

Is Nocturnal Foraging in a Tropical Bee an Escape From Interference Competition?

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Abstract

Temporal niche partitioning may result from interference competition if animals shift their activity patterns to avoid aggressive competitors. If doing so also shifts food sources, it is difficult to distinguish the effects of interference and consumptive competition in selecting for temporal niche shift. Bees compete for pollen and nectar from flowers through both interference and consumptive competition, and some species of bees have evolved nocturnality. Here, we use tropical forest canopy towers to observe bees (the night-flying sweat bees *Megalopta genalis* and *M. centralis* [Halictidae], honey bees, and stingless bees [Apidae]) visiting flowers of the balsa tree (*Ochroma pyramalidae*, Malvaceae). Because *Ochroma* flowers are open in the late afternoon through the night we can test the relative influence of each competition type on temporal niche. Niche shift due to consumptive competition predicts that *Megalopta* forage when resources are available: from afternoon into the night. Niche shift due to interference competition predicts that *Megalopta* forage only in the absence of diurnal bees. We found no overlap between diurnal bees and *Megalopta* in the evening, and only one instance of overlap in the morning, despite the abundance of pollen and nectar in the late afternoon and evening. This supports the hypothesis that *Megalopta* are avoiding interference competition, but not the hypothesis that they are limited by consumptive competition. We propose that the release from interference competition enables *Megalopta* to provision cells quickly, and spend most of their time investing in nest defense. Thus, increases in foraging efficiency directly resulting from temporal shifts to escape interference competition may indirectly lead to reduced predation and parasitism.

Key words: competition, temporal niche, resource partitioning, niche overlap

Competition for floral nectar and pollen is typically treated as consumptive competition (competition to consume resources before others do). Consumers who arrive first find abundant resources, while later arrivals are relegated to the dregs (Heinrich 1976, Inouye 1978, Pleasants 1983, Abrol 2012). However, foragers are also subject to interference competition (driving away or otherwise preventing competitors from accessing resources). Because flowers renew nectar and pollen, they are often monopolized by aggressive foragers to deter access to potential competitors (reviewed by Roubik 1992, Kronfeld-Schor and Dayan 2003, Willmer 2011, Abrol 2012). Avoiding this interference competition may result in novel temporal niches when one species shifts its activity patterns to avoid aggressive interactions from another (Morse 1974, Case and Gilpin 1974, Carothers and Jaksić 1984). For example, subordinate hummingbird species forage at flowers early in the day when dominants are away hunting insects (Lara et al. 2009), and less aggressive stingless bee species forage earlier or later than the dominant species that control

flowers during peak resource availability (Nagamitsu and Inoue 1997). Disentangling the effects of each competition type can be difficult. For instance, some bee species have shifted temporal activity even further, into the night. Consumptive competition may have driven this niche shift, as nocturnal species have new sources of food (nocturnal flowers) and first access to early opening diurnal flowers (Wcislo and Tierney 2009). However, such a shift also eliminates interference competition with diurnal bees. Here we hypothesize that avoiding interference competition from aggressive diurnal bees may be an important reason for nocturnal foraging.

We used observations of the Neotropical, night-flying bees *Megalopta genalis* and *M. centralis* on flowers of the balsa tree, *Ochroma pyramalidae*, to test if escaping interference competition structures nocturnal foraging. *Megalopta* (Halictidae) are solitary or weakly social (typically 2–3 colony members) bees that forage from both diurnal flowers that remain open past sunset or open before sunrise, and flowers with nocturnal anthesis (Janzen 1968, Roulston 1997,

