Foraging patterns of bees in watermelon (*Citrullus lanatus* Thunb.) flowers in Panama

Juan Carlos Di Trani | Virginia Meléndez Ramírez | Anovel Barba | Yostin Añino

1. Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mexico.
2. Instituto de Innovación Agropecuaria de Panamá, Divisa, Panamá.

**Abstract** The foraging patterns of bees in watermelon (*Citrullus lanatus* Thunb.) flowers were investigated in Los Santos, Panama, over a period of 84 observation days. The study aimed to identify the bee species visiting the flowers, their daily visitation rates, and the resources they foraged. The majority of visits were made by native bees, particularly stingless bees, suggesting their crucial role in pollinating watermelon crops in the area. The most frequently observed bee species visiting the flowers were *N. perilampoides* (58.7%), *A. mellifera* (23%), and *P. peckolti* (4%). Nectar was the primary resource foraged by most bees, with comparable visitation rates for both male (staminate) and female (pistillate) flowers. Honeybees allocated nearly half of their visits (47.7%) for pollen collection, and the majority of their daily visits occurred between 7:00 and 8:00 hours. In contrast, stingless bee visits peaked between 8:00 and 9:00 hours. Nectar visits were shorter in duration than pollen visits, with honeybees exhibiting the shortest durations when visiting watermelon flowers. Significant variations were observed in the daily foraging patterns among bee species during the 84-h observation period (Friedman $P < 0.05$). Additionally, bee characteristics such as size, color, and sociability, along with the time of day, significantly influenced flower visits for resources (GLMM $P < 0.05$). These findings contribute to the understanding of Central American bee species' behavior, aid in their conservation and management and have implications for enhancing fruit production in local watermelon crops.

**Keywords**: bee foraging, duration, nectar, pollen, visits, watermelon

1. Introduction

Watermelon, which produced approximately 101.6 million metric tons worldwide in 2020 (FAO 2020), ranks among the most significant fruit crops globally. Being a monoecious plant, watermelon produces flowers with separate male (staminate) and female (pistillate) sexual parts (Adlerz 1966; Delaplane and Mayer 2000). Consequently, these flowers heavily rely on external agents for pollination and the subsequent production of commercially viable fruits (Adlerz 1966; Stanghellini et al. 1998; Gianini et al. 2015). Therefore, factors such as visitation frequency and bee foraging behavior play crucial roles in determining the quantity and quality of watermelon fruits by facilitating the transfer of pollen grains from staminate to pistillate flowers (Adlerz 1966; Stanghellini et al. 1998; Walters 2005; Bomfim et al. 2014; Garantonakis et al. 2016; Campbell et al. 2018).

Although honeybees are globally recognized as the most important species for watermelon pollination (Delaplane and Mayer 2000; Bomfim et al. 2013), a diverse array of other bee species also visit watermelon flowers, contributing significantly to crop pollination (Meléndez et al. 2002; Pinkus-Rendon et al. 2005; Henne et al. 2012; Bomfim 2013; Garantonakis et al. 2016; Campbell et al. 2019; Rodrigo et al. 2021). To ensure watermelon pollination, common practice involves introducing honeybee hives to crops (Delaplane and Mayer 2000; Bomfim et al. 2013), often leading to the placement of local bee species (Meléndez et al. 2002; Pinkus-Rendon et al. 2005; Machinis and Forrest 2019; Layek et al. 2021). This practice, coupled with intensive apiculture and habitat destruction (Roubik 1992b; Buchmann and Nabhan 2012), can diminish the contribution of native bees to crop pollination. This is particularly noteworthy because certain native bee species have demonstrated a complementary role in watermelon pollination and, at times, exhibit greater efficiency than honeybees (Njoroge et al. 2004, 2010; Spicer 2007; Campbell et al. 2018). Additionally, in temperate zones, certain bumblebee species have been employed as alternative pollinators in watermelon crops (Stanghellini et al. 1998, 2002; Spicer 2007).

