

Effects of social organization and resource availability on brood parasitism in the facultatively social nocturnal bee *Megalopta genalis*

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Abstract Understanding the ecological benefits that may select for the evolution of living in groups rather than solitarily is key to understanding the evolution of social cooperation. Defense against natural enemies, such as parasites and predators, is generally acknowledged to be such a benefit, but most studies focus only on predators. Among the bees, parasitism is a major source of brood mortality. Here we use the nocturnal, Neotropical, facultatively social bee *Megalopta genalis* (Halictidae) to directly compare parasitism rates between social and solitary nests at the same site during times of high and low resource availability. We focus on four parasites: one that eats some pollen but does not kill host offspring [the fly *Fiebrigella* sp (Chloropidae)] and three that kill host offspring (the beetle *Macrosiagon gracilis* (Rhipiphoridae), the wasp *Lophostigma cincta* (Mutillidae), and the congeneric bee *M. Noctoraptor byroni*). We found no difference in parasitism between social and solitary nests for the four parasites tested. Across all nests, 25–31% of brood cells were parasitized by *Lophostigma* sp., with parasitism

increasing from the dry to wet season, although this seasonal effect was significant only for social nests. Only ~4% of brood cells were parasitized by one of the other three parasites, and *M. byroni* was only found in social host nests. Our data reveal that *Megalopta* have low rates of parasitism overall, and that this is not a function of social organization or resource availability. Limited nocturnal foraging time and foraging offset from the activity patterns of diurnal parasites may instead play a larger role in keeping parasitism rates low.

Keywords Brood parasitism · Parasitoid · Cleptoparasitism · Social evolution

Introduction

Enhanced defense against natural enemies—parasites and predators—may be one of the ecological benefits that select for the evolution of cooperative social groups in animals (Lin and Michener 1972). Among the nest-making Hymenoptera (bees, wasps and ants) social groups can always leave a guard at the nest, but solitary nests must be left unattended during foraging, potentially leaving them more exposed to natural enemies (Wcislo and Fewell 2017). Facultatively social species nest either in groups or alone, and are thus powerful study organisms for directly testing the ecological costs and benefits of social and solitary nesting (Smith et al. 2003; Wcislo 1997; Schwarz et al. 2007). Previous studies used facultatively social bees to demonstrate increased defense of offspring against predators as a benefit of social nesting (Smith et al. 2003; 2007; Kukuk et al. 1998; Hogendoorn and Zammit 2001; Schwarz et al. 1997). However, the effect of social cooperation on defense against brood parasites is less studied (but see Rehan et al. 2011).

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Here we compare social and solitary nests of a facultatively social bee to directly test whether social nesting enhances defense against brood parasites.

Bees provision cells with pollen and nectar for their developing offspring. These provisions or the offspring themselves may be targeted by parasites in various taxa and with different life-history strategies. Parasites may consume the developing offspring directly, kill it indirectly by consuming all of its food, or eat only some food, so that the host offspring completes development, albeit at a smaller size (e.g. Smith et al. 2008; Michener 2007). Parasitism is a major source of brood mortality for bees (reviewed in Wcislo 1996; Wcislo and Cane 1996). Parasitism rates vary across species and environments, but brood loss of ~20% of offspring to parasites is the approximate average for reported studies (Wcislo 1996).

Parasitism rates in bee nests may be influenced by social organization and resource limitation. Social nests may be better defended against parasites than solitary nests because one individual can guard the nest while others forage, whereas solitary bees must leave the nest unattended to forage (Lin and Michener 1972). Rehan et al. (2011) showed that social nests of a facultatively social bee species (*Ceratina australensis*) did not have significantly lower rates of parasite attack, or intensity of infestations, but did have more surviving brood after parasite attack than solitary nests. No other study has directly compared parasitism rates between social and solitary nests of the same species. Resource limitation may also increase parasite pressure. If bees must spend more time foraging to provision each cell when resources are scarce, nests will be left unattended and susceptible to parasites more often (Goodell 2003).

To test these hypotheses, we used the Neotropical sweat bee *Megalopta genalis* (Halictidae) because they are facultatively social, with both solitary and social nests present in the same population. Social nests have one queen and one or more worker(s); Wcislo et al. 2004. These bees also experience seasonal decline of resource availability. On Barro Colorado Island (BCI), Panama, *Megalopta* provision nests from January to July, but productivity is higher in the dry season (January–April) when floral resources are more abundant than during the early wet season (May–July; Wcislo et al. 2004; Smith et al. 2012).

