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Daily foraging activity of the Maya bee (*Melipona beecheii*) in Chetumal, México

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Abstract The Maya bee, *Melipona beecheii*, has been an integral part of Mayan culture on the Yucatan Peninsula for several centuries. In the present study, we explore the daily food-foraging behavior of *M. beecheii* during the year and compare its foraging behavior during summer and winter with the foraging behavior of honeybees during the same periods in the Yucatan Peninsula. Annual behavior showed a remarkable tendency toward pollen foraging during the early hours of the day, whereas nectar foraging peaked at midday. Factors such as season, resource, and hour significantly influence the daily activity of *M. beecheii and A. mellifera*. We detected noticeable differences in foraging behavior between summer and winter in both Maya bees and honeybees. Honeybees preferred foraging earlier pollen during winter and nectar during summer, whereas Maya bees preferred foraging pollen earlier during summer. Finally, we observed that both bee species made far more foraging trips during winter than in summer.

Keywords: foraging, nectar, pollen, maya bees, honey bees

1. Introduction

The Maya bee *(Melipona beecheii)* was bred intensively by Yucatan peninsula natives much before the arrival of Europeans on the continent (Echazarreta et al., 1997, Quezada-Euán et al., 2001, Villanueva et al., 2005). This activity, called meliponiculture, is an integral part of Mayan culture in which honey, pollen wax, and other materials are obtained (Quezada-Euán et al., 2001, Villanueva et al., 2005, Pat-Fernández et al., 2018).

Unfortunately, since the middle of the XX century, there has been a noticeable decrease in both meliponiculture and natural populations of bee species (Villanueva et al., 2005, Villanueva et al., 2013a). Multiple factors seem to be causing this decline, such as a loss of knowledge of the technique used to breed and multiply bee nests, deforestation, pollution, and competition with Africanized *honey bees*, among others (Echazarreta et al., 1997, Quezada-Euán et al., 2001, Villanueva et al., 2005, Villanueva et al., 2013b).

In recent decades, some important efforts have been made to recover the Maya species in the zone (Quezada-Euán et al., 2001, Villanueva et al., 2005, Acereto et al., 2006, Villanueva et al., 2013), but to improve the results, it is necessary to understand the biology of the species. Foraging behavior is one of the most important aspects for the survival of bees, for which they provide food for the members of the nest (adults and immatures) (Michener 1974, Roubik 1989, Willmer 2011).

Bee foraging behavior tends to be flexible, so a species can choose different resources from different flowers under different conditions (Kajobe & Echazarreta 2005, Jha & Vandermeer 2009, Ogilvie & Forrest 2017). These foraging choices seem to depend on both internal and external factors (Iwama 1977, Roubik 1989, Biesmeijer et al., 1998, Slaa et al., 2003, Kajobe 2005, Aleixo et al., 2017). Some of the most important internal factors are the brood population in the nest, the number of adults, the reproductive state of the nest, and the amount of food reserves (Eckert 1990, Stone et al., 1999, Hilário et al., 2000, 2007, Nunez-Silva et al., 2010, Oliveira et al., 2012, Di Trani & Villanueva 2018).

In contrast, some of the most important external factors affecting bee foraging are the availability, quantity, and quality of food (Pierrot & Schlindwein 2003, Biesmeijer et al., 1999, Abrol 2006, Fowler et al., 2016). Another important external factor impacting bee foraging is environmental conditions. Numerous studies have demonstrated the influence of factors such as temperature, solar radiation, humidity, and wind speed on the foraging patterns of bees (Iwama 1977, Inoue et al., 1985, Bruijn et al., 1997, Polatto et al., 2014, Di Trani et al., 2022). Environmental conditions can significantly change from one day to the next, but they tend to change much more during the year, either between the four seasons (temperate regions) or between the rainy and dry seasons (tropics) (Roubik 1989, Heard & Hendrikz 1993, Nascimento & Nascimento 2012, Gobatto et al 2013, Vossler 2010, Aleixo et al 2017, Vijayan et al 2018, Di Trani et al., 2022).