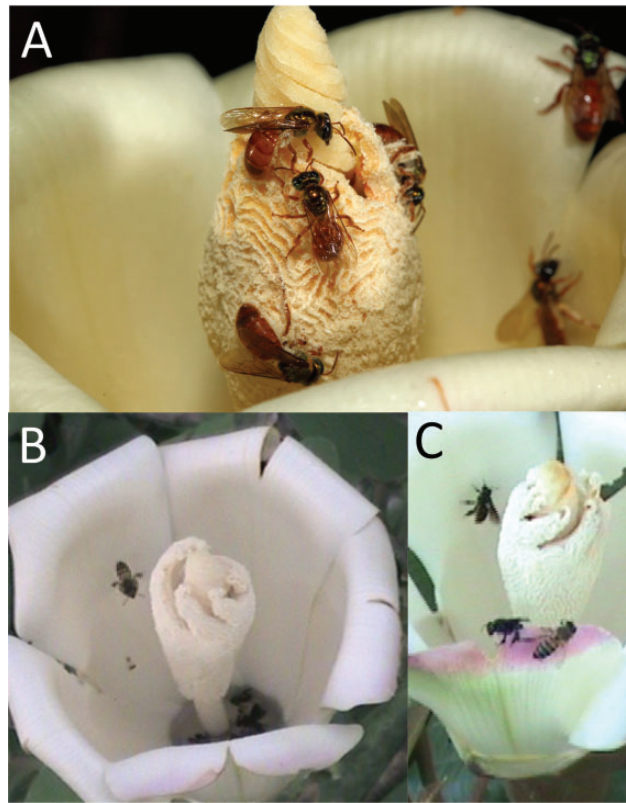


Fig. 1. (A) *Megalopta* foraging for pollen on the anther of an *Ochroma* flower, Photo by CZ. (B) Diurnal honey bee, flying, and stingless bees, drowned in copious nectar in bottom of the flower. (C) Honey bee (right) and stingless bees foraging. B and C are screenshots from videotape.

Hopkins et al. 2000, Wcislo et al. 2004, Kelber et al. 2005, Franco and Gimenes 2011, Smith et al. 2012, Krug et al. 2015, Oliveria et al. 2016, Cordeiro et al. 2016). *Megalopta* are generalist foragers, with 64 species of pollen recorded from nests at a single site, an active nesting season of ~9 months and opportunistic shifts among pollen sources based on availability (Smith et al. 2012). *Megalopta* have numerous morphological and neurobiological adaptations that allow them to fly in near-darkness, during which time most other sympatric bees are in their nests. However, because they cannot navigate beyond astronomical twilight, they stop foraging about one hour after sunset, and do not resume again until about an hour before sunrise. As a result, they rarely venture from their nests for >2 h per day, and usually much less (Kelber et al. 2005, Theobald et al. 2007, Warrant 2008). Flying during the approximately one hour after sunset and before sunrise offers access to night blooming flowers with little competition from other bees, and may also offer an escape from diurnal predators and parasites (reviewed in Wcislo et al. 2004, Wcislo and Tierney 2009, Smith et al. 2012).

Low light levels constrain *Megalopta* foraging times at night, but why not extend foraging into the late afternoon and early morning? Because their foraging period is so short, even a modest expansion would translate into a substantial increase in the number of provisioning trips and thus reproductive output, all other things being equal (Neff 2008). We hypothesize that interference competition from behaviorally aggressive eusocial honey bees and stingless bees (*Apis mellifera* and Melliponini) may reduce the rewards of foraging when other bees are active. These bees can displace other bees from flowers, often aggressively (Johnson and Hubbell 1974, Roubik 1992, Nagamitsu and Inoue 1997, Gross and Mackay 1998, Paine 2004, Lichtenberg et al. 2010, Abrol 2012). *Megalopta* can nest solitarily or in small social groups with a queen and worker(s), but foragers work

alone and do not recruit to flowers like honey bees and stingless bees do (Wcislo et al. 2004; Smith et al. 2003, 2007). Thus, interference competition from eusocial bees may cause *Megalopta* to refrain from foraging even when floral resources are abundant. To test this hypothesis, we observed bees foraging on canopy flowers of the balsa tree (*Ochroma pyramalidae*, Malvaceae) in Central Panama. *Ochroma* flowers open about an hour before sunset and remain open for a single night. Each flower produces ~ 25 ml of nectar, enough that bees sometimes swim in it (Fig. 1B), so consumptive competition is not an issue: pollen and nectar are still abundant after both diurnal bees and *Megalopta* stop foraging when the trees' known pollinators, kinkajous and bats, begin visiting (Kays et al. 2012). The timing of *Ochroma* floral resource availability offers the chance to disentangle the relative effects of consumptive and interference competition.

If *Megalopta* foraging time is determined by resource availability, we predict that bees will begin foraging when the flowers open in order to maximize floral resource acquisition before it becomes too dark to forage.