M. genalis and *M. centralis* are parasitized by four different macroparasites that attack the hosts in different ways. The beetle *Macroisiagon gracilis* (Rhipiphoridae) infects nests by ovipositing within flowers and the phoretic triungulin larvae climb on a foraging bee, to hitchhike a ride to the nest cells (Falín et al. 2000). There they wait for *Megalopta* larvae to complete feeding before attacking and consuming them (Clausen 1976). Thus, it is unlikely that increased adult presence at the nest would prevent *M. gracilis* attack. Indeed, if individual foraging rates are greater in social nests relative

to solitary bees, then social nests are expected to be more exposed to rhipiphorids due to their sampling more flowers.

The three other parasites must enter the nest to lay the eggs that parasitize brood cells. A parasite congeneric bee, *M. (Noctoraptor) byroni*, attacks *Megalopta* nests. *M. byroni* presumably kills the developing host egg and consumes the pollen provisions, although within-nest observations in naturally parasitized host nests are not available. *M. byroni* readily enter *M. genalis* nests in controlled laboratory settings: parasites that are able to gain entry to the nest interior are generally aggressive toward nest residents, may inspect brood cells, and can remain in the nest interior for at least a few hours (CJK personal observations). These parasitic bees have enlarged ocelli, similar to other *Megalopta*, suggesting similar nocturnal habits (Engel et al. 1997; Biani and Wcislo 2007), and have been observed flying near nests at night (W. T. Wcislo and V. H. Gonzalez, pers. obs.). The mutillid wasp *Lophostigma cincta* has never been observed entering a *Megalopta* nest in a natural setting, but females have been observed walking on the forest floor and along branches during the day (Cambra et al. 2005), including along the top of a nest (CJK pers. obs.). In other mutillid species, females enter the host nest to lay eggs (Brothers et al. 2000; Bergamaschi et al. 2010). In laboratory assays, *L. cincta* will enter host nests, inspect brood cells by tapping their antennae on the cell caps, and may open cells and inspect the contents (CJK personal observations). *L. cincta* only attack immature hosts after they have completed larval feeding. Lastly, a cleptoparasitic fly (*Fiebrigella* sp., Chloropidae) enters the nest to lay eggs (Smith et al. 2008). Its larvae consume pollen provisions, but usually do not kill the developing bees because the flies are so small (~2 mm adult length) that sufficient pollen remains for the host, although host body size is reduced (Smith et al. 2008). For these species, *Megalopta* bees are the only known hosts (Falín et al. 2000; Cambra et al. 2005; Engel et al. 1997; Biani and Wcislo 2007; Luz et al. 2016), but studies of other potential hosts are scarce.

Based on the biology of the parasites and seasonal resource availability, we made two predictions about parasitism patterns in *Megalopta* bees. First, if sociality protects bees from parasitism, brood loss from parasites that enter the nest (*M. byroni*, *L. cincta*, *Fiebrigella* sp.), should be lower in social nests than in solitary nests because they are guarded. However, *M. gracilis* parasitism rates will either be unaffected, or higher, due to increased foraging rates in social nests (Wcislo et al. 2004; Smith et al. 2007). Second, if resource limitation influences parasitism rates, then brood loss from all parasites should increase in both social and solitary nests in the wet season, when less abundant floral resources force bees to take more trips per provisioned cell (Smith et al. 2012), leaving nests unguarded more often. The hypotheses that these predictions test are not mutually exclusive; if sociality confers strong defensive benefits to

bees, then effects of seasonal resource reduction would only be seen in solitary nests. Also, *Megalopta* bees lower their reproductive rate in the wet season, perhaps mitigating the effect of potentially longer foraging trips by simply reducing overall provisioning (Wcislo et al. 2004; Smith et al. 2012). Both hypotheses assume that adult bees at the nest can effectively guard against parasites and that the parasites do not have their own seasonal patterns, yet we know almost nothing about their biology (Falin et al. 2000; Cambra et al. 2005; Biani and Wcislo 2007; Smith et al. 2008).