In contrast, the Neotropics, where highly social bees predominate (Roubik 2012), have seen only a limited number of studies focused on bees visiting watermelon, with a few conducted in Mexico (Meléndez et al. 2002; Pinkus-Rendon et al. 2005) and Brazil (Malerbo-Souza et al. 1999; Souza and Malerbo 2005; Bonfim 2013; Chaves 2013). Moreover, most studies on bees in watermelon have primarily described bee frequency or diversity rather than analyzing their behavior within the flowers. This is significant because a bee's contribution to pollination depends not only on the number of visits but also on other factors, such as bee morphology, collected resources, visit duration, and the time of day they visit the flowers (Willmer 2011; Freitas 2013). In this study, the aim is to analyze bee visitors to watermelon crops in Los Santos, Panama. Specifically, we investigate their daily
foraging patterns on staminate and pistillate flowers, the resources they collect, the duration of their visits, and the impact of certain bee characteristics on their foraging behavior.

2. Materials and Methods

2.1. Study Area

The study area focused on the observation of visitors to watermelon flowers within crops located in Villa Lourdes, Los Santos, Republic of Panama (coordinates: 7°48′59.8″N 80°28′30.8″W). This region falls within the Azuero Peninsula, characterized as a dry forest area based on the Holdridge classification. The area predominantly consists of lowlands, with an elevation of approximately 15 meters above sea level, and experiences an average annual rainfall ranging from 1000 to 1600 mm (ANAM 2009).

Cucurbit crops, including watermelon, melon, and squash, are commonly cultivated in the region, with their production primarily taking place during the dry season from January to April (Barba et al. 2015). While a few forested patches remain in the peninsula, most of the original vegetation has been degraded to make way for agriculture and cattle ranching (Bennett 1965). The prevailing tree species include Jatropha curcas, Bursera simaruba, Gliricidia sepium, Spondias mombin, Cedrela odorata, Guazuma ulmifolia, and Cordia alliadora (Metzel and Montagnini 2014).

Observations were conducted between December and April 2020 in six crops spread across four adjacent fields, with two fields being replanted. Each crop covered an area of approximately one hectare, and they were planted alternately to ensure noncoinciding flowering periods (Figure 1). The observation period for each crop field lasted approximately three weeks, starting from the initial flowering stage of the crop.

![Figure 1 Panama map with details of the study site (7°48′59.8″N 80°28′30.8″W).](image)

2.2. Observations

Observations were conducted for a total of 84 days, during which we employed a random selection process to choose one plant daily within a watermelon crop. The focus of our observations was on insects visiting both male (staminate) and female (pistillate) flowers. Each hour, from 7:00 to 13:00, we allocated 20-minute intervals to observe these flowers. The observation distance ranged from 1 to 2 meters, and we followed a modified methodology based on Vededele et al. (2006) and Polatto et al. (2014).

During these observations, we recorded various details for each visiting insect, including their identity, duration of the visit, the gender of the flower visited, and the floral resources they collected. Specifically, we considered visits only when the insect made contact with the sexual structures of the flower and remained on the flower for more than one second. To identify the bees, we relied on previous sampling of bees that had been observed visiting watermelon flowers in the crops. Additionally, we conducted manual net collections of bees visiting watermelon flowers for 20-minute intervals at 8:00 and 9:00 hours daily over a period of three weeks.

The collected bees were subsequently identified using a combination of identification keys, including Schwarz (1934), Michener (1954), Roubik (1992a), Michener et al. (1994), Michener (2000), Gonzáles et al. (2009), and Bonet and Vergara (2019).

2.3. Statistical analysis

For the statistical analysis, bee species were included only if they accounted for at least 1% of the total visits recorded during the 84-day observation period. The daily foraging patterns of each bee species on each floral resource (pollen/nectar) were determined by totaling the visits per hour. Subsequently, a comparison of daily patterns between bee species was conducted using the nonparametric Friedman test.

To assess the influence of bee characteristics (size, color, sociability) and the timing of visits on the number of visits for food resources (pollen/nectar) on the flowers, a generalized linear mixed model (GLMM) test was performed. The size of the bee species or genus utilized in the test was determined based on the average length of 30 individuals collected during the preliminary sampling whenever possible.
When species-specific information was unavailable, the size was determined based on the genus (Table 2).

Regarding the classification of bee color, species were categorized as "dark bees" if more than two-thirds of their cuticle exhibited dark colors (black or brown). Conversely, species were classified as "light-colored bees" if more than one-third of their cuticle was dark (Table 2). The social networking of bee species was classified as either highly social or solitary/primitively social based on available information about the genus or species from sources such as Michener (1954), Michener (2000), Gonzáles et al. (2009), and Bonet and Vergara (2019).

