

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



Juan Carlos Di Trani^a 💿 🖂 | Virginia Meléndez Ramírez^a | Anovel Barba^b | Yostin Añino^c

^aCampus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mexico.
^bInstituto de Innovación Agropecuaria de Panamá, Divisa, Panama.
^cMuseo de Invertebrados G. B. Fairchild, Universidad de Panamá, Panama.

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 (Melendez 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 displacement 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 Nabhann 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 (Stanghelini 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).

2

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.

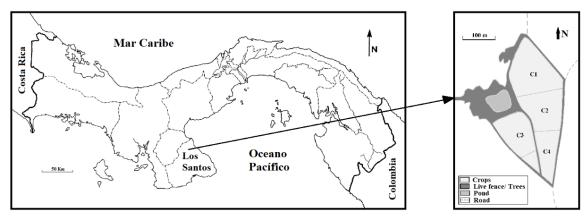


Figure 1 Panama map with details of the study site (7°48'59.8"N 80°28'30.8" W).

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 Veddeler 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.

3. Results

3.1. Floral visitors

Watermelon flowers were predominantly visited by *N. perilampoides* 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%), *Augochlora* 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).

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.

Bee Species	Staminate Flowers	Pistillate Flowers	Relative Abundance (%)
Apis mellifera	984	351	22.7
Nannotrigona perilampoides	1933	1481	58.0
Partamona peckolti	130	100	3.9
Trigona corvina	14	11	0.4
Trigona fulviventris	11	4	0.3
Tetragona perangulata	58	21	1.3
Frieseomelitta paupera	56	26	1.4
Melipona phenax	10	2	0.2
Melissodes tepaneca	3	1	0.1
Calliopsis hondurasica	1	-	0.0
Megachile sp.	1	-	0.0
Lasioglossum spp.	99	94	3.3
Augochlora spp.	86	100	3.2
Augochloropsis spp.	63	98	2.7
Non-Bees			
Vespidae	10	12	0.4
Muscidae	6	7	0.2
Syrphidae	3	3	0.1
Hesperiidae	42	40	1.4
Pieridae	8	4	0.2
Lycaenidae	2	3	0.1
Nymphalidae	8	3	0.2

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. perilampoides* was the second most frequent visitor for pollen, representing approximately one-third (37.8%) of their

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 \pm SE s) than nectar visits (12.2 \pm 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 \pm SE and 23.4 \pm SE s, respectively) (Figures 3a, 3b and 3c).

Δ

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

Species	Body Size				VISITS	
	(mm)	Color	Sociability	Pollen (Stam)	Nectar Stam.	Nectar Pistil.
Apis mellifera	10.7	Light	Higly Social	637	347	351
Nannotrigona perilampoides	4.1	Dark	Higly Social	469	1464	1481
Partamona peckolti	5.2	Dark	Higly Social	74	56	100
Tetragona perangulata	7.0	Light	Higly Social	37	21	21
Frieseomelitta paupera	5.3	Dark	Higly Social	22	34	26
Lasioglossum spp.	6.2	Light	solitary/primitiv soc	6	93	94
Augochlora spp.	6.8	Light	solitary/primitiv soc	0	86	100
Augochloropsis spp.	6.9	Light	solitary/primitiv soc	0	63	98

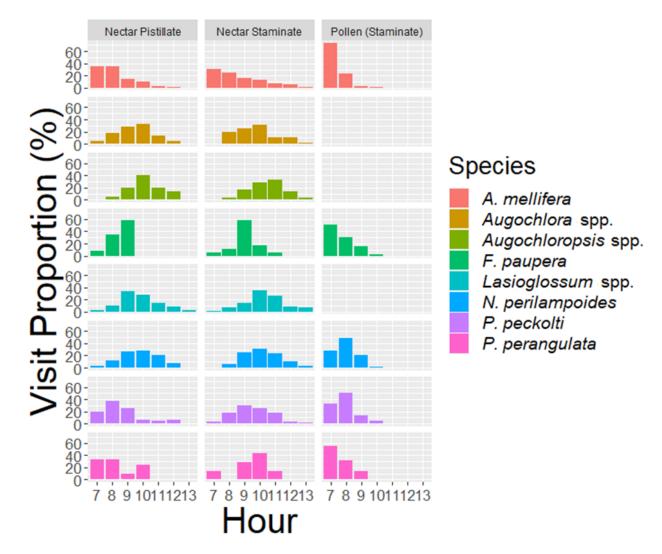


Figure 2 Visit proportion (%) for each floral resource and flower sex for each bee species during the 84-day observation period.