The competition for food resources is yet another external factor influencing bee foraging patterns (Roubik 1980, Thomson 2004, Roubik 2009, Yokoi & Fujisaki 2011, Wojcik et al., 2018). Some bee species can aggressively defend their food resources (Johnson & Hubbell 1974, Cairns et al., 2005, Nagamitsu 1997, Reyes-Gonzalez & Zamudio 2020), but exploitative

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interference is seemingly the most common form of competition (Inouye 1978; Schaffer et al., 1979, Balfour et al., 2015). By this approach, a competitor completely or partially consumes the available food resources, leaving the other with an energetic deficit (Jensen 1987, Chouvalova & Limeri 2023), which could hinder its short- or long-term survival. When examining the foraging patterns of a bee species, all these factors need to be considered.

In this work, we attempt to contribute to the understanding of the daily foraging behavior of Maya bees and compare it to honeybee foraging behavior in Quintana Roo (Yucatan Peninsula). This can be decisive in improving bee management, conservation, and exploitation (Carvalho-Zilse et al., 2007, Batista et al., 2018, Freitas et al., 2022).

2. Methodology

The present study took place between 2008 and 2009 in Othon P. Blanco municipality in Chetumal, Quintana Roo. All the Maya bees observed belong to Colegio de la Frontera Sur meliponary, with coordinates 18.5441315-88.2661828.

The climate at the site is tropical semihumid, with average annual rainfall between 1100 and 1300 mm. The average temperatures are between 18.8°C and 33°C, but each winter, the zone is impacted by cold fronts, causing a remarkable drop in temperature. Most of the vegetation in the region is low ever-green, and some of the most common plant species are *Piscidia piscipula, Talisia olivaeformis, Sideroxylon foetidissimum, Poteria campechiana, Swartzia cubensis, Sabal yapa, and Brosimnum alicastrum* (SEDATU 2024).

For the first part of this study, we registered the bees that returned to three nests of M. beecheii and the food resources they carried (pollen or nectar) during the first 15 minutes each hour, from 6:00 to 16:00 hours. The observations were carried out for nine consecutive days every two months, from June 2008 to June 2009, at Colegio de la Frontera Sur meliponary.

For the second part of the study, we registered the bees returning to three Maya bees' nests and three honeybee hives every 15 minutes on three lapses on the day, at 6:00--8:00 hours, 11:00--13:00 hours, and from 16:00--18:00 hours. The observations took place for 15 consecutive days, once in winter (January) and once in the summer of 2009 (July). For the honeybee observations, we placed three honeybee hives on a secondary forest patch approximately 2 km from Colegio de la Frontera Sur meliponary, and for the Maya bee observations, we selected three nests on the meliponary.

The information was introduced in tables, processed, and graphed. The observations of *M. beecheii and A. mellifera* were analyzed with a Generalized Additive Model for Location Scale and Shape (GAMLSS) with a Negative Binomial distribution, and P-splines for continuous predictors were employed, where these continuous predictors include time (transformed continuously) and days. The variables “season” and “resource” complement the model, which has “bee abundance” as the dependent variable. The gamlss package in R was used.

3. Results

3.1. Foraging patterns during the year

We observed low accumulated foraging activity during the first observation hour (6:00 hrs) for nectar and more intense activity for pollen trips. Most pollen-foraging trips occurred during the first five observation hours (6:00 to 11:00), peaking at 7:00 and 8:00 hours. Nectar foraging, on the other hand, followed a bell pattern, with activity peaking around midday (11:00 and 12:00 hours).