In the GLMM model, the hour of the visit was considered the fixed factor, while the foraged resource (pollen or nectar) was the random factor. The statistical analysis was performed using R Studio with the "Tidyverse" package for the Friedman test and the "Nml" package for the GLMM tests.

### Table 1 Visitors observed watermelon flowers during the 84 days of observation, detailing the sex of the visited flower and relative abundance (%) for each species.

<table>
<thead>
<tr>
<th>Bee Species</th>
<th>Staminate Flowers</th>
<th>Pistillate Flowers</th>
<th>Relative Abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apis mellifera</em></td>
<td>984</td>
<td>351</td>
<td>22.7</td>
</tr>
<tr>
<td><em>Nannotrigona perlampoides</em></td>
<td>1933</td>
<td>1481</td>
<td>58.0</td>
</tr>
<tr>
<td><em>Partamona peckolti</em></td>
<td>130</td>
<td>100</td>
<td>3.9</td>
</tr>
<tr>
<td><em>Trigona corvina</em></td>
<td>14</td>
<td>11</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Trigona fulviventris</em></td>
<td>11</td>
<td>4</td>
<td>0.3</td>
</tr>
<tr>
<td><em>Tetragona perangulata</em></td>
<td>58</td>
<td>21</td>
<td>1.3</td>
</tr>
<tr>
<td><em>Frieseomelitta paupera</em></td>
<td>56</td>
<td>26</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Melipona phenax</em></td>
<td>10</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Melissodes tepaneca</em></td>
<td>3</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td><em>Calliopsis hondurasica</em></td>
<td>1</td>
<td>-</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Megachile sp.</em></td>
<td>1</td>
<td>-</td>
<td>0.0</td>
</tr>
<tr>
<td><em>LasioGLOSSUM spp.</em></td>
<td>99</td>
<td>94</td>
<td>3.3</td>
</tr>
<tr>
<td><em>Augochloropsis spp.</em></td>
<td>86</td>
<td>100</td>
<td>3.2</td>
</tr>
<tr>
<td><em>Augochloropsis spp.</em></td>
<td>63</td>
<td>98</td>
<td>2.7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Non-Bees</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Vespidae</td>
<td>10</td>
<td>12</td>
<td>0.4</td>
</tr>
<tr>
<td>Muscidae</td>
<td>6</td>
<td>7</td>
<td>0.2</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>3</td>
<td>3</td>
<td>0.1</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td>42</td>
<td>40</td>
<td>1.4</td>
</tr>
<tr>
<td>Pieridae</td>
<td>8</td>
<td>4</td>
<td>0.2</td>
</tr>
<tr>
<td>Lycaeidae</td>
<td>2</td>
<td>3</td>
<td>0.1</td>
</tr>
<tr>
<td>Nymphalidae</td>
<td>8</td>
<td>3</td>
<td>0.2</td>
</tr>
</tbody>
</table>

### 3. Results

#### 3.1. Floral visitors

Watermelon flowers were predominantly visited by *N. perlampoides* bees, accounting for 58% of the visits. The second most frequent bee species were honeybees, which accounted for approximately one-quarter of the total flower visits (22.7%). Other bee visitors included *P. peckolti* (4%), *LasioGLOSSUM* spp. (3.3%), *Augochloropsis* spp. (3.2%), and *Augochloropsis* spp. (2.7%) (Table 1). Staminate flowers were preferred by most social bees, and the proportion of visits to staminate and pistillate flowers was similar in Halictid species (Table 1). Among nonbee visitors, Hesperiidae butterflies, particularly of the *Urbanus* genus, were the most frequent, representing approximately 1% of the total flower visits (Table 1).