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* < 0.0001).

5

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).

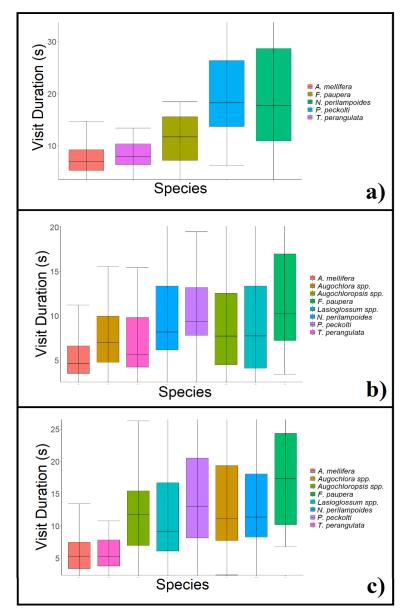


Figure 3 Average visit duration (seconds) for each bee species foraging on a) pollen (staminate flowers), b) nectar on staminate flowers, and c) nectar on pistillate flowers during the 84 days of observation.

Table 3 Calculated GLMM values for each bee characteristic on visits for floral resources for the observed bee species.

Characteristic	F-value	P-value*
Body Size	4.88	0.0271
Color	60.34	<0.0001
Sociability	236.89	<0.0001
Hour of Visits	29.56	<0.0001
Intercept	6.33	0.0119

*Significant when P < 0.05

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 (Ureña 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

4.2. Floral resources foraging
et al 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.
ig. 3), gion.
4.2.1. Pollen

al 2015; Da Cruz 2020).

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 Pisanty 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.

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

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 scopae 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

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; Vaudo 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 Crailsheim 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/scopae and 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 staminate 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.

7

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 Crailsheim 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 (*Lasioglossum, 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

8

a b

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

Abou-Shaara HF, Owayss AA, Ibrahim YY, Basuny NK (2017) A review of impacts of temperature and relative humidity on various activities of honeybees. Insectes sociaux 64:455-463.

Abrol DP (2012) Pollination Biology. Springer, Dordrecht.

Adlerz WC (1966) Honeybee visit numbers and watermelon pollination. Journal of Economic Entomology 59:28-30.

ANAM. (2009) Atlas de las Tierras Secas y Degradadas de Panamá, Autoridad Nacional del Ambiente, República de Panamá.

Barba A, Espinosa J, Suris M (2015) Adopción de prácticas para el manejo agroecológico de plagas en la sandía (*Citrullus lanatus* Thunb.) en Azuero. Panamá. Revista de Protección Vegetal 30:104-114.

Bennett CF (1965) Beekeeping with stingless bees in western Panama. Bee World 46:23-24.

Bernauer OM, Tierney SM, Cook JM (2022) Efficiency and effectiveness of native bees and honeybees as pollinators of apples in New South Wales orchards. Agriculture, Ecosystems and Environment 337:108063.

Bishop JA, Armbruster WS (1999) Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny, and ecology. Functional Ecology 13:711-724.

Bomfim IGA (2013) Uso de abelhas sem ferrão (Meliponinae: Apidae) em casa de vegetação para polinização e produção de frutos de minimelancia [*Citrullus lanatus* (Thunb.) Matsum. andNakai] com e sem semente. Dissertation, Universidad Federal do Ceará.