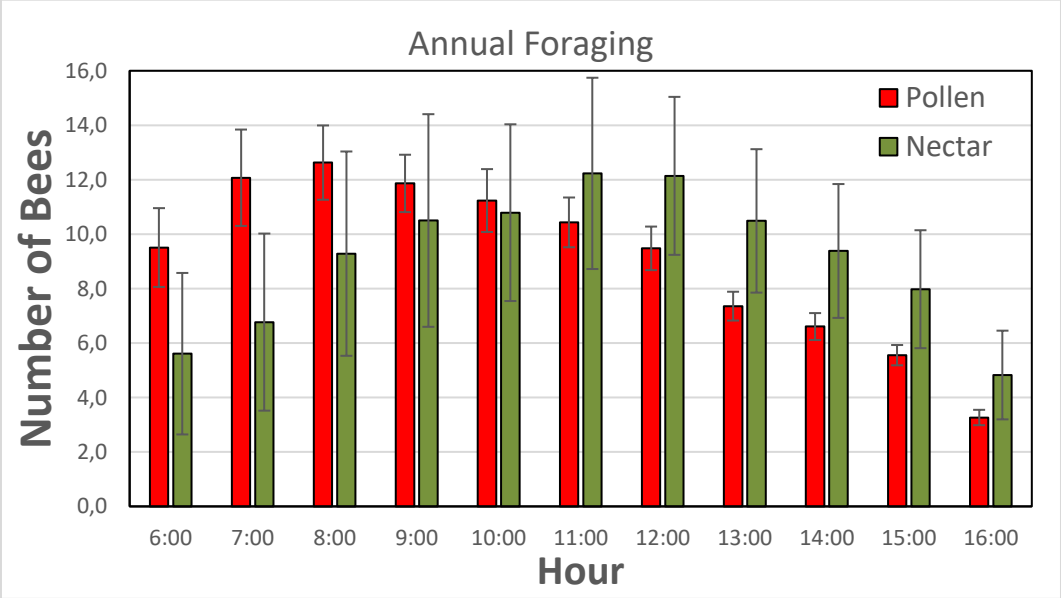

Figure 1 Daily food foraging of Maya bees. *Source*: *M. Beecheii* (June 2008 to June 2009).

3.2. Bimonthly foraging patterns

Bees showed a clear preference for pollen foraging in the first hours of the day, between 6:00 and 8:00 hours, particularly at 7:00 hours, when peak foraging activity occurred for most of the months. Then, activity tends to decline after 9:00 hours and is minimal after midday, except for the winter months (December and February), when there is still noticeable activity late in the day.

In general, August had the most pollen-foraging trips in an hour (7:00 hours), but February was the month with the most pollen-foraging trips, when pollen-foraging trips occurred between 9:00 and 12:00 hours.

The number of nectar foraging trips was low during the first hour and then gradually increased until peaking around midday, after which it declined again from 14:00 to 15:00. The nectar peak hour was variable during the months, occurring at 9:00 hours for June 2008, June 2009, and December, at 12:00 hours for August and October, and at 14:00 hours for February.