#### 3.2. Floral resources foraging

##### 3.2.1. Pollen

Pollen foraging, represented by staminate flowers, accounted for approximately one-third (31.5%) of the total visits recorded (Table 1). The highest proportion of pollen visits among bee species was observed in honeybees, with more than half of the visits (51.4%) (Table 1). *N. perlampoides* was the second most frequent visitor for pollen, representing approximately one-third (37.8%) of their visits.
total visits (Table 2). The remaining species accounted for only approximately 10% of pollen visits (Table 2). The majority of pollen visits occurred between 7:00 and 9:00 hours, after which pollen visits ceased (Figure 2). Honeybees, *T. perangulata*, and *F. paupera* had peak pollen visits at 7:00 hours, followed by a decline, while *N. perilampoides* and *P. peckolti* peaked at 8:00 hours. On average, pollen visits took longer (17.2 ±SE s) than nectar visits (12.2 ±SE s). Generally, honeybee visits were the shortest, both for pollen and nectar, while pollen visits of *N. perilampoides* and *P. peckolti* were the longest (23.5 ± SE and 23.4 ± SE s, respectively) (Figures 3a, 3b and 3c).

**Table 2** Bee characteristics and number of visits for each floral resource for the analyzed bee species during the 84-day observation period.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apis mellifera</em></td>
<td>10.7</td>
<td>Light</td>
<td>High Social</td>
<td>637</td>
<td>347</td>
<td>351</td>
</tr>
<tr>
<td><em>Nannotrigona perilampoides</em></td>
<td>4.1</td>
<td>Dark</td>
<td>High Social</td>
<td>469</td>
<td>1464</td>
<td>1481</td>
</tr>
<tr>
<td><em>Partamona peckolti</em></td>
<td>5.2</td>
<td>Dark</td>
<td>High Social</td>
<td>74</td>
<td>56</td>
<td>100</td>
</tr>
<tr>
<td><em>Tetragona perangulata</em></td>
<td>7.0</td>
<td>Light</td>
<td>High Social</td>
<td>37</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td><em>Frieseomelitta paupera</em></td>
<td>5.3</td>
<td>Dark</td>
<td>High Social</td>
<td>22</td>
<td>34</td>
<td>26</td>
</tr>
<tr>
<td><em>Lasioglossum spp.</em></td>
<td>6.2</td>
<td>Light</td>
<td>solitary/primitiv soc</td>
<td>6</td>
<td>93</td>
<td>94</td>
</tr>
<tr>
<td><em>Augochlora spp.</em></td>
<td>6.8</td>
<td>Light</td>
<td>solitary/primitiv soc</td>
<td>0</td>
<td>86</td>
<td>100</td>
</tr>
<tr>
<td><em>Augochloropsis spp.</em></td>
<td>6.9</td>
<td>Light</td>
<td>solitary/primitiv soc</td>
<td>0</td>
<td>63</td>
<td>98</td>
</tr>
</tbody>
</table>

**Figure 2** Visit proportion (%) for each floral resource and flower sex for each bee species during the 84-day observation period.
3.2.2. Nectar

A similar proportion of nectar visits was observed between staminate and pistillate flowers for most bee species, except for *P. peckolti* and *Augochloropsis* spp., which showed a preference for nectar from pistillate flowers (Table 2). The majority of nectar visits were made by *N. perilampoides*, accounting for almost two-thirds of the total observed nectar visits (Tables 1 and 2). Honeybees followed with nectar visits, representing only 17% of the total visits (Table 1). The remaining bee species accounted for less than 10% of the total nectar visits (Table 1). Nectar visits on staminate flowers for most bee species were concentrated between 9:00 and 10:00 hours. In contrast, honeybees made most of their nectar visits at 7:00 and gradually declined thereafter (Figure 2). Nectar visits on pistillate flowers by honeybees and *T. perangulata* primarily occurred between 7:00 and 8:00 hours. On the other hand, *N. perilampoides* and *F. paupera* peaked at 9:00 hours (Figure 2), and *P. peckolti* peaked at 8:00 (Figure 2). Visits for nectar on pistillate flowers took longer (13.2 ±SE s) than visits for nectar on staminate flowers (11.2 ±SE s). *F. paupera* had the longest visits for nectar on both staminate and pistillate flowers, averaging 16.9 ±SE and 22.2 ±SE seconds, respectively. Significant differences were found in the daily foraging pattern between bee species for pollen collection (Friedman *P* < 0.0001), nectar on staminate flowers (Friedman *P* = 0.0000832), and nectar on pistillate flowers (Friedman *P* < 0.0001).