Methods

We collected nests from the forest in BCI, (9°09'N, 79°51'W), Republic of Panama, which is a lowland tropical semi-deciduous moist forest (Leigh 1999). *Megalopta* nest in sticks and provision individual cells in which each offspring is reared. They are nocturnal bees with short foraging periods (about 1 h each) before sunrise and after sunset; even solitary nests typically have a female present ≥ 22 h/day (Wcislo et al. 2004; Kelber et al. 2006). Thus, the bees spend very little time away from the nest, which is outside the activity period of diurnal parasites and predators (Wcislo et al. 2004). We collected during the day when all adults are present. We opened nests in the lab and either opened brood cells and recorded their contents and developmental stage, or transferred individual brood cells into tissue culture plates for rearing at ambient temperature. We recorded the number of adult males and females present in the nest at collection. We classified nests with multiple adult females as social, and those with only one female as solitary. In some cases, nests were abandoned or female(s) escaped at collection. We used these nests to calculate seasonal parasitism rates, but not social–solitary comparisons.

Parasitism

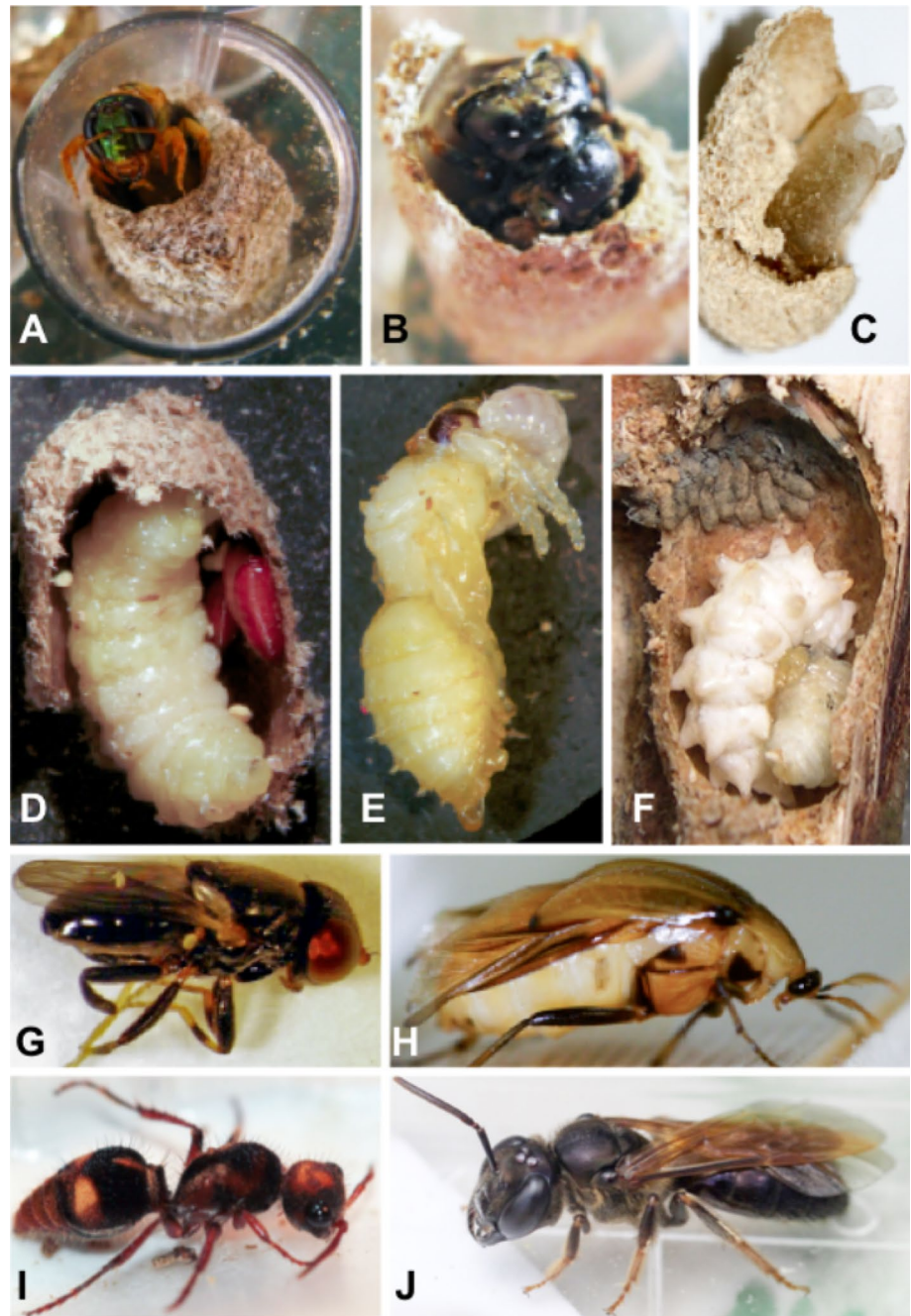
We recorded emergences of *Fiebrigella* sp. adults from reared brood cells collected in 2007 on BCI. We did not record fly emergences from the other rearing datasets (2010, 2015, 2016, Table 1). *L. cincta* and *M. gracilis* parasitism is apparent when the host has reached the pre-pupal (after the larvae has finished feeding and defecated) and pupal stages. At this point the parasite larvae begin feeding on the host. *L. cincta* larvae are transparent with a visible reddish gut (Fig. 1). *M. gracilis* larvae are white or cream colored with lateral conical projections. *L. cincta* pupae are encased in a brown cocoon, while *M. gracilis* pupae are visibly beetle-shaped; *Megalopta* pupae do not cocoon (Fig. 1). If opened brood cells contained a host pre-pupa or pupa, we recorded parasitism status and estimated the emergence date based on developmental stage. Parasitism is not apparent in cells with host eggs or feeding larvae, and we, therefore, excluded these cells from our analyses of parasitism. For analysis of *M. byroni* parasitism, we included only cells that were reared to adulthood, because we could not distinguish the host and parasite immatures. As adults, *M. byroni* are distinguishable from host *Megalopta* due to their black color (hosts are green and copper colored), as well as other morphological features (Engel et al. 1997).