If *Megalopta* foraging time is influenced by interference competition, we predict that the cessation of diurnal bee foraging, rather than flower opening, will determine when *Megalopta* begin foraging. Alternatively, if *Megalopta* do not wait for diurnal bees to stop foraging, we predict that they will suffer aggressive displacement from flowers.

Methods

All observations were conducted from the platforms of scaffolding towers built into the canopies of three *Ochroma* trees for a photography project (Angier and Ziegler 2011). All trees were located in

second growth tropical moist forest in central Panama. One was near the town of Gamboa (9°7'40.8", -79°41'48.8394"), one was near Pipeline road in Parque Nacional Soberania (9°7'57", -79°43'34.32"), and the third was on Barro Colorado Island field station (BCI) near the lab clearing (9°9'59.0394", -79°50'12.8394"). All were ≥ 10 m crown diameter (for more details of tree sites see Kays et al. 2012).

We conducted observations between 2 January and 23 February, 2010. We chose flowers opportunistically based on the ~ 2 m range of our video equipment from the scaffolds. We recorded one flower at a time with a Sony (Tokyo, Japan) MiniDV camera and infrared light, and recorded presence or absence data from the resulting video tapes. To standardize for slight differences in start and finish times, we only recorded data beginning 10 min before sunset to 50 min after sunset in the evening, as this is when *Megalopta* typically stop foraging due to their inability to navigate back to their nests in low-light conditions; both species of *Megalopta* have similar foraging times and behavior (Kelber et al. 2005, Theobald et al. 2007, Smith et al. 2012). The data used from morning recordings began 65 min before sunrise and continued until 25 min after. We include data from 27.5 h of observations, including 9 morning (810 min total) and 14 evening (840 min total) filming sessions. We have 8 sessions from the Pipeline road tree, 7 from Gamboa, and 8 from BCI.

We recorded the number and type of insect visitors seen in ten-second scans taken at one minute intervals (*Ochroma* also receive many vertebrate visitors; Angier and Ziegler 2011, Kays et al. 2012). We recorded the presence of *Megalopta*, honey bees (*Apis mellifera*), stingless bees (Meliponini), moths, and the nocturnal vespid wasp *Apoica pallens*. We could not identify species of *Megalopta*, moths, or stingless bees from the videos, although nearly all of the stingless bees appeared to be *Trigona sp.* We analyzed foraging time relative to sunrise or sunset to standardize for change in day length across the study: negative values reflect minutes before sunrise or sunset, and positive values minutes after sunrise or sunset. Because our data were not normally distributed, we use a Kruskal-Wallis test followed by Conover post-hoc comparisons to test for differences between groups. Sunrise, sunset, moonrise and moonset times, and moon phase data were downloaded from the US Naval observatory (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). For analysis of moon visibility, days in which the moon had not yet risen before foraging were counted as "no moon". Days were counted as "visible" if the moon was up and 60–100% full. Our recordings included no days with risen moons at <60% visibility or cloudy days. Due to our narrow field of view, which focused on one flower, as well as our scan methodology and unmarked animals, we could not distinguish between repeat visits of a single forager and visits of two separate foragers (Fig. 1). Since we could not differentiate between individual foragers, we did not attempt to classify visits as nectar versus pollen collecting. For instance, a bee that flew from the anther of the flower out of the field of view and then quickly returned to drink nectar would appear the same as two different bees arriving in sequence to collect pollen and nectar, making such a classification difficult.

We recorded potentially aggressive interactions between bees. These included "push", when a bee moved toward another bee and pushed it away, either forwards or backwards, "bite", when a bee closed its mandibles on another bee, "no land" when a bee occupied the space another bee was attempting to land in, preventing the flying bee from landing, "delay land", which is similar to "no land" above, but the flying bee was able to land nearby, and "land and displace" in which the flying bee forced the bee on the flower to move so as not to be landed on. For "push" and "bite" the pushing or

Table 1. All scans of floral visitors included in our study

	Evening	Morning	Total
Honey bee	254	17	271
Stingless bee	457	70	527
<i>Megalopta</i>	108	16	124
<i>Apoica pallens</i>	18	0	18
Moth	14	13	27

biting bee was classified as the aggressor. For "no land" and "delay land" the stationary bee was classified as the aggressor. For "land and displace" the landing bee was defined as the aggressor.