3.4. Bee characteristics and number of visits

The number of visits for resources recorded on the flowers was influenced by bee characteristics (size, coloration, and sociability) and the hour, as indicated by our analyses (GLMM *P* < 0.05) (Table 3).

![Figure 3](https://www.jabbnet.com/a.png) Average visit duration (seconds) for each bee species foraging on a) pollen (staminate flowers), b) nectar on staminate flowers, and c) nectar on pistillate flowers during the 84 days of observation.
4. Discussion

4.1. Floral visitors

Watermelon flowers are predominantly visited by the relatively common stingless bee species *N. perilampoides* in Panama and Central America (Urefia et al. 2022). Similar findings have been reported in Brazil, where other stingless bee species were identified as the most frequent visitors to watermelon crops (Malerbo-Souza et al. 1999; Souza and Malerbo-Souza 2005). In contrast, honeybees were reported as the most frequent visitors to watermelon crops in Kenya, possibly due to nearby apicultural activities (Njoroge et al. 2004, 2010).

In addition to their high-frequency visitation to watermelon flowers (Table 1), *N. perilampoides* also made prolonged contact with the flower’s sexual structures (Fig. 3), suggesting their vital role in crop pollination in the region. Honeybees have been recognized as efficient pollinators in watermelon crops (Adlerz 1966; Njoroge et al. 2004, 2010; Campbell et al. 2018), and considering that they represent the second most common species visiting flowers (Table 1), they likely play a significant role in crop pollination as well. It is worth noting that these honeybees were feral, as no hives were introduced to the crops, and there were no apiaries nearby. The remaining flower visitors accounted for nearly one-fifth of the total visits, suggesting that together they also contribute significantly to crop pollination. Among all the recorded visitors, bees are likely the most important for pollination due to their specialized structures for carrying pollen (Michener et al. 1978; Thorp 1979, 2000; Michener 2000).

While the most frequent visitors usually play a crucial role in flower pollination, occasional visitors can sometimes be even more important or efficient in pollinating flowers. This has been demonstrated in previous studies on watermelon crops with occasional visitors, such as *Lasioglossum* (Njoroge et al. 2010; Garantonakis et al. 2016; Layec et al. 2021) and *Halictus* (Layec et al. 2021). Furthermore, frequent visitors can sometimes have negative effects on flower pollination by reducing the available food resources for other more efficient bee species (Westerkamp 1991; Zych et al. 2013; Willmer 2011; Buchmann and Nabhan 2012; Kendall et al. 2022).

The abundance of native bees is likely associated with the proximity of their nests to the crops and the presence of alternative food resources in the area (Bomfim et al. 2013). As watermelon food resources are only available for a few months each year and most of the observed bee nests are found in trees (Roubik 1983; Roubik 2006), it is strongly recommended to protect the remaining vegetation near the crops. Additionally, the introduction of box nests for stingless bees could promote the establishment of their nests in close proximity to the crops. This is a common practice in meliponiculture (Oliveira et al. 2013; Silva et al. 2014; Jaffé et al. 2015; Da Cruz 2020).

4.2. Floral resources foraging

Differences in preferences for floral resources, flower sexes, and the timing of flower visits were observed among the bees, which is expected due to the significant variations in the biology of the visiting bees.

4.2.1. Pollen

Pollen collection was strongly preferred by honeybees, with nearly half of their visits dedicated to this resource. In contrast, watermelon pollen was largely ignored by Halictid bee species (Table 1). The preference of honeybees for watermelon pollen aligns with observations made by Souza and Malerbo-Souza (2005) in Brazil and differs from the findings of Pisansky et al. (2016). This suggests that bees may forage for pollen or nectar on watermelon crops depending on the availability of other resources in the area.

Based on our observations, honeybees were the primary removers of pollen from the crop (Tables 1 and 2), although pollen removers are often inefficient pollinators (Tepedino 1981; Thomson and Thomson 1992; Westerkamp 1996; Young et al. 2007). Due to their grooming behavior and collection of pollen grains on specialized structures (corbiculae for Apidae and scape for other bees), only a small number of grains are transferred to the stigmas, while the majority of the collected pollen is transported to the bee nests (Wilson and Thomson 1991; Lau and Galloway 2004; Young et al. 2007; Njoroge et al. 2010). Additionally, most honeybee visits occurred at 7:00 AM (or even earlier), when some female flowers had not yet opened, resulting in limited contribution to pollination. Furthermore, it was common to observe honeybees visiting male flowers early in the day (7:00 to 8:00 AM), disregarding adjacent female flowers or briefly landing on female flowers without contacting the stigmas.

