cell production per female, was greater in the dry season than the wet, likely reflecting floral resource availability. Per nest productivity was greater in social nests than solitary, but this difference was only significant in the dry season. Conversely, per capita productivity was greater in solitary than social nests, but again only in the dry season. Nest failure rates were also higher in the wet season, although roofs protecting nests from rain did not increase survival, suggesting that increased foraging effort in the face of declining resources rather than wetness per se led to nest failure. Newly initiated nests had higher failure rates than established nests, but these were not affected by season. Social nests collected late in the wet season after reproduction has largely ceased show that *M. genalis* can live in social groups without reproduction; these bees are likely waiting together until provisioning resumes in the subsequent dry season. Our results suggest that the productivity benefits of social nesting are greatest in the dry season, but that insurance-based benefits to social nesting may be greater in the wet season. This reveals that the costs and benefits underpinning sociality are dynamic across seasons, even in tropical systems.

Keywords Social evolution · Halictidae · Augochlorini · Tropical seasonality · Ecological constraints

Introduction

Extrinsic environmental factors such as predation, climate, and resource availability influence the costs and benefits of living in social groups, and thus are central to understanding how social nesting with non-reproductive helpers is selected for (Hamilton 1964; Lin and Michener 1972; Hatchwell and Komdeur 2000; Korb and Heinze 2008). The sweat bees (Halictidae) are an especially useful group for comparing the costs and benefits of sociality because they include many species with intraspecific variation in behavior, including some that are facultatively eusocial, which allows direct comparison of the two strategies (Wcislo 1997; Schwarz et al. 2007; Kocher and Paxton 2014).

Studies of environmental variation and its effects on sweat bee sociality typically focus on the length of the brood rearing season in temperate habitats, which is the time when flowers are available to provide nectar and pollen and temperatures are warm enough for immature bee development. One approach is to use populations across latitudinal or altitudinal gradients to reveal the effect of seasonal variation on social behavior. Two general trends have emerged from these gradient studies in temperate sweat bees (Schwarz et al. 2007). First, many facultatively eusocial species are solitary in habitats in which the favorable period is too short

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for both a worker brood and reproductive brood to be reared, but are social in milder climates (lower latitudes and altitudes) in which they can rear multiple broods (Sakagami and Munakata 1972; Eickwort et al. 1996; Wcislo 1997; Schwarz et al. 2007; Field et al. 2010, 2012; Purcell 2011; Kocher et al. 2014; Kocher and Paxton 2014; Davison and Field 2016, 2018). Second, in some eusocial species, longer summers lead to larger worker broods which can no longer be controlled by queens, and thus an increase in worker reproduction (Richards and Packer 1995; Strohm and Bordon-Hauser 2003; Richards 2004; Richards et al. 2005, 2015).

Another approach to studying environmental variation is to study a single population for multiple years to correlate year-to-year variation in weather with productivity, survival, and social outcomes (we use the term 'productivity' to refer to brood production; Sakagami and Hayashida 1968; Richards and Packer 1995; Richards 2004; Packer et al. 1989). Studies of single species across a reproductive season can also yield insights into how parameters like survival, productivity, and group size change over the course of a season (e.g. Michener and Wille 1961; Sakagami 1977; Sakagami and Fukuda 1989). However, for temperate species, it is difficult to disentangle the relatively synchronous developmental effects of colony cycle (all nests begin in the spring or early summer, and group size increases as offspring emerge later) with the environmental changes in resource availability or other parameters that also change seasonally.

In tropical species, the temperature is more stable and can be discounted as a contributing factor in brood rearing seasons (Wolda 1988). Reproduction may be relatively asynchronous (new nests initiated while established nests continue) and occur through most or all of the year (Michener and Seabra 1959; Wcislo et al. 1993). Even in the absence of winter, wet-dry seasonality and fluctuations of floral resource availability can be strong in the tropics (Wolda 1988). For instance, Wille and Orozco (1970) and Eickwort and Eickwort (1971) showed dramatic differences in the social behavior of the sweat bee *Lasioglossum umbripenne* between a dry forest with strong wet-dry seasonality and a moist forest with a less distinct dry season in Costa Rica. However, there are few studies relating the environmental parameters that affect the costs and benefits of sweat bee sociality to seasonal variation in tropical habitats.

Our previous research on the social behavior of the Neotropical sweat bee *Megalopta genalis* suggests that tropical seasonality, either through rainfall destroying nests or through resource availability, might change the survival and productivity parameters that determine the costs and benefits of eusocial and solitary nesting throughout the year. We have previously compared eusocial and solitary nests of *M. genalis* in order to understand the costs and benefits of social and solitary nesting (Smith et al. 2003, 2007, 2009; Wcislo et al. 2004; Kapheim et al. 2013, 2015). Social nests suffer less nest failure than solitary nests because in solitary nests the death of the adult leaves the offspring orphaned and exposed to ant predation, whereas social nests maintain at least one adult to protect the offspring (Smith et al. 2003, 2007; Kapheim et al. 2013), consistent with brood-insurance based models for the evolution of social behavior (Queller 1989, 1994; Gadagkar 1990). Moreover, workers increase colony productivity, generating indirect fitness benefits (Smith et al. 2007). However, these indirect fitness benefits are less than the direct fitness benefits accrued by dispersers, and thus are not sufficient to select for social, rather than solitary nesting. This suggests a role for direct fitness benefits to the queen and maternal manipulation of offspring to stay as workers (Kapheim et al. 2013, 2015). The nature of these benefits, though, may vary depending on the season.

The results of these previous studies are based primarily on data collected during the tropical dry season. At Barro Colorado Island (BCI), Panama, where we have studied *M. genalis,* there is a pronounced dry season from mid-December to mid-April, followed by a wet season for the rest of the year (Leigh 1999). Most ovipositing and brood provisioning in *M. genalis* occurs from December-July, with nests collected later in the year having few provisioned cells or developing offspring (Wcislo et al. 2004). Floral resources on BCI peak in the dry season, decline in the early wet season (mid-April—July), and decline further still in the later, wetter, part of the wet season (August—December) (Wright and Calderon 1995). Smith et al. (2012) showed that brood rearing in *Megalopta* nests tracks the availability of the bees' pollen sources from the dry to early wet season, although they did not distinguish between social and solitary nests, and did not collect nests in the late wet season. Parasitism by a non-lethal cleptoparasitic fly (but not other lethal brood parasites) increases from the dry to early wet season (Smith et al. 2008, 2018), and sex ratio varies seasonally as well (with a peak in male production in the middle of the dry season; Smith et al. 2019). In a collection done in the early wet season across the rainfall gradient of central Panama, which ranges from drier than BCI on the Pacific coast to wetter on the Atlantic coast, *M. genalis* shows variation in productivity, body size, and ovary size—but not variation in social group size or frequency of social groups (Tierney et al. 2013). All of these results show seasonal influence on factors that may affect the costs and benefits of social vs. solitary nesting. This presents an opportunity to evaluate the effect of seasonal conditions on sociality in the tropics.