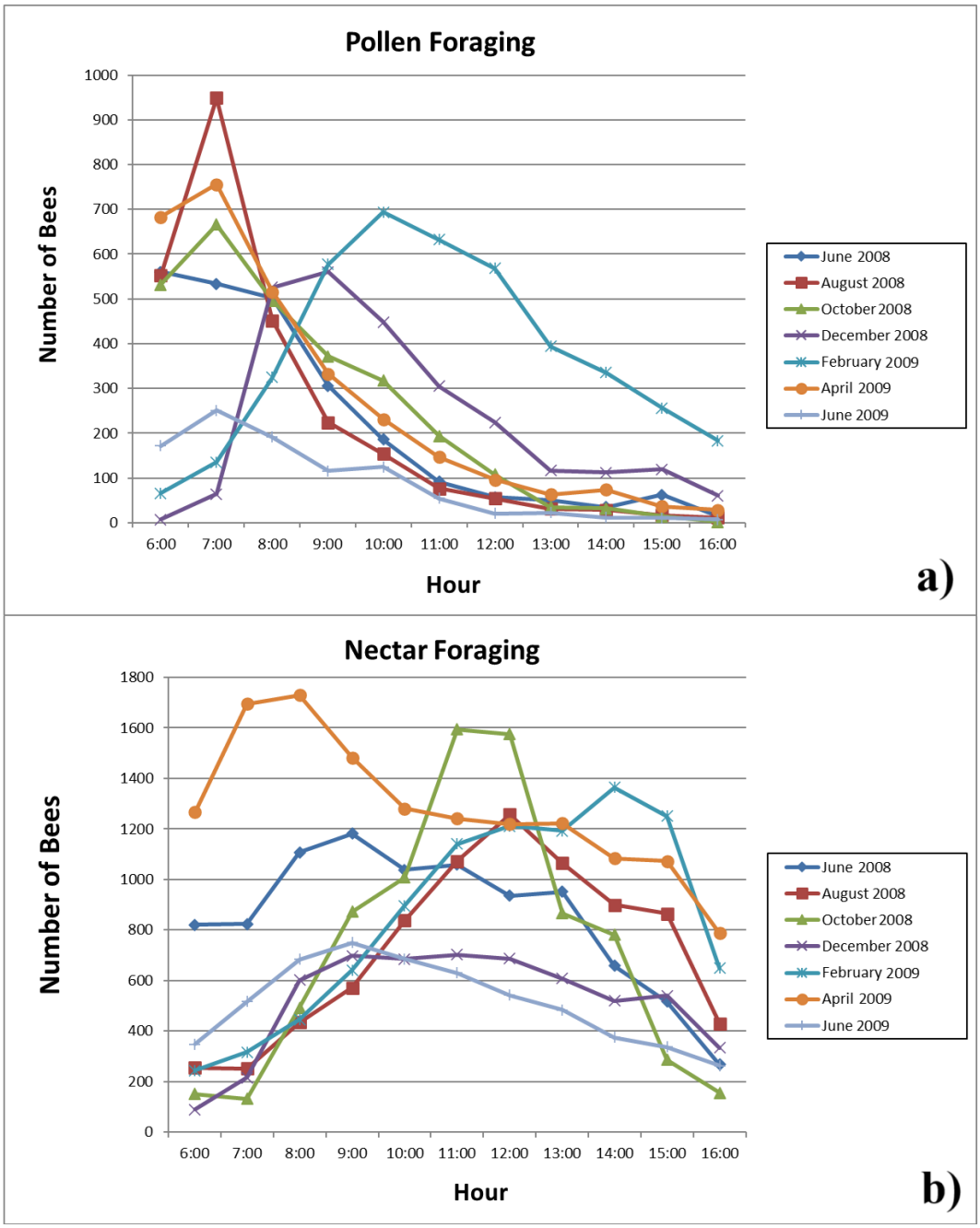

Figure 2 Bimonthly daily foraging activity of *Maya bees* from June 2008 to June 2009.

3.3. Maya bees and honeybees: Comparative observations

3.3.1. Pollen foraging

Honeybees exhibited a similar pollen foraging pattern between winter and summer; they were especially active during the early hours of the day, peaking at approximately 7:00 hours and then declining. However, during winter, the pollen-foraging peak extended to 8:00.

The Maya bees, on the other hand, presented a contrasting pollen foraging pattern between winter and summer. In summer, pollen foraging peaked at approximately 7:00 (similarly to honeybees), then declined and ceased at 17:00. During the winter, the Maya bee activity peaked late in the morning, between 11:00 and 12:00, and then decreased, but the bees remained active after 17:00 hours.

When we compared the bee species, we detected a noticeable difference when they began foraging for pollen, with honeybees beginning before 6:00 and Maya bees beginning after 6:15 hours.

Finally, the total number of pollen-foraging trips in winter almost doubled the number of summer foraging trips for both bee species.