The notable pattern of Halictidae bees (Lasioglossum, Augochlora, and Augochloropsis) rejecting watermelon

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Calculated GLMM values for each bee characteristic on visits for floral resources for the observed bee species.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Characteristic</td>
<td>F-value</td>
</tr>
<tr>
<td>Body Size</td>
<td>4.88</td>
</tr>
<tr>
<td>Color</td>
<td>60.34</td>
</tr>
<tr>
<td>Sociability</td>
<td>236.89</td>
</tr>
<tr>
<td>Hour of Visits</td>
<td>29.56</td>
</tr>
<tr>
<td>Intercept</td>
<td>6.33</td>
</tr>
</tbody>
</table>

*Significant when P < 0.05
pollen could be attributed to their preference for pollen from herbaceous plants associated with the crop, where they were frequently observed collecting pollen, particularly on Portulaca oleracea. It is likely that the pollen of these plants is more attractive to Halictidae bees, as different bee species can exhibit preferences for specific types of pollen grains (Rasheed and Harder 1997; Cook et al 2003; Vuadoo et al 2016; Nicholls and Hempel 2017). A future study could investigate whether associated herbs in the crop compete with watermelon flowers for pollinators or if they promote the presence of bees on the crop.

Most pollen visits occurred early in the morning, consistent with the observations of Stanghellini et al. (2002). They reported that approximately 77% of the pollen on watermelon staminate flowers was removed by honeybees within the first two hours after anthesis. Since pollen is a limited resource produced by flowers and its availability decreases after flower visitation throughout the day (Roubik 1992b; Tepedino et al 2016), ensuring an adequate supply of pollen can be crucial for bees, especially for highly social bees with a large brood to feed (Velthuis 1992; Eckert et al 1994; Schmickl and Grillsheim 2004). Analyzing the duration of bee visits is also relevant, as visit duration has been shown to play a significant role in pollination in some cases (Thomson and Plowright 1980; Thomson 1986; Galen 1989; Fishbein and Venable 1996; Ivey et al 2003). The variation in visit duration for pollen and nectar observed in our study is expected since manipulating pollen is a considerably more complex task than sipping nectar (Raine and Chittka 2009), and this pattern has been observed in numerous studies (Heinrich 1976; Harder 1990; Thomson and Goodell 2001; Bernauer et al 2022).

4.2.2. Nectar

It is widely recognized that nectar-foraging bees can play a crucial role as pollinators (Young et al 2007). In contrast to pollen removers, nectar foragers do not store pollen on their corbiculae/scopa or groom themselves frequently, allowing pollen grains to remain on their bodies. When these bees visit pistillate flowers, pollen grains can be transferred to the stigmas (Westerkamp 1996; Young et al 2007). The concentration of nectar in female flowers appears to be slightly higher than that in male flowers (19.24/18.45) (Taha and Bayoumi 2009). However, we observed a remarkably similar number of visits for nectar on stamine and pistillate flowers (Table 2). The difference in nectar concentration may have been insufficient to influence bee preferences for either flower sex.

The proportion of visits by honeybees to pistillate flowers was relatively low (approximately one-fourth), and due to their large size and long tongues, they often had limited contact with the stigmas. This could potentially limit their contribution to crop pollination (Figure 4a and 4b). In contrast, smaller observed bees, such as N. perilampoides, tended to insert their entire bodies into the base of the female flowers when feeding on nectar, facilitating the transfer of pollen grains from their bodies to the stigmas (Figure 4c and 4d). This behavior of stingless bees, coupled with their high frequency of visits to pistillate flowers, suggests their significant involvement in flower pollination. Visits for nectar on pistillate flowers slightly exceeded those on staminate flowers. In this case, the higher sugar concentration in female flowers (Taha and Bayoumi 2009) could influence the duration of time bees spend on the flowers.

4.3. Bee Characteristics and Number of Visits

The number of visits for food resources was significantly influenced by bee characteristics and hour of visitation (Table 3), an idea previously examined by Rodrigo et al. (2021) for crops in Spain but rarely explored in tropical regions.