Here we analyze data from multiple sources collected over several years at BCI, Panama, across wet and dry seasons to test the hypothesis that tropical seasonality influences social strategy in *M. genalis* (Supplementary Information Table 1). Specifically, we investigate seasonal patterns in nest failure and nest productivity, as it relates to social status.

Social groups confer increased protection against nest failure due to brood orphanage in the dry season (assured fitness returns; Smith et al. 2003, 2007). If nest failure is more likely in the wet season, the survival benefits of social nesting may be higher during this period. We tested this prediction by comparing rates of nest failure for established nests in the wet and dry season. We also measured failure rates for newly initiated nests, as this is a crucial parameter for calculating the benefit of reproductive dispersal (which is also the opportunity cost of forgoing dispersal to stay in the natal nest as a worker). If new nest failure rates are high, then the benefit of dispersing to reproduce decreases because many nesting attempts yield no reproductive success. If the benefit of dispersal decreases, then the opportunity cost of forgoing reproduction also decreases. Finally, we experimentally investigated the effect of weather on nest failure by protecting naturally-occurring nests from the rain with artificial roofs. Rain has the potential to cause nest failure by soaking through the dead sticks in which the bees excavate their nests (Wcislo et al. 2004).

We also used several sources of data to investigate seasonal patterns of productivity. Nests collected in the field in both the dry and wet season provided measures of the proportion of nests that are social, the number of females in nests, and the productivity of nests across seasons. We complemented these data with data from observation nests, which allow us to compare wet and dry season productivity while controlling for foundress age and nesting substrate. We used these data to determine how sociality influences productivity across tropical seasons.

Methods

Natural history of *Megalopta genalis*

Megalopta genalis (Halictidae, Augochlorini) construct nests by excavating tunnels into dead sticks that fell from trees and are caught in lianas or the lower branches of trees suspended above the ground (Wcislo et al. 2004). Nests are initiated by single females (not co-foundresses) that are singly mated (Kapheim et al. 2013). Foundress females forage and provision their first brood. In social nests, 1–3 daughters stay in the nest as non-reproductive workers. These workers now assume foraging duties, and the foundress, now a queen, ceases foraging. Subsequent siblings disperse from the natal nest to reproduce. In solitary nests, all offspring disperse from the natal nest to reproduce, and the foundress continues foraging and provisioning new cells. When young reproductives disperse from the natal nest, the queen or solitary reproductive and worker(s), if any, are left behind, so that should not lead to nest failure. Nest sticks are not typically re-used, although we have never systematically observed sticks over multiple seasons to quantify this statement. Foundresses may re-nest if their original nest is destroyed, but we have no observations foundresses otherwise leaving an existing nest to nest elsewhere, although such behavior would be difficult to detect. *Megalopta genalis* forage only in the approximately 90 min before sunrise and after sunset (Wcislo et al. 2004). We collected nests during the day to ensure that all adults were present. *Megalopta genalis* fly year-round based on flight trap data (Wolda and Roubik 1986; Roubik and Wolda 2001).

Survival censuses of field nests

These were 5-week (or longer) censuses of naturally occurring nests in the field to measure rates of nest failure. We located nests for the census by walking through the forest and checking apparently suitable sticks for signs of nesting—a ring of sawdust lining a ~ 4 mm diameter hole in the center of the stick. We did not randomize our search patterns, and our census nests are thus not a random sample of nests in the population. We confirmed an adult female was present in each nest before including it in the census by shining a light into the entrance of the nest. In some censuses, we checked nest status (i.e., whether at least one adult female was still present) at regular intervals during the study period, while in other censuses we simply collected the nests at the end of the study (see Table 1). Nests without at least one adult present at the time of collection were counted as failed, while those with an adult present were counted as

Table 1 Survival censuses of naturally occurring nests in the field used in this study

Year	Season	Start date	Duration, days	Total nests	Surviving nests	Avg. daily rain (mm)
2000	Dry	3 Jan–17 Feb	40	25	21 (22)	0.3
2003	Dry	23 Feb	35	32	26	0.1
2004	Dry	2 Feb–12 Feb	35	30	23	0.9
2001	**Wet**	**18 Apr**	**35**	**48**	**29**	**5.2**
2003	**Wet**	**20 May**	**50**	**36**	**21 (24)**	**8.8**

Dry season censuses are in white, wet season censuses are bolded. For census with duration > 35 days, 35-day survival estimates are listed in parentheses. "Avg. daily rain, mm" lists the average daily rainfall, in mm, recorded at the BCI weather station during the census surviving. In all censuses, we collected all nests at the final day by plugging the entrance with cotton wool, wrapping the nest stick in a plastic bag or mesh insect net bag, and bringing it back to the lab for dissection. In two of our censuses (2000 dry season and 2004 dry season), we included nests as they were discovered, which resulted in a range of starting and ending dates (see Table 1). In the other three censuses, we waited until we found all the nests that we would use before beginning the censuses, which resulted in uniform starting and ending dates (Table 1). All censuses ran for at least 35 days. This is an ecologically relevant time period, as it is approximately the egg-adult development time in *M. genalis* (Wcislo et al. 2004; Kapheim et al. 2013). Some censuses ran longer than 35 days. In order to compare across all censuses, we estimated the number of surviving nests in the censuses that ran longer than 35 days from the slope of the line between the final two data points, which included day 35, and rounded to the nearest whole integer to facilitate statistical comparison (Table 1). The results of the 2001 wet season census and 2003 dry season census were previously reported (Smith et al. 2003, 2007). New nests are initiated throughout the dry and early wet seasons, so there should be no nest-age bias in the censuses. However, foundresses in the dry season were likely born the previous July or August, if not earlier, because reproduction largely ceases during the late wet season (see Results, Social nesting does not affect productivity in the late wet season, below). Foundresses in the wet season may be only a week or two old.

Survival of newly initiated nests

To monitor the success of newly initiated nests, we placed marked sticks without nests in the field and checked them weekly for the presence of a new nest. We first collected sticks that appeared to be suitable nesting substrate, confirmed that they contained no existing nests, and placed them in the freezer (− 20 C) for at least 24 h to ensure that no undetected nests were present. We then placed these sticks in the field and checked them weekly for nesting activity. Nests were monitored and checked weekly for survival as soon as they were discovered. Nests used for the analysis were initiated between 22 March 2008 (dry season) and 14 June 2008 (wet season). This is similar to the use of trap nests used for monitoring cavity-nesting bees and wasps (Staab et al. 2018), except that we did not drill a cavity into the sticks.