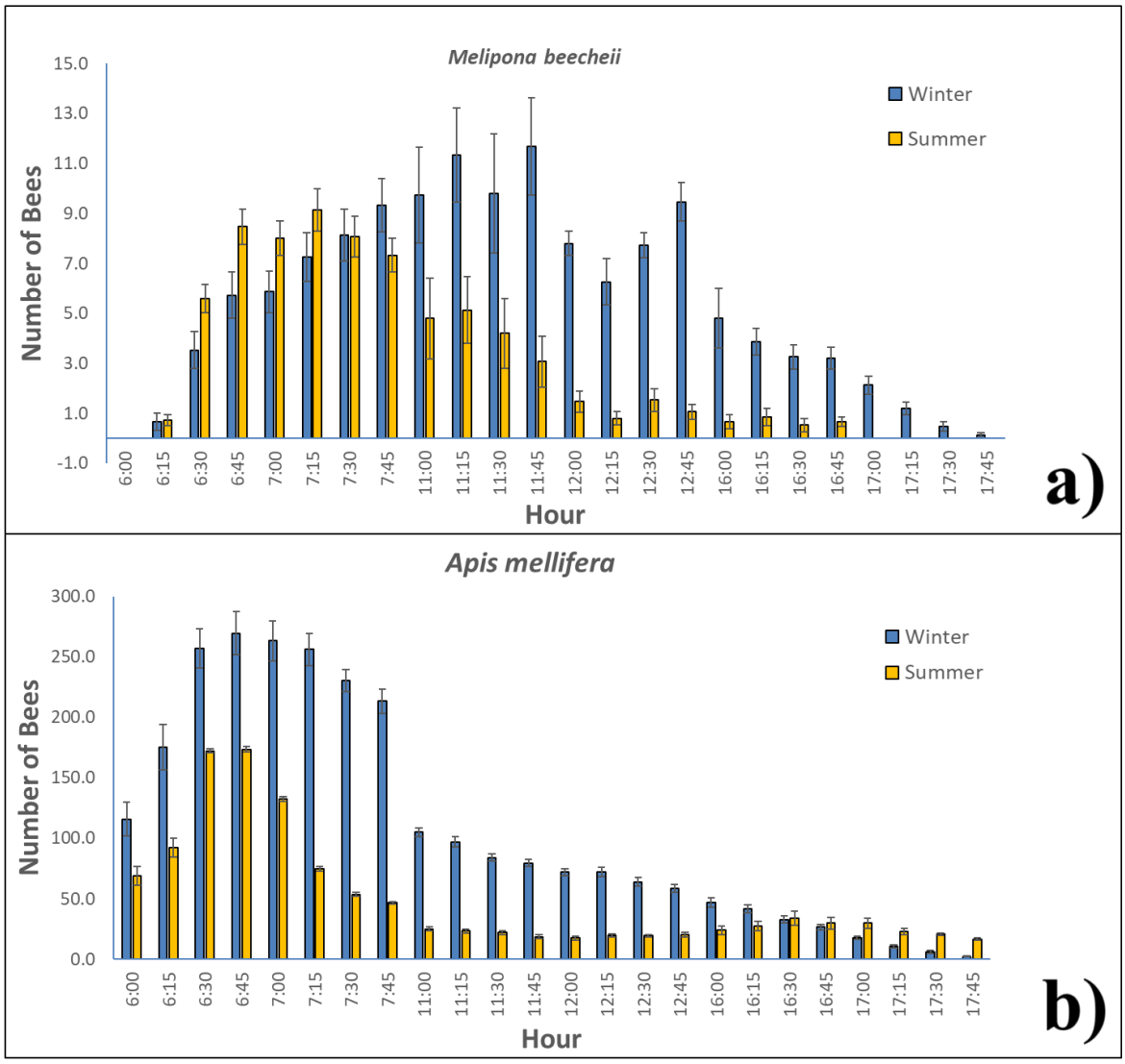

Figure 3 Daily pollen-foraging behavior of Maya bees (a) and *honey bees* (b) in winter and summer.

3.3.2. Nectar foraging

Nectar foraging patterns for honeybees differ between summer and winter. During winter, activity peaks early in the morning, between 6:00 and 7:00, and then decreases. In contrast, nectar-foraging activity in the summer was more uniform, with similar values occurring between 7:00 and 16:00 hours.

The Maya bees presented a similar nectar-foraging pattern between summer and winter, peaking around midday.

Nectar foraging also began earlier for honeybees, with honeybees active before 6:00 hours, and limited Maya bees foraging trips during 6:00 and 6:15 hours.

Similar to the total number of pollen-foraging trips, nectar-foraging trips during winter almost doubled the number of foraging trips during summer.