Results

Observations of Flower Visitors

We recorded 967 visits across all *Ochroma* flowers (Table 1). Visitor species composition varied between sites ($\chi^2 = 31.05$, $df = 2$, $P < 0.001$) but there was no significant effect of site on foraging time for *Megalopta*, honey bees or stingless bees. No honey bees were observed at the Pipeline Road tree, and only a single *Megalopta* was observed at the BCI tree even though the species is common on BCI; stingless bees were common at all three trees.

All flowers were open when evening filming began, and the evening observations typically had diurnal bees already present at the flower. Mean *Megalopta* foraging time was significantly later than both diurnal bees, but there was no significant difference between stingless bees and honey bees (Kruskal-Wallis $\chi^2 = 288.84$, $df = 2$, $P < 0.001$). Conover post hoc tests for *Megalopta* versus stingless and honey bees both $P < 0.001$, stingless versus honey bee $P = 0.57$). We observed honey bees in 10 of our 14 evening foraging observation periods. The latest we observed honey bees foraging was 24 min after sunset (mean latest visit \pm SD = 11 ± 10 min after sunset; Fig. 2). We saw stingless bees in 13 of 14 observations. The latest stingless bee was 27 min after sunset (mean = 13 ± 10 min). *Megalopta* visited during only 8 of our 14 evening foraging observation periods. The earliest *Megalopta* visit we recorded was 16 min after sunset (mean first visit = 26 ± 10 min).

We recorded fewer visits during morning foraging observation periods than evening periods (Table 1). Mean *Megalopta* foraging time was significantly earlier than both diurnal bees, but there was no significant difference between stingless and honey bees (Kruskal-Wallis $\chi^2 = 38.18$, $df = 2$, $P < 0.001$). Conover post hoc tests for *Megalopta* versus stingless and honey bees both ($P < 0.001$), stingless versus honey bee ($P = 0.18$). We observed honey bees in 3 of our 9 morning foraging observation periods. The earliest we observed honey bees foraging was 16 min before sunrise (mean earliest visit \pm SD = 14 ± 2 min before sunrise; Fig. 2). We saw stingless bees in 5 of 9 observations. The earliest stingless bee was 24 min before sunrise (mean = 6 ± 13 min). *Megalopta* visited during 6 of our 9 morning foraging observation periods. The latest *Megalopta* visit we recorded was 14 min before sunrise (mean last visit = 32 ± 15 min before sunrise).

We recorded few visits of moths or the nocturnal paper wasp *Apoica pallens* during our observation periods (Table 1), but both groups likely continued foraging past the end of our evening observation periods (Hunt et al. 1995, Nascimento and Tannure-Nascimento 2005, Camargo et al. 2016).

Foraging Overlap

Across all evening samples pooled together, *Megalopta* foraging overlapped with diurnal bees. However, within each foraging