Effect of keeping nests dry in the late wet season

To test for the direct effect of rain on nests, we covered some nests with a roof to keep them dry. We randomly assigned nests in the field to either treatment or control categories. A roof made of plastic approximately 15 cm wide and folded to a peak in the middle running the length of the stick and extending at least 3 cm beyond the entrance and rear end of the stick, was hung from surrounding branches over the nest stick in its natural location. We attached the stick to the roof with metal wire (see Supplementary Information Fig. 1 for a diagram). To control for effects of handling, we attached control nests to surrounding branches with metal wire in their natural locations as well, but without the roof. We included 42 nests in the study in 2006 beginning between 27 July and 13 August. We included 45 nests in the study in 2007, beginning between 5 July and 9 July. All nests were confirmed to have at least one live female at the beginning of the study. Nests were collected 48 days after the beginning of the experiment.

General collections for productivity calculations

We collected nests in the field in the dry and early wet seasons of 2007 ($N = 118$, collected 3 February to 4 July), 2008 ($N = 133$, collected 2 January to 27 April), and 2009 ($N = 328$, collected 14 January to 6 May). We brought nests back to the lab where we opened them to record the number of brood cells, the number of empty brood cells, and the number of adult females in each nest. We report overall productivity for each nest, as it is relevant to the direct fitness of queens and solitary reproductives, and also per-capita productivity as an estimate of the effects of workers on reproductive output.

Late wet season collections to study social nesting when provisioning has largely stopped

We collected nests in the late wet season when little reproduction occurs (Wcislo et al. 2004). The late wet season females include the surviving nests from the roof experiments (see “effect of keeping nests dry in the late wet season”, above), which were collected 13—30 September 2006, and 22—26 August 2007, as well as 27 additional nests collected 17–29 November 2009. We measured the ovary development of females in these nests by removing the tergites to view the ovaries dorsally through a dissecting microscope. We assigned each ovary a rating of 1–5 following Michener and Wille (1961). Ratings of 3–5 were considered “developed”, as these indicated at least one developing oocyte nearing completion. For the November 2009 collections, we also examined the spermetheca for presence or absence of sperm to determine matedness. The presence of sperm in the spermetheca shows that the female has mated. Ovary samples were lost for bees from 8 nests, and in one female from the November 2009 collection we could not find the spermetheca, thus sample sizes for these data are less than the nest collection total.

Observation nests

We use provisioning data from standardized observation nests to measure the effect of seasonality on productivity. These were the nests used by Kapheim et al. (2013). We made observation nests by placing balsa wood with a predrilled tunnel between two panes of plexiglas and placing the nest in the field with a newly emerged female reared from collected natural nests (see above) in order to observe in-nest behavior; see Kapheim et al. (2013) for details. We report the number of brood cells provisioned within 35 days of the first observation of an open cell as a measure of first-brood, pre-offspring emergence, productivity; 35 days is the approximate egg-adult development time of *M. genalis* (Wcislo et al. 2004; Kapheim et al. 2013). Because foundresses often took many days to provision their first cell (Kapheim et al. 2013), first brood provisioning often continued beyond 35 days. We use 35 days as a conservative measure, and to have a standardized period for comparing productivity across nests and seasons. Nests were censused every three or four days. Censuses recorded the presence of new, open cells, and when these cells were closed, signaling the end of provisioning. We report data from 229 observation nests: 51 nests initiated in 2007 (first open cell observations between 15 February and 6 May), 73 nests initiated in 2008 (first open cell observations between 9 February and 19 May), and 105 nests in 2009 (first open cell observations between 3 February and 14 May).

Statistical analyses

For the censuses of natural nest survival, we used a stepwise binary logistic regression to analyze the effect of census, season (wet or dry), and rainfall on nest failure to 35 days. For rainfall, we used the mm of rain measured at the BCI lab clearing during the days of the census by the Physical Monitoring Program of the Smithsonian Tropical Research Institute. We also used a binary logistic regression to test for an effect of season on the failure of newly initiated nests, but in this case season was treated as a continuous variable (days since 1 Jan) because nests were initiated throughout the year. We used Kaplan–Meier survival analysis to test whether the survival rate measured by the new nest census was significantly different from the other censuses. We used generalized linear mixed models (GLMM) to analyze the effect of season (days since 1 Jan) on number of adults per nest and productivity (brood cells per nest), while including sample year as a random effect. When comparing social and solitary nests, we also included social status as a fixed effect. To analyze the effect of seasonality on whether nests were solitary or social (a binary response variable) we used a binary logistic regression model in the GLMM. For other analyses, we used a linear regression model. For our analysis of the effect of season on the number of females in social nests, we used a regression including days since 1 Jan and a quadratic term in the model because the distribution of the data suggested a curvilinear relationship between date and number of females. For comparing groups in the late wet season collections and roof nest experiment, we used non-parametric statistics because data were not normally distributed. All statistics were performed in SPSS.

Results

Social status does not depend on season, but group size does

Most nests from 2007, 2008, and 2009 dry season and early wet season had one female at the time of collection, although some of these nests would likely have become social if not collected (75%, mean group size = 1.43 ± 0.92, median = 1), and most social nests (58%) contained two females (mean social group size = 2.71 ± 1.07, median = 2, maximum = 7; Fig. 1a). We did not find a significant effect of season or year (a random effect) on whether or not a nest was occupied by more than one female (season $F_{1,789} = 1.87$, $p = 0.17$, year $Z = 0.33$, $p = 0.74$; Fig. 1b). Among social nests, group size increased through April, and then decreased later in the season (regression with quadratic term full model $r^2 = 0.10$, $p < 0.001$, Fig. 2).

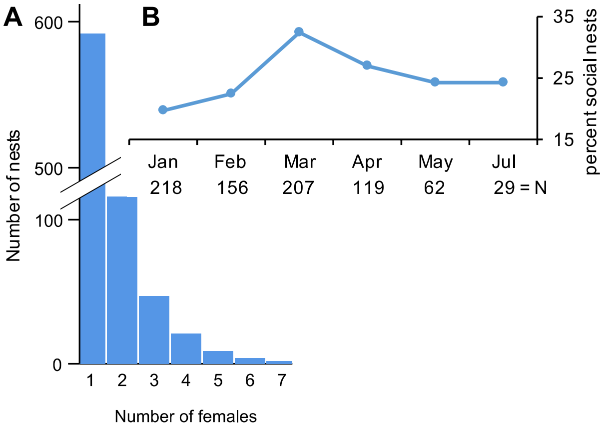

Fig. 1 **a** Most nests were solitary, and most social nests had two females. Note the break in the vertical axis. $N = 791$ nests. **b** Percent of all collected nests that were social by month for 2007–2009 combined. Note that no nests were collected in June. Monthly sample sizes are listed below each month in (**b**), the wet season begins approximately 15 April