The observed influence of body size and color on bee foraging patterns can be attributed, at least partially, to how environmental conditions affect bees. As indicated in numerous studies, larger bees tend to initiate foraging earlier due to their better tolerance of low temperatures (Bishop and Armbruster 1999; Pereboom and Biesmeijer 2003; Hrncir and Maia-Silva 2013a, b). Our observations align with this pattern, as the largest observed bees (honeybees) visited the flowers earlier in the day. In contrast, N. perilampoides, the smallest stingless bee, exhibited lower activity (particularly in nectar foraging) during the first hours compared to other larger stingless bee species observed, namely, P. peckolti, T. perangulata, and F. paupera (Figure 2, Table 2).

Insect color can influence insect tolerance to high temperatures and low relative humidity. Dark-colored insects exhibit greater absorptivity of solar radiation, enabling them to begin foraging at lower temperatures (Pereboom and Biesmeijer 2003). However, high absorptivity can also lead to overheating of insects under elevated temperatures (Willmer and Unwin 1981; Pereboom and Biesmeijer 2003; Hrncir and Maia-Silva 2013a, b). In our study, honeybees (light-colored) may not have been at risk of overheating, but their large bodies likely made foraging trips energetically costly under elevated temperatures (Heinrich 1974, 1975, 1993; Abrol 2012).

Furthermore, we observed that sociability influenced the foraging patterns of bees. As mentioned earlier, highly social bees require a substantial supply of protein to feed their offspring, making it a priority for them to forage pollen in the early hours of the day before the resource is depleted from the flowers (Velthuis 1992; Eckert et al 1994; Schmickl and Grillsheim 2004). Additionally, at high temperatures, some highly social bees shift their activities from food foraging to water foraging and engage in “fanning” inside the nest to prevent overheating of the brood (Southwick and Heldmaier 1987; Engels et al 2008; Vollet-Neto et al 2015; Ostwald et al 2016; Abou-Shaara et al 2017).

The case of Halictid bees (Lasiglassum, Augochlora, and Augochloropsis) is noteworthy, as they possess small bodies and light colors and exhibit solitary/primitive social characteristics (Table 2). This can explain their lower activity in the early hours of the day, but they continue foraging until the last hours of observation (Fig. 2), even during the highest
temperatures, as demonstrated in a previous study conducted in the same locality, suggesting a strong correlation between temperature and visitation frequency for Halictid bees (Di Trani et al 2022).

Figure 4. a, b) Honeybees feeding on the nectar of pistillate flowers, c) *N. perilampoides* feeding on the nectar of a pistillate flower, d) *P. peckolti* feeding on the nectar of a staminate flower.

5. Conclusions

Watermelon flowers in Panama were primarily visited by stingless bees, particularly *N. perilampoides*, suggesting their potential role in pollinating the crops.

The foraging patterns of local bees appear to be influenced by bee characteristics, including their tolerance to environmental conditions and preferences for specific food resources throughout the day. This information can be valuable in predicting bee foraging behavior in other watermelon crops, optimizing the management of these bee species, and providing recommendations for crop management, such as the timing of fumigation, irrigation, and fruit harvest.

Further studies are necessary to assess the pollination efficiency of the observed bee species, particularly those exhibiting "advantageous" characteristics for crop management, such as high availability, increased activity during the receptive stage of flowers, high sociability, low aggressiveness, and aerial nesting habits. These bees could serve as alternative pollinators for watermelon crops in the region, avoiding the drawbacks associated with introducing honeybees.

Acknowledgments

The authors express their gratitude to Cooperativa El Progreso in Los Santos for their contributions of various materials and equipment. Special thanks also go to Francisco Morales, a local farmer from Villa Lourdes, for providing the crops used in this study.

Ethical considerations

Not applicable.

Conflict of Interest

The authors declare no competing interests.

Funding

Funding for this study was provided by the International Scholarships program of SENACYT Panama (No. 270-2018-980) and by SENACYT through the National Research System (SNI) (Dr. Anovel Barba).

References

Cardoso MWR. (2017) Eficiência das abelhas sociais Melipona scutellaris na polinização de minúmelos em ambiente protegido. XIV Seminário Estudantil de pesquisa e Extensão – FAMAM.