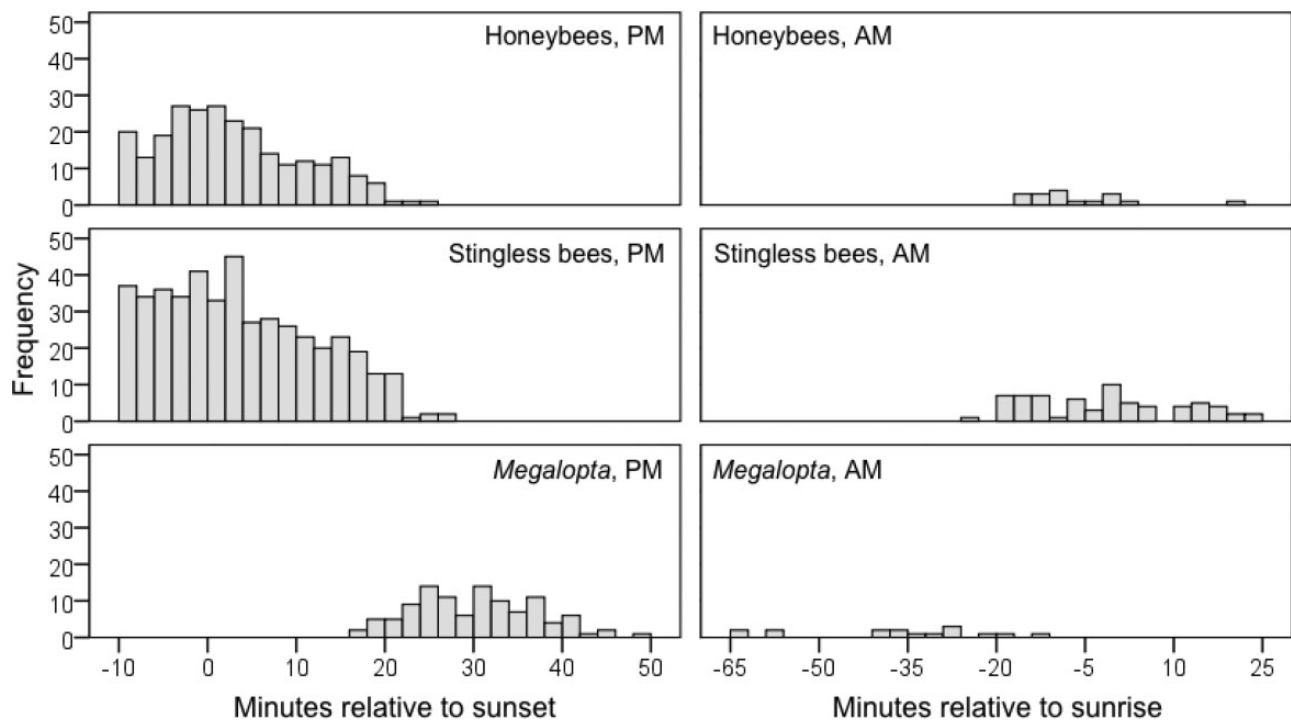


Fig. 2. Frequency histogram of bee foraging patterns. The X-axis origin on the left and right panels represents time of sunset and sunrise, respectively. Bars in the left panels represent 2 min intervals, bars in the right panels represent 3 min intervals.

period, *Megalopta* always began foraging after the final diurnal bee visit. The mean time between the last diurnal bee visit and first *Megalopta* visit was 14 ± 15 min (range: 2–40, $n = 7$). There was slight overlap of *Megalopta* foraging with diurnal bees in the morning samples. In one session, we observed one instance of a *Megalopta* foraging 1 min after the first stingless bee arrived. In the every other sample, the last *Megalopta* visit occurred before the first diurnal bee visit. The mean time between the last *Megalopta* visit and the first diurnal bee visit was 23 ± 18 min (range: –1 to 52, $n = 5$).

Moonlight affected diurnal bee foraging, but in opposite directions. Honey bees were more likely than expected to forage until or after 16 min post-sunset (the minimum for overlap with *Megalopta*) on nights when the moon was visible (11 to 17 instances of foraging past 16 min occurred on moonlight nights, with expected probability of 0.4 because moon was visible two of the five nights, exact binomial test two-tailed $P = 0.047$). However, stingless bees were less likely to forage until or after 16 min after sunset on nights when the moon was visible (16 of 50 instances occurred on moonlight nights, expected probability of 0.5 because moon was visible three of the six nights with foraging past 16 min, binomial $P = 0.015$). There was no correlation between the latest diurnal bee visit and first *Megalopta* visit for each day (Spearman's $Rho = 0.26$, $P = 0.57$, $n = 7$). There were also no significant correlations between the number of diurnal bees and *Megalopta* foraging on a given day, nor between stingless bees and honey bees on a given day, nor were there any significant partial correlations between the same variables after controlling for tree site.

Aggression

We observed 101 instances of potentially aggressive behavior (45.5% push, 1% bite, 6.9% no land, 23.8% delay land, 22.8% land and displace). No instances of aggression were observed

between *Megalopta*, even though 24.5% of the scans with *Megalopta* ($N = 106$) contained >1 individual. Of the potentially aggressive interactions that we observed, 30.7% were from honey bees directed toward stingless bees, 28.7% were between honey bees, 11.9% were from stingless bees directed toward honey bees, and 28.7% were between stingless bees. The single instance of biting was between honey bees.