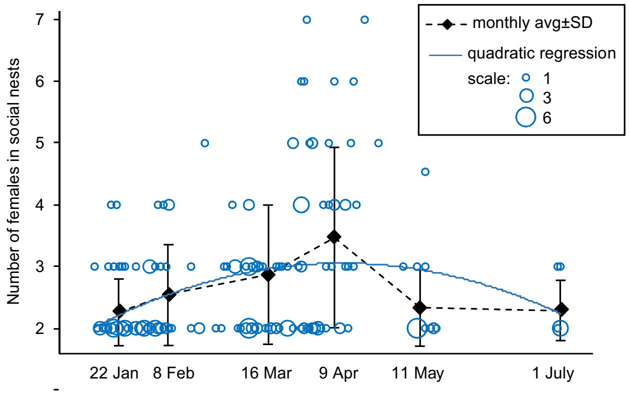

Fig. 2 Number of females in social nests by date, 2007–2009. Open blue circles represent each nest, and overlapping data points are represented by larger circles, scaled for the number of nests at that point (see scale). The filled diamonds show mean ± SD for each month, plotted at the average date for each month's collections. The wet season begins approximately 15 April. $N = 199$ social nests (colour figure online)

Nest failure is higher in the wet season

The wet season censuses showed more nest failure than the dry season censuses (Fig. 3). 2003 was the only year for which we have both wet and dry season data, but the data from other years is consistent with this trend. In a stepwise binary logistic regression analyzing nest survival that included season (wet/dry), census, and rainfall, only season was included in the final model ($p = 0.008$). After season was included, neither census ($p = 0.81$) nor rainfall ($p = 0.66$) were significant. The overall 35-day survival rate for all nests included in Table 1 and Fig. 3 is 72.5%; wet season survival rate was 63.1%, dry season survival was 81.6%.

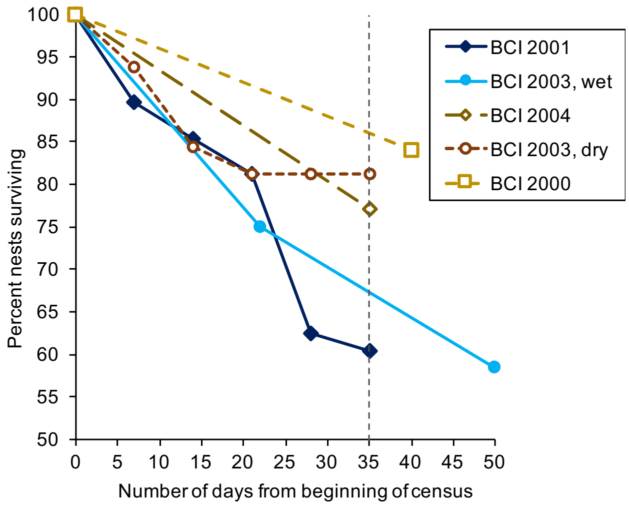

Fig. 3 Percent survival of naturally occurring nests on BCI. Dry season censuses are shown in dashed brown lines with open markers, wet season censuses are shown in solid blue lines with closed markers. The dashed reference line shows survival at 35 days. See Table 1 for details of each census (colour figure online)

Newly initiated nests have high failure rates in both wet and dry seasons

Newly initiated nests ($N = 44$) showed high failure rates in the first weeks after initiation, with 45.2% (20/44) surviving for 35 days (Fig. 4). There was no effect of season, measured as initiation date, on the probability to survive to 35 days (binary logistic regression $p = 0.15$), although our census only spanned the end of the dry season and beginning of the wet season. The nest failure rate was higher than in our other censuses of established nests (Kaplan–Meier survival analysis log-rank pairwise comparisons $p < 0.05$ for all other census, except 2001 wet season, $p = 0.08$). The 35 day survival of newly-initiated nests is also significantly lower than the pre-emergence foundress survival observed in *M. genalis* observation nests during the dry seasons of 2008 and 2009, which are the only other data we have monitoring newly initiated nest failure rates (113/180, $\chi^2 = 4.40$, $p = 0.04$) (Kapheim et al. 2015).

Keeping nests dry during the wet season does not improve survival or productivity

The nests protected under a roof were dry upon collection, while both the inside and outside of the control nests were

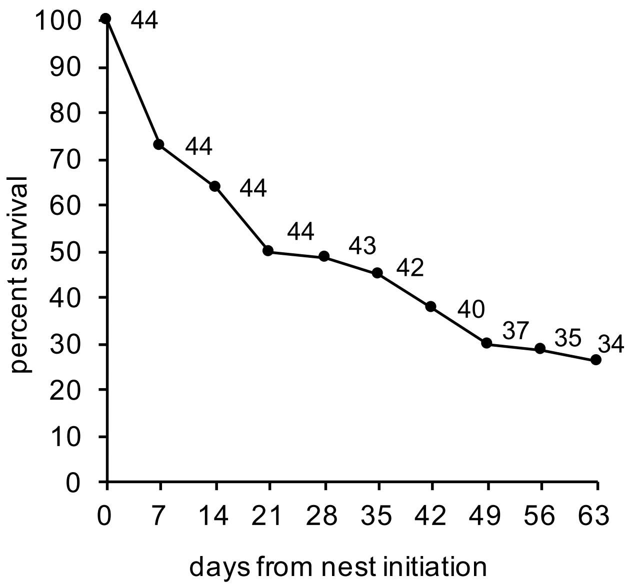

Fig. 4 Weekly survival of newly initiated nests. There were 44 nests included in the study, but some nests were initiated < 63 days before collection. Weekly percentages were calculated based on the maximum number of nests (shown at each point) that could have survived that long

wet. However, there was no effect of experimentally keeping nests dry in the late wet season (roof treatment) on nest failure, nor was there a difference between the two years of the study in nest failure (binary logistic regression effect of treatment $p = 0.97$; year $p = 0.25$). Overall, 23 of 43 (53%) treatment nests survived and 24 of 44 (55%) control nests survived. In 2006, 20 of 42 nests survived (48%), and in 2007, 27 of 45 nests survived (60%). For comparison with the censuses in Fig. 3, 35-day estimates of survival are 61.8% for 2006 and 70.8% for 2007, similar to the other wet season survival censuses. Most surviving nests (40 of 47) had no brood cells. There was no effect of treatment on productivity, measured as brood cells (treatment mean ± SD = 0.35 ± 0.74, control = 0.17 ± 0.64, Mann–Whitney $U = 312$, $p = 0.22$). Nearly half the surviving nests contained multiple females at collection (23 of 47), but there was no effect of treatment on number of females (treatment mean = 1.91 ± 1.00, control = 1.67 ± 1.13, Mann–Whitney $U = 326.5$, $p = 0.24$) or likelihood of being social ($\chi^2 = 1.04$, $p = 0.31$), suggesting that emerging females did not use the moisture level of the nest as a cue for staying or leaving. See "*Social nesting without reproduction*", below, for comparisons of social and solitary reproduction in these nests.