For brood cells that we reared to adulthood, we recorded the emergence date and species identity (host or parasite) of each emergence. For *M. byroni* we also included emergences from the observation nests censused in 2003 by Smith et al. (2007). We are unsure if our census methods (checking every 5 days) would have detected *L. cincta* and *M. gracilis* emergences, so we only used these cells for analysis of *M. byroni* parasitism. The individual *M. byroni* discovered in these nests all remained for several days. We assume, but do not know, that *L. cincta* and *M. gracilis* leave immediately after emergence. The inclusion of the 2003 nests for *M.*

Table 1 Collection sample sizes and date ranges

	Year	N cells				N nests				Date range	Used for
		Social	Solitary	Unknown	Total	Social	Solitary	Unknown	Total		
<i>Fiebrigella</i> <i>M. byroni</i> <i>L. cincta</i> and <i>M. gracilis</i>	2003	53	20	0	73	13	8	0	21	23 February–30 March	<i>M. byroni</i>
	2007	124	106	0	230	39	47	0	86	8 February–24 July	All parasites
	2010	396	433	0	829	87	127	0	214	24 January–3 April	<i>M. gracilis</i> & <i>L. cincta</i>
		190	159	0	349	71	89	0	160		<i>M. byroni</i>
	2015	217	312	125	654	80	145	55	280	29 January–6 August	All except <i>Fiebrigella</i>
	2016	138	99	60	297	47	51	30	128	10 January–22 June	All except <i>Fiebrigella</i>
	Total	124	106	0	252	39	47	0	86		
	Total	722	696	185	1603	250	340	85	675		
	Total	875	950	185	2010	253	370	85	708		

Fig. 1 Photos of an uninfected *M. genalis* emerging from its brood cell in a rearing tray (**a**) and examples of parasitism (**b–f**) and adult parasites (**g–j**). **b** *M. byroni* emerging from brood cell. **c** Cocoon of emerged *L. cincta* inside *Megalopta* brood cell. **d** Three brown *Fiebrigella* sp. cocoons next to a host larva. The host survived to adulthood. **e** *L. cincta* larvae on head of host *Megalopta* pupa, consuming host. **f** *M. gracilis* larva (left) consuming host (remains at right). Note the host feces at the top of the brood cell. The parasite waited until the host had completed feeding before attacking. **g** Adult *Fiebrigella* sp. **h** Adult *M. gracilis*. **i** Adult female *L. cincta*. **j** adult female *M. byroni*. **g–j** were reared from brood cells. Photos not to same scale



byroni and exclusion of opened, but not reared, cells from 2010 for *M. byroni* accounts for the unequal sample sizes in Table 1. Individual analyses may have lower sample size in cases where social status ($N=212$ cells) or emergence dates ($N=12$ cells) were unknown.