General Observations

Pooled nectar was still present at the end of all the evening observation periods in which the bottom of the flower was visible (in four cases it was not visible), and was present at the beginning of 4 of the 6 morning observation flowers in which the bottom of the flower was visible. The anther had at least some pollen available during all observed foraging periods. Many flowers contained dead, apparently drowned, honey bees or stingless bees floating in the nectar (Fig. 1b, Kays et al. 2012, Brighenti and Brighenti 2010). We never found a dead *Megalopta* floating in the nectar, although we did occasionally see one fall into the nectar and then climb back out. Because the flowers are so large, bees could not gather pollen and nectar at the same time. They either landed on the anther to collect pollen, or climbed down the petals to drink nectar (Fig. 1). Although we could not distinguish nectar versus pollen visits because bees were unmarked and often flew out of the field of view (see Methods), *Megalopta* occasionally switched between nectar and pollen collecting in the same visit without leaving the camera field of view. We never observed males or mating in any of the observed bee species.

Discussion

Megalopta foraging behavior was consistent with the hypothesis that they avoid interference competition from diurnal bees.

Megalopta did not overlap with diurnal bees on *Ochroma* flowers. Ours is the first study of *Megalopta* to analyze data minute by minute and separate observations by flower to explicitly test for overlap, although studies of other *Megalopta* species show results similar to our Fig. 2 (Franco and Gimenes 2011, Krug et al. 2015, Oliveria et al. 2016, Cordeiro et al. 2016).

Moonlight may extend the foraging time of diurnal bees past sunset (reviewed in Kelber et al. 2005, Somanathan et al. 2009, Wcislo and Tierney 2009). However, our data show only a modest and inconsistent effect of moonlight on extending foraging time. *Megalopta* do not extend their foraging with moonlight because they are limited by their ability to navigate back to their nest below the canopy, where moonlight does not penetrate (Kelber et al. 2005), although in a study of other *Megalopta* species in a Brazilian agricultural setting, bees did begin foraging earlier in the morning when moonlight was present (Krug et al. 2015).

As assumed by previous authors (Wcislo et al. 2004), *Megalopta* face little competition for *Ochroma* nectar and pollen after sunset. We saw few *Apoica* and moths. Kays et al. (2012) report that two species of bats and five species of arboreal nocturnal mammals visited *Ochroma* and often left flowers empty, but this typically occurred after the *Megalopta* foraging period; in our observations, we saw one opossum visit and no other vertebrates. Because flowers produced little nectar after midnight (Kays et al. 2012), it is unsurprising that overall visitation rates were low in the morning. Other species of flowers that open late at night are visited by *Megalopta* more frequently in the pre-dawn foraging period (Roulston 1997, Franco and Gimenes 2011, Smith et al. 2012, Krug et al. 2015, Oliveria et al. 2016, Cordeiro et al. 2016).

Our data do not support the hypothesis that *Megalopta* are trying to maximize resource acquisition: flowers were open with copious nectar and pollen well before *Megalopta* began foraging. Floral resources were not limited—there was still enough nectar to literally swim in when *Megalopta* stopped foraging at night—but time was restricted. *Megalopta* typically forage for 20–45 min in the evening, and again in the morning (foraging bouts over an hour are rare; Kelber et al. 2005, A.R.S. pers. obs.). Nevertheless, *Megalopta* did not extend their foraging into daylight to take advantage of available resources—why not?

We can rule out an alternative hypothesis, that the optical adaptations that enable nocturnal vision render *Megalopta* blind in bright light. *Megalopta* that flee their nest upon disturbance during the day return a few minutes later, and, if the nest was removed, orient to the now-empty space where their nest used to be, before starting to search for the nest in expanding circles (A.R.S. pers. obs.). This demonstrates functioning visual navigation during daylight.

Would the eusocial bees displace *Megalopta* if their foraging periods overlapped? Among tropical species, the literature on aggressive monopolization of floral resources by bees focuses on competition between species of stingless bees and honey bees (Johnson and Hubbell 1974, Roubik 1992, Nagamitsu and Inoue 1997, Lichtenberg et al. 2010). Our study found 101 instances of potential aggression, although it is difficult to tell to what extent the interference we observed is incidental or aggressive, with the exception of the single bite that we observed. It seems likely that bee species intolerant of foragers from other social nests would be equally intolerant of solitary foragers, but this hypothesis is untested.