Productivity benefits of sociality are higher in the dry season

Productivity, measured as the number cells with developing brood, was generally high for nests collected in the dry season, and lower in the early wet season. Social nests were more productive than solitary nests, and there was no effect of year (GLMM social status $F_{1,788} = 210.20$, $p < 0.001$, season $F_{1,788} = 68.43$, $p < 0.001$, year $Z = 0.90$, $p = 0.37$; Supplementary Information Fig. 2). Overall, solitary nests averaged 3.08 ± 2.08, and social nests 5.59 ± 2.86, brood cells; maximum = 13 for both groups. However, the productivity advantage of social nests was present only in the dry season: social nests did not have more brood cells than solitary nests in the wet season. When analyzed by month, social-solitary pairwise comparisons were significant January—April (all Bonferroni corrected p values < 0.001) but not for May ($p = 0.12$) or July ($p = 0.84$; Fig. 5a). Per capita productivity also declined from the dry to wet season, and solitary nests had higher per capita productivity than social nests (GLMM social status $F_{1,788} = 33.23$, $p < 0.001$, season $F_{1,788} = 89.39$, $p < 0.001$, year $Z = 0.90$, $p = 0.37$; Supplementary Information Fig. 2). Average per capita productivity for solitary nests is equal to total productivity listed above. Social nests averaged 2.17 ± 1.10 brood cells per female; the maximum was 5.0. However, like absolute productivity, the difference between solitary and social nest per capita was strongest in the dry season. When analyzed by month, pairwise comparisons show significant differences in per capita productivity between social and solitary nests for January—March (Bonferroni corrected pairwise comparison $p \leq 0.002$ for each month) and May ($p = 0.04$) but not April ($p = 0.76$) or July ($p = 0.14$; Fig. 5b).

Analysis of productivity by female number (treated as a categorical variable) shows that nests with more females had higher productivity. Because only 15 nests (1.9%, see Fig. 1) contained more than four females, we grouped together all nests with > 3 females. We found a significant effect of group size ($F_{3,787} = 83.99$, $p < 0.001$) and no effect of year ($Z = 0.75$, $p = 0.45$) on the number of brood cells.

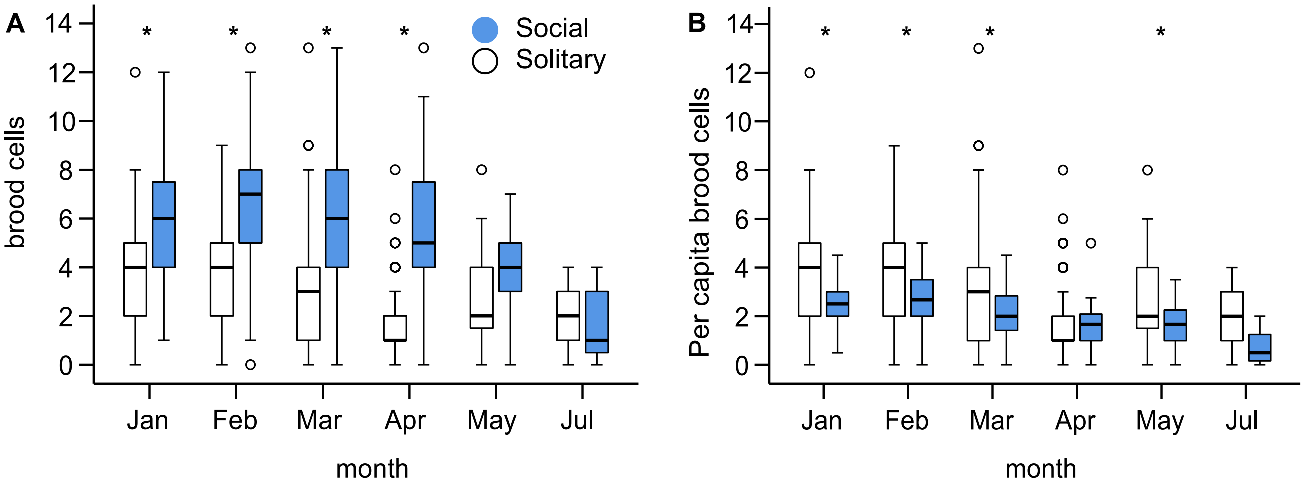

Fig. 5 Productivity by month. Social nests (blue filled boxes) have more brood cells than solitary nests (open boxes) during the dry season (Jan–April, asterisks (*) indicates significant posthoc pairwise comparisons for that month). Note that the solitary (open) boxes are the same in each panel. Upper and lower bounds of boxes are one interquartile range (IQR) above and below the median. Whiskers represent data within 1.5(IQR), and open circles are points > 1.5(IQR) from the median. $N = 791$ nests (colour figure online)

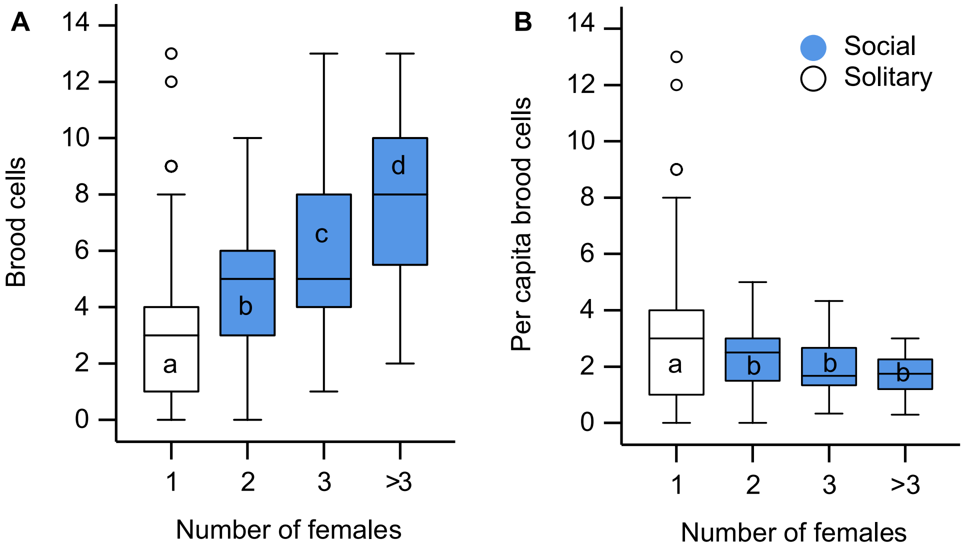

Fig. 6 Productivity **a** increased as group size increased, but per capita productivity **b** decreased. Social nests are blue-filled boxes and solitary nests are open boxes. Boxes with different letters significantly differed in posthoc pairwise comparisons. Note that the solitary (open) boxes are the same in each panel. Upper and lower bounds of boxes are one interquartile range (IQR) above and below the median. Whiskers represent data within 1.5(IQR), and open circles are points > 1.5(IQR) from the median. $N = 791$ nests (colour figure online)

Pairwise comparisons showed a significant increase in the number of brood cells with each additional female (all Bonferroni corrected p values < 0.005; Fig. 6a). Per capita productivity, however, showed the opposite trend, as solitary females had higher per capita productivity than social groups ($F_{3,787} = 12.78$, $p < 0.001$; there was no effect of year, $Z = 0.60$, $p = 0.55$). Pairwise comparisons showed that solitary females had greater per capita productivity than all other group sizes (all Bonferonni corrected p values ≤ 0.001), but that increasing group size beyond two females had no effect on per capita productivity (all p values > 0.05; Fig. 6b).