Our collections encompass the entire *Megalopta* nesting period, but contain many more cells (80% of total) from the dry season (Fig. 2). This is partly due to sampling effort in 2010 and partly due to increased productivity (more cells per nest on average) in the dry season (Wcislo et al. 2004; Smith et al. 2012). The proportion of cells from solitary and social

nests was similar (50.2 and 49.8%, respectively). We did not use 2003 samples in our analyses of seasonality because they included such a narrow range of dates.

Statistical analyses

We compared parasite occurrence (0 or 1 for each cell) using a generalized linear mixed model (GLMM) with binomial distribution and logit link function in SPSS version 24. We used social status (social or solitary) of the nest from which the cells were collected and date (measured as days from

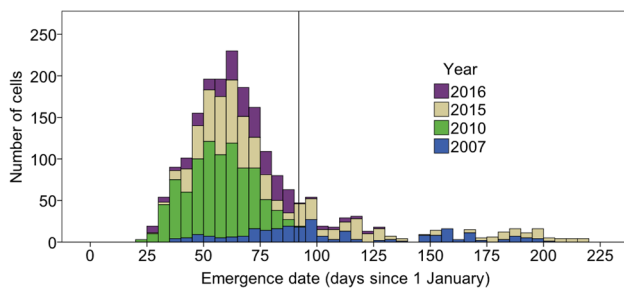


Fig. 2 Distribution of nest cells used in the study by year and season. 83% of the cells used in our study emerged before 1 April (vertical line)

January 1, to compare across years) as fixed factors, and nest identity and year as random factors. We did not use year in our analyses of fly parasitism because all samples were from 2007. We used a similar approach to analyze flies per cell, and flies per infected cell, but with a Poisson distribution and log link, as these are count, rather than binary data.

Results

Fly parasitism

Of the 106 brood cells that came from solitary nests 27 (25.5%) were parasitized by flies, while 38 of the 124 cells from social nests were parasitized by flies (25.8%). This difference was not significant ($F_{1,225} = 0.58$, $P = 0.45$). The effect of date, however, was significant: parasitism increased from the dry to wet season ($F_{1,225} = 5.13$, $P = 0.02$). Nest identity was also significant as a random effect ($Z = 3.83$, $P < 0.001$). There were no significant differences between

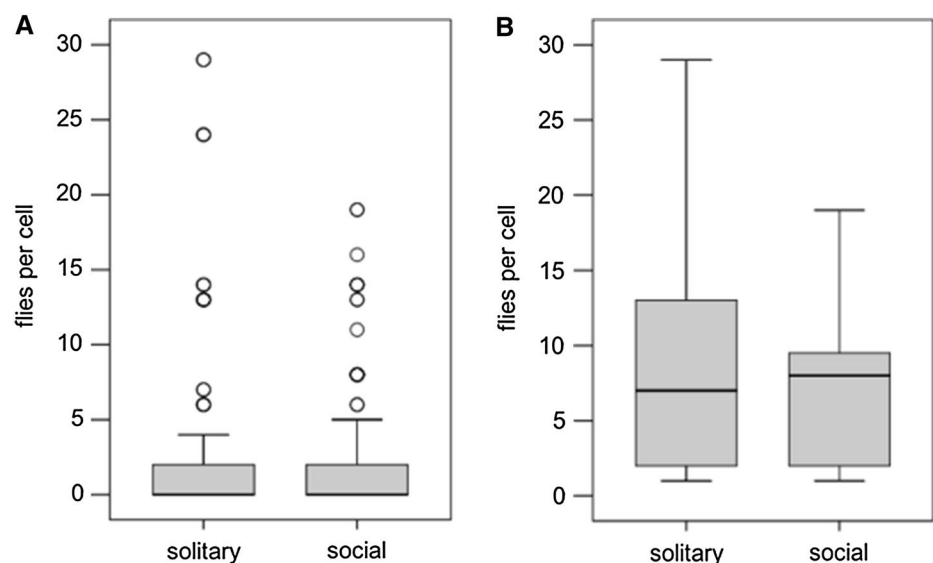
solitary and social nests in the intensity of parasitism, nor effects of date. This was true when parasite intensity was measured as the number of flies per cell (social status: $F_{1,225} = 0.53$, $P = 0.47$, date: $F_{1,225} = 2.29$, $P = 0.13$. Nest $Z = 4.76$, $P < 0.001$) and when measured as flies per infected cell, excluding all cells without flies (social status: $F_{1,70} = 0.002$, $P = 0.97$, date $F_{1,70} = 0.10$, $P = 0.75$. Nest $Z = 3.03$, $P = 0.002$; Fig. 3). The effect of date appears to be driven principally by cells from social nests, as the effect of date remains when only cells from social nests are included (date $F_{1,120} = 5.20$, $P = 0.02$. Nest $Z = 2.66$ $P = 0.008$) but not when only cells from solitary nests were included (date $F_{1,104} = 1.10$, $P = 0.23$. Nest $Z = 2.73$ $P = 0.006$; Fig. 4), although there was no significant social status by date interaction effect in the full model.