Bomfim IGA, Bezerra ADDM, Nunes AC, Freitas BM, Aragão FASD (2015) Pollination requirements of seeded and seedless mini watermelon varieties cultivated under protected environment. Pesquisa Agropecuária Brasileira 50:44-53.

Bonet FM, Vergara CH (2019) Abejas silvestres de un cafetal orgánico en Veracruz, México. Universidad de las Américas Puebla. Puebla, México.

Buchmann SL, Nabhan GP (2012) The forgotten pollinators. Island Press, Washington, DC.

Campbell JW, Daniels JC, Ellis JD (2018) Fruit set and single visit stigma pollen deposition by managed bumble bees and wild bees in *Citrullus lanatus* (Cucurbitales: Cucurbitaceae). Journal of Economic Entomology 111:989-992.

Campbell JW, Stanley-Stahr C, Bammer M, Daniels JC, Ellis JD (2019) Contribution of bees and other pollinators to watermelon (*Citrullus Ianatus* Thunb.) pollination. Journal of Apicultural Research 58:597-603.

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

Carr RV (1967) Factors affecting honeybee foraging behavior in watermelon, *Citrullus lanatus* (Thunb.) Mans. Dissertation, University of Arizona.

Chaves L (2013) Efeitos de abelhas na frutificação e qualidade de melancia (cv. Crimson Sweet) na região Central do estado do Piauí. Dissertation. Universidade Estadual Paulista.

Cook SM, Awmack CS, Murray DA, Williams IH (2003) Are honeybees' foraging preferences affected by pollen amino acid composition? Ecological Entomology 28:622-627.

Cruz IAD (2020) Eficiência de ninhos-isca na atração e na obtenção de enxames, por nidificação espontânea, de abelhas sem ferrão amazônicas. Dissertation, Instituto Nacional de Pesquisas da Amazonia

Delaplane KS, Mayer DF (2000) Crop pollination by bees. CABI publishing, New York.

Di Trani JC, Ramírez VM, Añino Y, Barba A (2022) Environmental conditions and bee foraging in watermelon crops in Panama. Journal of Animal Behavior and Biometeorology 10:2234-2234.

Eckert CD, Winston ML, Ydenberg RC (1994) The relationship between population size, amount of brood, and individual foraging behavior in the honeybee, *Apis mellifera* L. Oecologia 97:248-255.

Engels W, Rosenkranz P, Engels E (1995) Thermoregulation in the nest of the Neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees. Studies on Neotropical fauna and Environment 30:193-205.

FAO (2020) Production Quantities of Watermelons by Country. Food and Agriculture Organization of the United Nations). FAOSTAT (Food and Agriculture Data. http://www.fao.org/faostat/en/#data/QC/visualize. Accessed in December 2020.

Fishbein M, Venable DL (1996) Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. Ecology 77:1061-1073.

Freitas L (2013) Concepts of pollinator performance: is a simple approach necessary to achieve standardized terminology? Brazilian Journal of Botany 36:3-8.

Galen C, Stanton ML (1989) Bumble bee pollination and floral morphology: factors influencing pollen dispersal in the alpine sky pilot, *Polemonium viscosum* (Polemoniaceae). American Journal of Botany 76:419-426.

Garantonakis N, Varikou K, Birouraki A, Edwards M, Kalliakaki V, Andrinopoulos F (2016) Comparing the pollination services of honeybees and wild bees in a watermelon field. Scientia Horticulturae 204:138-144.

Giannini TC, Cordeiro GD, Freitas BM, Saraiva AM, Imperatriz-Fonseca VL (2015) The dependence of crops for pollinators and the economic value of pollination in Brazil. Journal of Economic Entomology 108:849-857.

Gonzáles Betancourt VH, Gonzáles M, Cuellar Y (2009) Notas biológicas y taxonómicas sobre los abejorros del maracuyá del género *Xylocopa* (Hymenoptera: Apidae, Xylocopini) en colombia. Acta Biológica Colombiana 14:3-40.

Harder LD (1990) Behavioral responses by bumble bees to variation in pollen availability. Oecologia 85:41-47.