Productivity is lower in observation nests in the wet season

Nest productivity of single females in standardized observation nests, measured as the number of cells provisioned and closed within 35 days of the first observation of an open cell, declined from the dry into the wet season (date $F_{1,227} = 36.35$, $p < 0.001$; Fig. 7); there was no effect of year on productivity ($Z = 0.59$, $p = 0.56$).

Social nesting in the late wet season does not affect productivity

Nests collected in the late wet season (September 2006, September–October 2007, both from the roof experiment, and November 2009) showed that *Megalopta* still nest in social groups even when there can be no effect on productivity because reproduction is not occurring. Of the nests from these three collections, 43% had more than one female in the nest, and most of both the social (78%) and solitary (74%) nests did not have provisioned brood cells, meaning that all the cells in that nest were empty

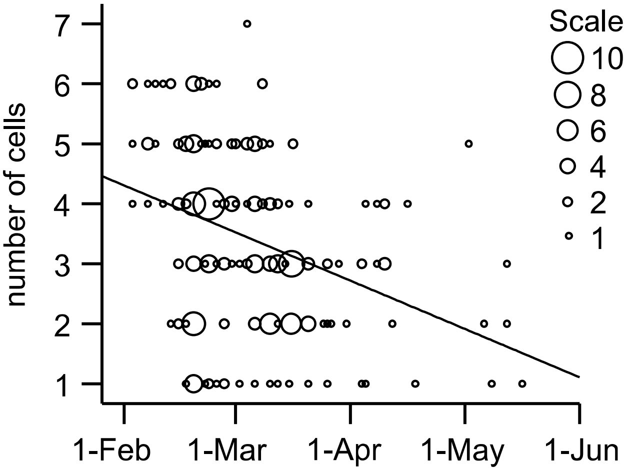

Fig. 7 Productivity in the first 35 days of provisioning in observation nests, 2007–2009. The vertical axis shows the number of offspring brood cells provisioned and closed within 35 days of the first observation of an open cell in the nest. The horizontal axis shows the date of first open cell for each nest. Larger marker sizes indicate overlapping data points, see legend for scale. The trendline is fitted values from a linear regression. The wet season begins approximately 15 April. $N = 229$ observation nests

Table 2 Number of social and solitary nests collected late in the wet season (August–November) with and without provisioned brood cells

	Nests	Social		Solitary	
		Brood	No brood	Brood	No brood
September 2006	20	2	10	0	8
September–October 2007	27	0	12	5	10
November 2009	27	5	3	6	13
Total	74	7	25	11	31

(Table 2, Supplementary Information Fig. 3). Social nests were not more likely than solitary nests to have provisioned brood ($\chi^2 = 0.18$, $p = 0.67$). The average number of provisioned cells per nest was 0.32 ± 0.64. The average number of brood cells in nests with provisioned brood was 1.33 ± 0.59. There was no correlation between the number of females and the number of provisioned cells ($N = 74$, rho = 0.19, $p = 0.11$), but there was a strong correlation between number of females and total cells (total cells include both empty and provisioned cells; $N = 74$, rho = 0.61, $p < 0.001$; Supplementary Information Fig. 3), suggesting that females that emerged into the nests remained there, but that further provisioning largely ceased and the empty cells from which they emerged were not re-provisioned. The few provisioned cells collected in each sample spanned the range from open with an incomplete pollen mass to pupae.

Ovary maturation, measured as the average of ratings for each ovary of the individual with the most developed ovaries in each nest (hereafter, "rank 1 female") differed between the three late-wet season samples (Kruskal–Wallis test = 7.91, $N = 67$, $p = 0.02$, 2006 = 2.06 ± 1.04, 2007 = 2.63 ± 1.11, 2009 = 3.17 ± 1.40). Pairwise comparisons showed that 2009 ovaries were larger than 2006 ovaries ($p = 0.02$); no other comparisons were significant. Of the 67 late wet season nests for which we have ovary measurements, 42 (63%) contained at least one individual with developed ovaries (2006: 8/17 with developed ovaries, 2007: 16/23, 2009: 18/27). The rank 1 females in social nests had larger ovaries than the females in solitary nests, showing a social effect on ovary development (Mann–Whitney $U = 717.5$, $N = 67$, $p = 0.04$; solitary mean = 2.40 ± 1.25, social mean = 3.05 ± 1.25). Rank 1 females in nests with brood had larger ovaries than rank one females in nests without brood, showing an effect of reproductive activity on ovary development (Mann–Whitney $U = 624.5$, $N = 66$, $p = 0.001$; no brood mean = 2.44 ± 1.85, brood mean = 3.63 ± 1.15). Nests with brood were more likely to have a female with developed ovaries (14/16 nests) than were nests without brood (28/50 nests; $\chi^2 = 5.20$, $p = 0.02$). Of the 47 females who were not rank 1 (from the 36 social nests), only two, each from a different nest, had developed ovaries, suggesting that dominant females suppress ovary development of subordinates even when not reproductively active.

For the November 2009 collections, we also recorded matedness. One solitary nest contained an unmated female with undeveloped ovaries. The rank 1 female in the other 25 nests for which we have data was mated, showing that lack of reproduction did not result from lack of mating. No nests contained more than one mated female.

Discussion

While the costs and benefits of sociality have long been rooted in ecological constraints, studies of how seasonality influences these tradeoffs have primarily focused on temperate species. However, differences in food availability and habitat availability that accompany the tropical wet and dry seasons are also likely to influence the costs and benefits of social nesting. We tested this hypothesis by analyzing composite nesting data from *M. genalis*, a tropical sweat bee that can nest in eusocial groups or alone. We find that nest failure is higher in the wet season, but that this may not be the direct result of nest destruction due to increased rainfall. Our data are consistent with the hypothesis that increased nest failure is a result of the increased foraging effort required to provision brood cells with decreased resource availability. If foragers have to exert more time and energy foraging due to a decline in resources, they would be more likely to die. However, data on foraging trip number and duration, similar to Richards (2004) are required to test this hypothesis. We also find that nest initiation is a particularly risky phase of the *M. genalis* life cycle, independent of season. Together, these results suggest that established nests are vulnerable to failure due to forager loss and seasonal variation in resource availability, rather than increases in precipitation per se, but that seasonal factors are not likely to be a major influence on nest survival in the earliest stages of nest founding. If increased nest failure during the rainy season is due to premature death due to the increased foraging effort, then survival benefits should be an important driver of social nesting in the early wet season, because additional females would be available to take over nest defense and brood rearing.