Brood parasitism

We recorded 32 instances of *M. gracilis* brood parasitism, 21 of *L. cincta*, and 12 of *M. byroni*. Parasitism rates were low overall (4.43% of cells from social nests, 2.73% of cells from solitary nests) (Fig. 5). Binary logistic models including date and social status as fixed effects and year and nest identity as random effects showed no significant effects for any included variable. We never collected *M. byroni* from a solitary nest (0/697 solitary cells, 12/718 social cells), but because *M. byroni* parasitism tended to cluster by nest (see below), this difference is not significant after accounting for nest identity.

Nests parasitized by *M. gracilis* typically had only one parasitized cell (one nest had two cells, 30 had only one cell parasitized). Of the nests parasitized by *L. cincta*, eight had only one cell parasitized, five contained two parasitized cells, and one had three parasitized cells. Nests parasitized

Fig. 3 The intensity of fly parasitism did not differ between cells from solitary and social nests when measured as flies per cell (a) or flies per infected cell (b). Horizontal lines show the median, boxes the interquartile range (IQR), and whiskers up to $1.5 \times (\text{IQR})$. Dots represent data points $> 1.5 \times (\text{IQR})$ from the median



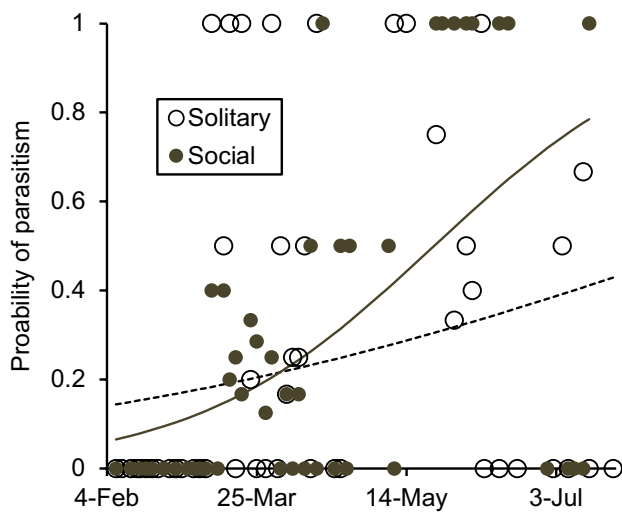


Fig. 4 The observed mean proportion of parasitized cells by emergence date for cells from solitary and social nests. Lines plot the probability of parasitism calculated by a binary logistic regression equation for each group separately. This relationship is significant only for the cells from social nests

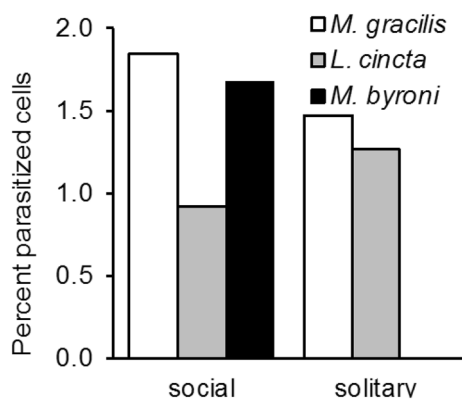


Fig. 5 Brood parasitism in social and solitary nests by parasite. Note the lack of *M. byroni* parasitism in social nests

by *M. byroni* contained 1, 2, 4, and 5 parasitized cells. Because not all reared cells survived to adulthood, our data may underestimate multiple parasitism.