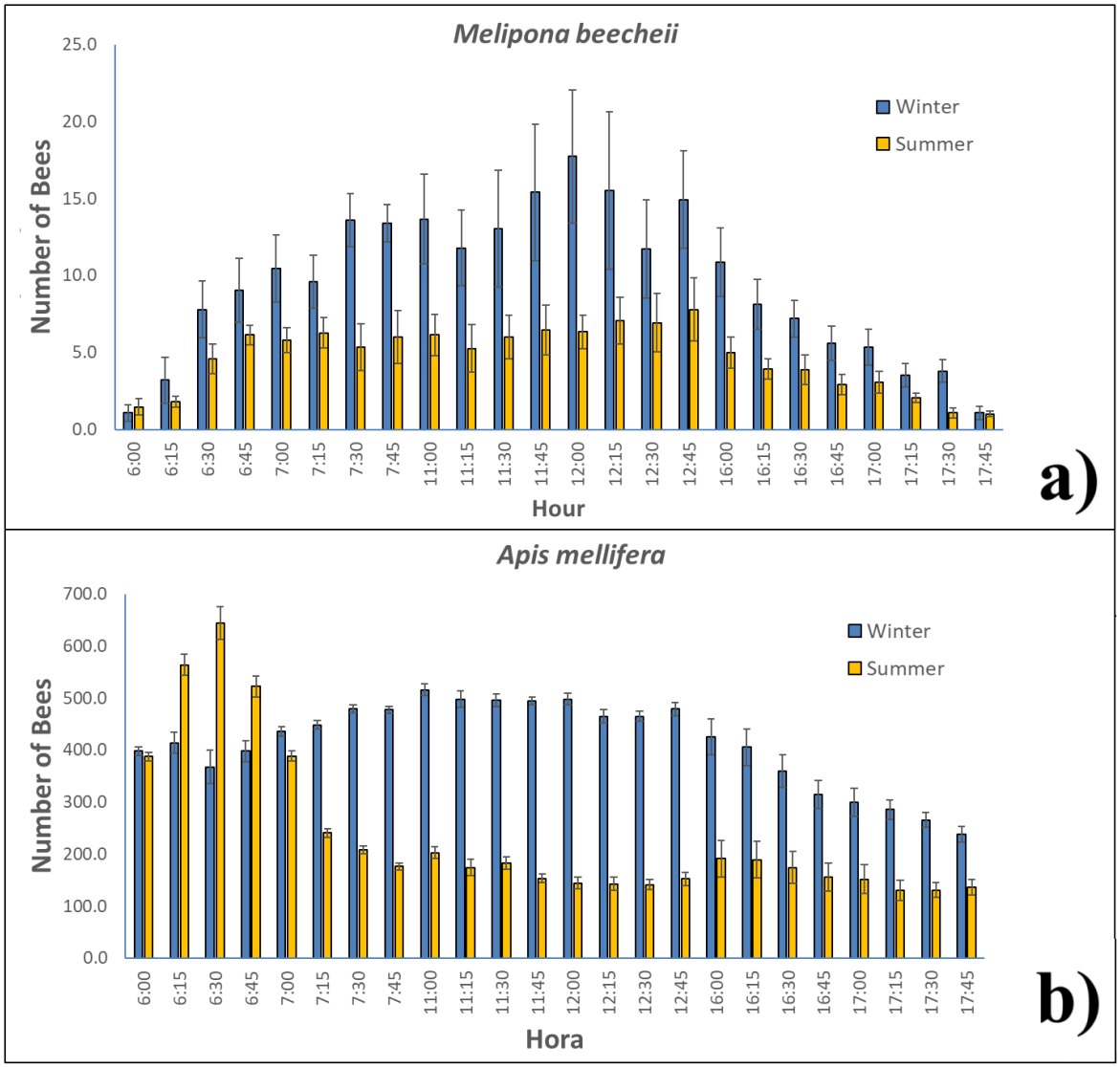

Figure 4 Daily nectar-foraging behavior of *Maya bees* (a) and *honey bees* (b) in winter and summer.

The analyzed variables had a significant influence on bee activity for both bee species, except for "Day", which was significant for only *A. mellifera.*

Table 1 P values obtained with the GAMLSS model for time, day, resource, and season variables for *M. beecheii and A. mellifera.*

Variable	*M. beecheii*	*A. mellifera*
Time	<0.0001	<0.0001
Day	0.266	0.023
Resource	<0.0001	<0.0001
Season	<0.0001	<0.0001

4. Discussion

4.1. Foraging patterns during the year

The daily food-foraging behavior we recorded during the year coincided with the foraging behavior observed for the *Maya bees* in Costa Rica (Bruijn & Sommijer 1997) and other Melipona species, such as *M. fasciata, M. quadrifasciata and M. rufiventris* (Bruijn & Sommijer 1997, Fidalgo & Kleinert 2007, Oliveira et al., 2014).