Seasonal differences are also apparent in productivity, where the differences in productivity between social and solitary nests are most pronounced in the dry season. Productivity is significantly reduced in the wet season, for both social and solitary nests. Our study thus reveals that *M. genalis* sociality may be driven by productivity benefits in the dry season and survival benefits in the early wet season. This demonstrates that seasonal variation in the costs and benefits of sociality are likely to be important factors in the tropics, and warrant further investigation.

Nest failure and seasonality

We previously showed that nest failure rates were higher for solitary than social nests, likely because when solitary foundresses died, ants consumed the orphaned brood, whereas brood in social nests was not orphaned if a forager died (Smith et al. 2003, 2007). Thus, if the increased nest failure rate in the wet season is due to higher rates of individual mortality, having more than one female in a nest during this time can act as an insurance policy to protect developing brood. These benefits are likely to diminish as the wet season progresses, however, because we observed a near halt to reproductive activity in the late wet season (Table 2, Supplementary Information Fig. 3, see also Wcislo et al. 2004). We know of no sweat bee study documenting seasonal effects on nest failure for nests of similar developmental stages (rather than, for instance, spring foundresses vs. summer social nests, e.g. Sakagami 1977), especially in a tropical habitat where nesting is not seasonally synchronized.

We hypothesize that the increased nest failure rates seen in the wet season are a result of increased adult mortality which results from increased foraging effort due to decreased resources. Productivity is lower in the wet season, which is also when less pollen is available (Smith et al. 2012). Foraging is dangerous (e.g. Wille and Orozco 1970; Packer 1986; Kukuk et al. 1998). In the temperate sweat bee *Halictus ligatus*, foundresses compensated for poor resource availability by increasing foraging effort (Richards 2004). If *M. genalis* similarly increase foraging effort, it may lead to increased mortality and resulting in nest failure. An alternative hypothesis is that bees do not adjust their foraging effort, and the reduced productivity reflects the diminishing returns for similar effort due to reduced resources.

Nest failure of newly initiated nests

The census of newly initiated nests shows that nest failure rates are higher for newly initiated nests than for established nests. The drop was especially steep in the first week, during which approximately one-quarter of newly initiated nests failed. We do not know if this represents foundress death or abandonment of the nest site. Also, we do not know how difficult it is for dispersing females to locate a suitable stick in which to initiate a nest after they disperse from their natal nest; our methods only allowed us to observe them once they begin nesting. Slightly fewer than half (45.5%) of nests monitored from initiation survived until 35 days when worker brood would first be expected to emerge (Fig. 4). However, given that cell provisioning takes about 6 days (Kapheim et al. 2013), a more realistic, but still conservative, the estimate for survival would be the 42-day result of 37.5% survival to brood emergence. Both estimates are lower than the survival rate of foundress females during the time until their first offspring emerge as adults (63%) for newly-emerged foundresses placed into observation nests in the field in 2008 and 2009 (Kapheim et al. 2015). This may be because the observation nests were initiated earlier in the dry season than the nests in this study (22 January—6 March, vs. 22 March—14 June; Kapheim et al. 2013), in which case there is a seasonal effect on new nest mortality that our data here could not detect. It might also occur if some of the 'mortality' observed in this study is actually nest abandonment and if females are less likely to abandon the observation nests, which are protected with a roof and hard sides than natural sticks. The newly initiated nest survival rate is also lower than the survival rate of 61.5% for solitary reproductives in established nests that we monitored in a previous study (Smith et al. 2007). Also, the newly initiated nest survival rate was lower than all but one of our individual censuses of established nests, and well below the overall 35-day survival rate of 72.5% from these censuses (Fig. 3). Together, these data suggest that the benefit of dispersing to reproduce directly, rather than staying in the natal nest to accrue indirect fitness as a worker, may be less than we previously estimated due to higher foundress attrition (Kapheim et al. 2015).

The survival rate we measured for newly initiated nests of *M. genalis* is within the range of newly initiated nest survival rates for other sweat bees. It is higher than the solitary foundress nest survival rate of *L. duplex* in Japan, in which 25% of nests initiated by solitary females in the spring survived to worker emergence, whereas 61–75% of nests that survived to worker emergence (summer) produced reproductives (Sakagami 1977; Sakagami and Fukuda 1989). *Megalopta genalis* new nest survival is similar to that of the tropical dry forest halictid *Lasioglossum umbripenne* (40%; Wille and Orozco 1970), but lower than that of the temperate halictid *Augochlorella aurata* in New York, 61.4% (Mueller 1996; the survival rate increased to 77.9% after worker emergence) or *Halictus ligatus* in Victoria, Ontario, 60.6% (Richards and Packer 1995; the survival rate increased to 93.5% after worker emergence, data from 1990 and 1991 nests). Additional studies of other halictids, as well as allodapine bees, show that nest failure rates fall dramatically with the addition of a second bee; the impact of additional workers is less clear (halictids: Yagi and Hasegawa 2011; Brand and Chapuisat 2014; allodapines: Schwarz et al. 1998; Hogendoorn and Zammit 2001; Zammit et al. 2008). In all of these studies, though, nest initiation and development are seasonally synchronized, so colony growth from solitary foundress to social post-emergence nest occurs along with seasonal changes. Our results from a tropical sweat bee reveal that nest initiation is a riskier stage of the nesting cycle, independent of seasonal variation.

Seasonal patterns in nesting

Our collections suggest that even though nests may be initiated throughout the reproductive season (Wcislo et al. 2004), there are still seasonal patterns in *M. genalis* nest initiation. Many nests are initiated in January, at the beginning of the dry season, and there is a second wave of new nesting in late April and May. The number of females in social groups peaks in April before declining into the wet season (Fig. 1), which suggests that many nests in January are newly initiated social nests into which workers have not yet emerged. The peak of mean group size, which coincides with the peak of overall productivity, at the end of the dry season suggests that some of the adult females in collected nests are recently emerged reproductive offspring waiting to disperse, rather than resident workers. In observation nests, newly emerged reproductives (both males and females) remain in their natal nest for about a week before dispersing (Wcislo and Gonzalez 2006; Kapheim et al. 2013). The drop in both the proportion of social nests and mean group size from April to May suggests that many newly emerged young reproductive females leave their natal nests at this time. Fewer newly emerged reproductive offspring in established nests, and more single female nests recently established by these dispersing reproductive offspring would cause both the proportion social and mean group size measures to decrease. Note that in Fig. 2 the two months that deviate from the regression line are April, which is well above the line, and May, which is well below, which is consistent with a wave of new foundresses emerging into their natal nests in April and then dispersing to initiate new nests in May.