Discussion

We found no support for the hypothesis that social nests are better defended against parasites. This was counter to our prediction for all species except *M. gracilis* that a guard at the nest would reduce parasitism. We predicted that *M. gracilis* parasitism may increase in social nests due to more foraging activity, but this did not occur.

It is not clear to what extent guards at the nest actually help deter parasites. One of us (ARS) once saw an adult

Fiebrigella sp. fly hovering ~5 mm in front of a *Megalopta* nest entrance. A resident female *Megalopta* appeared to track the fly's movements with her head, and nipped at the fly with her mandibles twice when the fly approached closely. This suggests that guards may deter *Fiebrigella* sp. parasitism, but we know nothing else about their biology. The significant effect of nest identity in all of our analyses of *Fiebrigella* sp. parasitism suggests that female flies either lay multiple eggs that may infect more than one cell in a nest, or that they visit the same nest repeatedly to lay eggs. We have no data on repeated visits, but larvae of *Fiebrigella* sp. are mobile (ARS, WTW, KMK & CJK personal observation) suggesting that a single invasion could lead to multiple infected cells.

Parasitism by the mutillid wasp *L. cincta* did not differ between social and solitary nests. While little is known about the host searching and nest entrance behavior of *L. cincta*, observations of other mutillids suggest that the wasps attempt to pass through the nest entrance, during which time they may be successfully repelled by guards, pass by the guards without reaction, or kill the guards to force their way in (Brothers et al. 2000; Bergamaschi et al. 2010). We saw no evidence of mutillids digging side tunnels to access nests (Polidori et al. 2009), but parasitized nests were so rare that this may not have been noted. Some mutillids parasitize multiple cells over days (or longer) in the host nest (Brothers et al. 2000). 40% of the mutillid-infected nests in our study contained more than one parasitized cell, suggesting that the *L. cincta* may have remained in the nest after entering, or returned to the nest repeatedly, although we have no data on this.

The most interesting case was the congeneric parasite *M. byroni*, which may target social nests or preferentially gain entry into social nests. However, Biani and Wcislo (2007) reported collecting *M. byroni* from one solitary nest. Host bees in social nests must solve the problem of nestmate recognition in determining which individuals to admit into and keep out of their nests. Solitary bees, on the other hand, can repel all other bees from their nest without risk of excluding nestmates, since they have no nestmates. Perhaps *M. byroni* exploit the recognition system of social bees to gain nest entry.

A second interesting characteristic of *M. byroni* parasitism was that three of the four infected nests in our sample contained multiple infected cells. In one nest, five cells were infected. This suggests that *M. byroni* females remain in the nest for some time, and may function as a social parasite—usurping the host queen and exploiting the continuing effort of the forager(s)—rather than simply an egg-dumping brood parasite (Michener 2007). This strategy would require social nests for successful reproduction. Similar social parasitism has evolved repeatedly in allodapine bees, another group with facultative sociality and small colonies (Smith

et al. 2006, 2013). Alternatively the parasites may learn the host location and return to a nest repeatedly (Wcislo 1987). Unfortunately, little is known about the biology of *M. byroni* or any of the other parasitic species of the *Megalopta* subgenus *Noctoraptor* beyond morphology (Engel et al. 1997; Biani and Wcislo 2007; Engel 2011).

The low rates of emergence by the parasites *M. gracilis*, *L. cincta*, and *M. byroni* may be due to adult females discarding infected cells. Quñones and Wcislo (2015) showed that *M. genalis* females discarded the contents of cells in which they had injected supplemental food, and interpreted this as a defense against potential parasitism. We have seen evidence of *M. genalis* opening and re-closing unmanipulated cells in observation nests (ARS & KMK, unpubl. obs.), as if checking on their contents. Plateaux-Quénu (2008) reviews similar behavior in other halictine bees. Thus, parasite infection rates may be higher than measured by rearing if many infected cells were discarded before collection, although the relatively high rates of *Fiebrigella* sp. parasitism suggest they may be less affected (Smith et al. 2008). The low rates of *M. gracilis*, *L. cincta*, and *M. byroni* occurrence mean that despite rearing thousands of cells, our sample size is small, and ability to detect social–solitary differences in nest defense is limited.