The early pollen foraging pattern (Figure 1) can be attributed to the limited nature of the resource, which has gradually decreased since dehiscence (Roubik 1989, Tepedino et al., 2016), so it represents a priority for social bees, who need to secure the food supply for numerous broods.

On the other hand, nectar is continuously produced by flowers, but its sugar concentration tends to change during the day due to environmental temperature and humidity (Deppe et al., 2000, Corbet 2003, Nicolson et al., 2013). In this case, the daily collection peak at midday (Figure 1) could reflect bee preferences for the specific properties of the nectar during those hours.

4.2. Bimonthly foraging patterns

The difference observed in daily foraging patterns between months, especially in pollen collection, seems to be related to the differences in environmental conditions due to seasonality. This is especially remarkable during the winter months (December and February), when Maya bees seem to delay the beginning of their foraging activities until later in the day, when conditions are warmer (Figure 2a). In any case, bees seem to "compensate" for the delay in their activities during winter by extending their foraging activities until later in the day (Figure 2a).

However, in the winter months, the beginning of bee foraging activity seems to be determined by temperature; during the remainder of the year, when temperatures are relatively stable, other environmental conditions, such as illumination, could determine the initiation of foraging activities, as suggested by Streinzer et al., (2016). They reported that before the beginning of foraging, bees piled up at the nest entrance until a critical value of illumination triggered the foraging activities of the bees. This critical value was different for each bee species and depended on their body size.

It would be interesting to learn if the food resources that bees collect later in the day are of the same quality as those that bees miss early in the day and if *M. beecheii* populations inhabiting zones not impacted by cold fronts show the same delay in their beginning of foraging activities during the winter.

During the remainder of the year, once again, we noticed that pollen collection was concentrated during the first hours of the day (Figure. 2a), as discussed previously.

Nectar, on the other hand, tends to be collected around midday, except in spring (April) and early summer (June), when nectar collection peaks earlier in the day (Figure. 2b), probably because of the abundance of flower rewards during those months (Juliani 1967, Winston 1980, 1987, Villanueva-Gutierrez et al., 2015).

4.3. Compared foraging activity

One of the most notable observations of foraging activity for both Maya bees and honeybees is that they are much more active during winter (January) than in summer (July) (Figures 3, 4).

The pollen foraging pattern seems to make little sense (Figure. 3a, b) if we consider that pollen is used for feeding the larvae and that many stingless bee species experience diapause during the winter. Additionally, previous studies in this zone revealed that Maya bee pollen reserves were at their maximum and that the brood cell averages were the lowest during winter (February) (Di Trani & Villanueva 2018). However, this could be the result of the bees preparing in advance for the explosion of the immature population during spring and summer, which is frequently observed in bees (Nogueira-Neto 1999, Borges & Blochtein 2006, Alves et al., 2009, Dos Santos et al., 2015).

On the other hand, the large number of nectar-foraging trips (Figure 4a, b) concurs with the lowest levels of honey reserves observed for Maya bees in the zone during the winter (Di Trani & Villanueva 2018). This pattern could be the result of the bees trying to restore the depleted honey reserves and the necessity of feeding a large number of bees foraging during the day.

An alternate explanation for the large number of foraging trips during winter could be that flowers are more scarce in winter (Juliani 1967, Winston 1980, 1987, Villanueva-Gutierrez et al., 2015), so more trips could be needed to satisfy food needs on the nest. However, pollen reserves were high during the winter in previous studies in the zone (Di Trani & Villanueva 2018), so bees did not have an immediate need for pollen.

As observed in the previous year's observations, we can see a remarkable delay in the beginning of the foraging activities of Maya bees during the winter (January) (Figures 3, 4). This coincides with the lowest temperatures for the zone during the year according to the local meteorological station (Colegio de la Frontera Sur, Chetumal), which registered temperatures as low as 10°C at 6:00 hours during the month.