Seasonal patterns in productivity

Our results suggest that seasonal patterns of productivity are driven by seasonal variation in resource availability. The number of brood cells is highest in the dry season and declines in the early wet season, before falling almost to zero in the late wet season. This pattern is apparent both in natural nests collected from the field and also observation nests controlling for nest quality and development time. *Megalopta genalis* productivity tracks the availability of their preferred pollen sources, which also are most abundant in the dry season and decline through the wet season (Smith et al. 2012).

This increased productivity (but not per capita productivity) in the dry season is particularly apparent for social nests. Our previous work showed that social nests were more productive than solitary nests, but these studies were limited to cell provisioning that occurred during the dry season (Smith et al. 2007, 2009; Kapheim et al. 2013). Here we show that social nests are more productive than solitary nests in the dry season, but not in the early wet season, although our study also contains many more nests collected in the dry than the early wet season. This suggests that the indirect fitness benefits associated with increased reproductive output in social nests (Smith et al. 2007) are seasonally dependent. Nevertheless, social nesting occurs in both seasons, as also found in a previous study (Fig. 1, Wcislo et al. 2004). Even during the early wet season when social nesting confers no apparent productivity advantage, the behavior continues (Supplementary Information Fig. 2, Fig. 5). This suggests that survival benefits drive sociality in the early wet season, but that increased productivity may favor social behavior in the dry season.

Per-capita productivity also decreased from the dry to wet season. Wcislo and Gonzalez (2006) showed that in nests with more than one worker, the youngest workers forage proportionally less as group size increases, which is consistent with a decline in per-capita productivity in large groups. Solitary nests had consistently higher per-capita productivity, however, these results should be taken with caution for two reasons. First, our field collections only include successful nests (those that were active at collection). Smith et al. (2007) showed that when higher rates of nest failure in solitary nests were taken into account, per capita productivity rates were similar in social and solitary *M. genalis* in a dry season collection. Because nest collections cannot include nests that failed prior to collection, they provide a biased estimate of per capita productivity if survival probability differs across group sizes (Clouse 2001; Smith et al. 2007; Brand and Chapuisat 2014). Studies of *M. genalis* in observation nests show that new foundresses pursuing a solitary or social nesting strategy are equally vulnerable to mortality before offspring emergence (Kapheim et al. 2013), but that social nests have lower nest failure rates post-emergence because at least one female remains if either the queen or forager die (Kapheim et al. 2015). Second, some of the females in social nests, especially those in the relatively large groups, were likely dispersing reproductives, which wait in their natal nest for about a week before dispersing (Kapheim et al. 2013), and should thus be counted as part of the reproductive brood rather than the adult workforce. Nevertheless, our previous studies of observation nests suggest that even with a careful accounting of per-capita productivity, solitary nesting females gain more fitness through direct reproduction than worker females do through indirect fitness (Kapheim et al. 2015). This suggests social nesting results from direct fitness benefits to the queen, as well as indirect benefits to the workers.

In summary, while the survival benefits of sociality may be stronger in the early wet season than in the dry season, the opposite appears to be true for productivity: the productivity benefits of social nesting are high in the dry season, perhaps higher than we measured depending on the interpretation of the per capita productivity data. However, our data did not show productivity benefits to social nesting in the early wet season.

Social nesting without reproduction in the late wet season

Our collections of nests in the late wet season (September–November) show that reproduction largely ceases during this time, but many bees nevertheless still live in social groups; Wcislo et al. (2004) showed a similar pattern. Bees were not inactive: some nests had provisioned cells, immature brood, and at least one female with developed ovaries, suggesting that they can reproduce opportunistically when resources are available. There was no synchrony among the few reproductively active nests in each sample, which suggests that nests were not responding to a widespread floral bloom in the late wet season. Social nests were not more or less likely to be reproductive than solitary nests, and there was no correlation between group size and productivity. We do not know if it is more difficult for bees to initiate nests in the wet substrate, and if so, how this affects late wet season nesting behavior. Some of our late wet season nests were placed under roofs, which may have affected bees' behavior, but our comparisons showed no significant differences between the roof nests and control nests.

Given the lack of brood rearing opportunity in the late wet season, it appears that there were no survival or productivity benefits to group nesting during the late wet season, as there were no brood to protect or produce. However, the cost to remaining in the natal nest—foregoing the opportunity to disperse and reproduce directly—was also apparently absent in the late wet season. This is in direct contrast to the results in the dry and early wet seasons when nearly all nests contained brood. We do not know how many of these females eventually disperse at the beginning of the subsequent dry season when there are again ample resources and reproductive opportunity. Given that some social nests are collected early in the dry season, often with improbably large numbers of offspring for a recently initiated nest (e.g. Supplementary Information Fig. 2), we suspect that at least some groups continue intact into the dry season, but we do not know how common this is. Tropical and subtropical sweat bees may pass the season that is unfavorable for reproduction with social groups intact and reproduction reduced, but not in a state of diapause (Michener and Lange 1958a, b, 1959; Michener and Seabra 1959; Eickwort and Eickwort 1971; Wcislo et al. 1993). In temperate zone halictid species, reproductives that initiate nests in cofoundress groups often show dramatically higher productivity than solitary foundresses (Packer 1993). While *M. genalis* groups passing the end of the tropical wet season together are not directly analogous to temperate cofoundresses emerging from winter diapause, the productivity benefits from 'starting' with a worker or workers in the dry season may be substantial given the positive relationship between group size and productivity (Figs. 5, 6, Supplementary Information Fig. 2 of this study; Smith et al. 2007). We hypothesize that *M. genalis* that begin the dry season already in a social group will have significantly higher productivity than newly initiated nests during this resource-rich period. This raises the intriguing possibility that the costs and benefits of social groups in June and July may be influenced by the potential for a larger payoff at the beginning of the subsequent dry season when resources are abundant.

Conclusions

Seasonal variation affects parameters of social costs and benefits through variation in resource availability, even in a tropical species. Our data suggest a three-part season to *M. genalis* productivity: first, high in the dry season, when resources are abundant, followed by lower productivity in the early wet season, when resource availability decreases, and lastly almost no productivity in the late wet season when floral resources are scarce. The ecological costs and benefits of helping are different in each of these three periods. In the dry season, workers increase productivity and reduce nest failure. In the early wet season resource scarcity apparently limits the productivity benefits of helpers, but survival benefits may promote sociality because overall nest failure rates are higher than in the dry season. In the late wet season, there is no evidence that additional females are workers at all, but some may be workers-in-waiting (and others dispersers-in-waiting) for when the subsequent dry season arrives.

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