The results of the current study contrast with other studies of facultatively social species, including *Megalopta*, that demonstrate a predator defense benefit to group living (Smith et al. 2003, 2007; Kukuk et al. 1998; Hogendoorn and Zammit 2001; Schwarz et al. 1997), but are consistent with Prager (2014). However, the anti-predator benefits demonstrated in those studies came not from having a guard at the nest during foraging, but from having an adult at the nest that could continue parental care if a nestmate died. To our knowledge, studies in which nests are experimentally orphaned or have worker number reduced have not tested for changes in brood parasitism rates (e.g. Field et al. 2000; Smith et al. 2003; Lucas and Field 2011). However, naturally orphaned nests of two other bee species suffered increased mortality from parasitic flies (Sakagami and Maeta 1977; Eickwort et al. 1996).

If bees forage longer as resources decline, thus leaving their nests unattended for longer and increasing susceptibility to parasite attack (Goodell 2003), parasitism should increase during the wet season in *Megalopta*. In the case of *Megalopta*, floral resources decline from the dry to the wet seasons, with corresponding decline in nest productivity measured as cells per nest (Wcislo et al. 2004; Smith et al. 2012). We found a significant effect of season on *Fiebrigella* sp. fly parasitism: infection rates, but not intensity per cell, were greater in the wet than dry season. This is consistent with Smith et al. (2008), who reported higher levels of fly parasitism in cells collected during the wet season than in the dry season, but their dry season

sample (2004) was from a different year than the wet season samples (2003, 2006). Our 2007 sample encompassed both the dry (January–April) and wet (May–July) part of the *Megalopta* nesting season. Interestingly, we found that the seasonal effect was present only in social nests. We do not know enough about the biology of *Fiebrigella* sp. to conclude that changes in *Megalopta* foraging patterns drive the seasonal changes in parasitism rates. We found no effect of season on the other three parasites in the study.

In evaluating hypotheses based on social defense and resource limitation, it is essential to note that even solitary *Megalopta* spend very little time away from their nest. *Megalopta* forage only for about an hour (often much less) after sunset and before sunrise (Warrant et al. 2004; Kelber et al. 2006; Smith et al. 2017). The rates of lethal parasitism (excluding the fly *Fiebrigella* sp.) that we measured (~4%) are similar to those of Wcislo et al. (2004) at the same site, and quite low compared to other bees (Wcislo 1996; Wcislo and Cane 1996). Even with a sample size of > 2000 cells, lethal parasitism was so rare that our statistical tests had little power.

Megalopta may benefit not only from foraging for very little time, but also from having that time not overlap with diurnal parasites (Wcislo et al. 2004). The asynchronous foraging time hypothesis (Lienhard et al. 2010) predicts that hosts may prevent parasitism by moving their foraging times outside of the active periods of their parasites. *Megalopta* may have escaped many diurnal parasites by becoming night-active (Wcislo et al. 2004). Unfortunately it is impossible to experimentally test this hypothesis with *Megalopta* because all species are nocturnal. However, the diurnal bee genus *Xenochlora* has similar nesting and social biology to *Megalopta* (Tierney et al. 2008) and is either the sister genus to (Tierney et al. 2012), or paraphyletically nested within *Megalopta* (Goncalves 2016). Comparisons of foraging effort and parasitism rates between sympatric species of diurnal *Xenochlora* and nocturnal *Megalopta* would likely be fruitful.

In summary, we found limited support for an effect of resource limitation on parasitism: non-lethal pollen cleptoparasitism increased in the wet season when host food resources were lowest. However, we do not know if increased foraging effort or another factor correlated with the wet season drive the pattern. We found no evidence that group living increased defense against lethal brood parasites. In fact, it may increase parasitism rates by exposing bees to *M. byroni* parasitism, although this effect was not significant. However, the most striking result was the rarity of lethal brood parasitism over all the years and seasons of our study. This may be due to nesting in sticks rather than the ground (Wcislo 1996), leaving their nest to forage for very short amounts of time (Goodell 2003; Smith et al. 2017), nocturnal foraging being offset from

the active period of most parasites (Wcislo et al. 2004) or a combination of the three.

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