Studies conducted on Maya bees by Macías-Macías et al., (2011) demonstrated that bees can survive at temperatures below 5°C; however, this species is sensitive to low temperatures, so it is expected to have a noticeable effect on the foraging behavior of bees. Studies on Melipona quadrifasciata and Melipona marginata have shown that the beginning of foraging activities occurred at 13°C and 14--18°C, respectively (Guibu & Imperatriz-Fonseca 1984, Kleinert-Giovannini & Imperatriz-Fonseca 1986).

In addition to the direct impact of low temperatures on the flying activity of forager bees, these bees could switch to thermoregulation activities inside the nest under low temperatures, as reported in other stingless bee species (Fletcher &

Crewe 1981, Engels et al., 1995, Jones & Oldroyd 2006). According to Hilario et al., (2000), this activity is especially crucial in "weak" nests (Hilario et al., 2000), which tend to delay their foraging activities for several hours at low temperatures.

The honeybees, in contrast, did not show a noticeable difference at the beginning of foraging activities between winter and summer (Figures 3, 4). Larger bees can fly under lower temperature conditions (Willmer 1983, Pereboom & Biesmeijer 2003, Texeira & Campos 2005, Gouw & Gimenes 2013). Additionally, honeybees have various internal temperature control mechanisms (Willmer & Stone 2004, Polatto et al., 2014). Furthermore, honeybee nests are considerably larger than Maya bee nests are (Van Veen & Arce 1999, Michener 2000, Hepburn et al., 2014), so honeybee nests probably do not need to invest a noteworthy part of the foraging bee population in thermoregulation duties due to heat retention (Roubik 1989, Goulson 2003).

The delay in foraging activities by Maya bees during the winter could be disadvantageous when they compete for food resources with honeybees. This competition can be caused by interference or exploitation. Previous studies in this zone (Quintana Roo) reported that honeybees attack other stingless bees when foraging (Cairns et al., 2005). On the other hand, it has been reported that Maya bees and honeybees can antagonize many of the same food resources in a locality (Leal-Ramos & León-Sánchez 2013). When Maya bees begin foraging during the winter, thousands of honeybees have already extracted some of their food resources from flowers, which is especially relevant for limited resources such as pollen (Roubik 1989, Tepedino et al., 2016). Dafni and Shmida (1996) observed in Mount Carmel, Israel, that introduced Bombus terrestris started foraging early in the day, causing a clear reduction in the food resources available for native bees, resulting in displacement. In the case of Maya bees vs. honeybees, the effect could be more severe due to the vast difference in the foraging force between honeybees and Maya bees. Therefore, especially during winter, Maya bees may be forced to forage in depleted flowers, fly farther distances or forage in flowers with inferior-quality food resources as a result of asymmetric competition with honeybees (Goulson 2003). This can be especially challenging for "weak" maya bee nests, leading to their collapse, as observed in a previous study in the zone (Di Trani & Villanueva-Gutiérrez 2018).

In general, bee activity was influenced by most of the considered variables (season, resources, and hour), except "Day" (Table 1). This was to be expected, since environmental conditions do not change much from one day to another in the area, according to the local weather station (Colegio de la Frontera Sur, Chetumal). In contrast, the environmental conditions between seasons (summer and winter) tend to sharply differ, influencing the foraging activity of the bees, with considerably more foraging trips during winter. On the other hand, pollen tends to be available in flowers only during the first hours of the day, so bees forage this resource only during a short lapse in the day, in contrast with nectar foraging, which takes place continuously until the end of the day. Thus, many more nectar-foraging trips are expected to occur, and there is a significant difference between trips for each resource.

5. Conclusion

The Maya bees in Quintana Roo exhibited different foraging patterns during the day for pollen and nectar and during the year, likely in response to the availability and quality of the food resources in the environment and the ability to reign environmental conditions such as temperature and illumination. The daily foraging behavior of Maya and honey bees also markedly differed, which can be attributed to the biology of each species and how they interact with the external conditions in the zone. The earlier foraging activity of honeybees probably gives the species a competitive edge over the Maya bees in the zone.

Acknowledgments

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Ethical Considerations

Bees were not harmed during the observations for this study.

Conflicts of Interest

The authors declare no conflicts of interests

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