We have anecdotal evidence that *Megalopta* may lose in competition with stingless bees. Two of us (A.R.S and C.Z.) cut a bud of the canopy tree *Pseudobombax septenatum* from a tree and allowed it to open overnight before taking it to a canopy tower on BCI before dawn. *P. septenatum* opens at night, and is gathered by

Megalopta during morning foraging flights on BCI when available. At sunrise we placed chilled *Megalopta* foragers on the flower. In <10 min, the flower, which was not near a *P. septenatum* tree, was discovered by a *Trigona* sp. forager, who proceeded to grab the slow-moving *Megalopta* and throw her off the flower. The same result occurred with a second *Megalopta* placed on the flower. While this interaction was contrived, and an ambient temperature *Megalopta* likely would have flown away, stingless bees are commonly seen foraging on *P. septenatum* flowers shortly after sunrise (A.R.S. pers. obs.). This suggests that pollen and nectar are still available, but that extending foraging time into the daylight would not be productive for *Megalopta* due to interference competition. Unfortunately, because *Megalopta* avoid interactions with diurnal bees, it is difficult to test this prediction in nature, although observations of interactions between stingless bees and diurnal solitary bees may be fruitful.

Perhaps *Megalopta* are not lazy, but efficient. Nocturnal foraging allows *Megalopta* to be such efficient foragers that they can afford to remain nestbound for ≥ 22 h per day guarding their offspring and still be as productive as day-active bees. *Megalopta* nests contain an average of 3.12–7.30 active brood cells, depending on the season and sample (Smith et al. 2007, 2012). These values are similar to other solitary and facultatively social species in the tribe Augochlorini, of which *Megalopta* is a member (see reviews by Sakagami and Michener 1962; Michener 1974; Eickwort and Sakagami 1979; also Packer 1990; Zillikens et al. 2001; Coelho 2002; Wcislo et al. 2003; Brosi et al. 2006; Tierney et al. 2008; Dalmazzo and Roig-Alsina 2012, 2015; Pietsch et al. 2016). Adult presence is required to defend the brood against predatory ants (Smith et al. 2003, 2007). *Megalopta* suffer much lower rates of brood parasitism than most solitary bees (Wcislo et al. 2004). Reducing foraging time, shifting it out of the activity time of parasites, and leaving a guard at the nest can reduce brood parasitism (Goodell 2003, Lienhard et al. 2010, Rehan et al. 2011). It is not clear how important shifting activity time is for brood parasites. Of the two brood parasites that attack the nest, one is a mutillid wasp with unknown temporal niche, and the other is a parasitic species of *Megalopta* that is also nocturnal (Cambra et al. 2005, Biani and Wcislo 2007). However, reducing the time a nest is left unattended likely reduces exposure to enemies (Smith et al. 2003). The ability to gather provisions in a short amount of time because foragers are unmolested may thus indirectly reduce *Megalopta* predation and brood parasitism. *Megalopta* are abundant on BCI (the only site where they have been systematically studied), widespread throughout the Neotropics, and have diversified into ~ 27 species, suggesting that their narrow temporal niche is successful (Wolda and Roubik 1986, Wcislo et al. 2004, Wcislo and Tierney 2009).

Ecologists generally appreciate that both escaping predation pressure and gaining access to new resources can lead to the evolution of new temporal niches (Rydell and Speakman 1995, McCauley et al. 2012, Monterroso et al. 2013, Lima et al. 1999), but interference competition is less often considered (but see Ziv et al. 1993, Kronfeld-Schor and Dayan 2003, Valeix et al. 2007, Harrington et al. 2009, Stuble et al. 2013, Camargo et al. 2016). Here we propose that escaping interference competition may also be important in selecting for a temporal niche shift. By foraging at night, *Megalopta* gain access to nocturnal flowers, but also to competitor-free space (Wcislo et al. 2004, Wcislo and Tierney 2009). Our observations on *Ochroma* flowers, where abundant resources are available but unused before sunset, suggest that interference competition may influence the evolution of nocturnality in *Megalopta*. We hypothesize that efficient foraging without interference, rather than just access to nocturnal flowers, may ultimately benefit *Megalopta* by allowing investment in nest

defense and reduced predation and parasitism. This perspective suggests that the quality of foraging rather than just the quantity of resources available may be a selective benefit of nocturnal foraging.

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