Heinrich B (1974) Thermoregulation in Endothermic Insects: Body temperature is closely attuned to activity and energy supplies. Science 185:747-756.

Heinrich B (1975) Energetics of pollination. Annual Review of Ecology and Systematics 6:139-170.

Heinrich B (1993) The hot-blooded insects: strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge.

Henne CS, Rodriguez E, Adamczyk JJ (2012) A survey of bee species found pollinating watermelons in the lower Rio Grande valley of Texas. Psyche 2012:1-5.

Hrncir M, Maia-Silva C (2013) On the diversity of foraging-related traits in stingless bees. In: Vit P et al. (eds) Pot-Honey. Springer, New York, pp 201-215.

Hrncir M, Maia-Silva C (2013) The fast versus the furious—On competition, morphological foraging traits, and foraging strategies in stingless bees. In Vit P, Roubik DW (eds): Stingless bees process honey and pollen in cerumen pots. Facultad de Farmacia y Bioanálisis, Universidad de Los Andes, pp 1-13.

lvey CT, Martinez P, Wyatt R. (2003) Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). American Journal of Botany 90:214-225.

Jaffé R, Pope N, Carvalho AT, Maia UM, Blochtein B, de Carvalho CAL, Imperatriz-Fonseca VL (2015) Bees for development: Brazilian survey reveals how to optimize stingless beekeeping. PloS one 10: e0121157.

Kendall LK, Stavert JR, Gagic V, Hall M, Rader R (2022) Initial floral visitor identity and foraging time strongly influence blueberry reproductive success. Basic and Applied Ecology 60:114-122.

Lau JA, Galloway LF (2004) Effects of low-efficiency pollinators on plant fitness and floral trait evolution in *Campanula americana* (Campanulaceae). Oecologia 141:577-583.

Layek, U, Kundu A, Bisui S, Karmakar P (2021) Impact of managed stingless bee and western honeybee colonies on native pollinators and yield of watermelon: A comparative study. Annals of Agricultural Sciences 66:38-45.

MacInnis G, Forrest JR (2019) Pollination by wild bees yields larger strawberries than pollination by honeybees. Journal of Applied Ecology 56:824-832.

Malerbo-Souza DT, Tadeu AM, Bettini PC., de Toledo VDAA (1999) Importância dos insetos na produção de melancia (*Citrullus lanatus* Thunb.)-Cucurbitaceae. Acta Scientiarum. Agronomy 21:579-583.

Meléndez RV, Magaña RS, Parra TV, Ayala BR, Navarro GJ (2002) Diversity of native bee visitor of cucurbit crops (Cucurbitaceae) in Yucatán, México. Journal of Insect Conservation 6:135-147

Metzel R, Montagnini F (2014) From farm to forest: factors associated with protecting and planting trees in a Panamanian agricultural landscape. Bois and Forets Des Tropiques 322:3-15.

Michener CD, McGinley RJ, Danforth BN (1994) The Bee Genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, D.C.

Michener CD (1954) Bees of Panamá. Bulletin of the American Museum of Natural History 104:1-176.

Michener CD (2000) The bees of the world. JHU press, Baltimore.

Michener CD, Winston ML, Jander R (1978) Pollen manipulation and related activities and structures in bees of the family Apidae. The University of Kansas Science Bulletin 51:575.

Mosseler A, Major J, Ostaff D, Ascher J (2020) Bee foraging preferences on three willow (*Salix*) species: Effects of species, plant sex, sampling day and time of day. Annals of Applied Biology 177:333-345.

Nates-Parra G, Palacios E, Parra A (2008) Efecto del cambio del paisaje en la estructura de la comunidad de abejas sin aguijón (Hymenoptera: Apidae) en Meta, Colombia. Revista de Biología Tropical 56:1295-1308.

Nicholls E, Hempel de Ibarra N (2017) Assessment of pollen rewards by foraging bees. Functional Ecology 31:76-87.

Njoroge, GN, Gemmill B, Bussmann R, Newton LE, Ngumi VW (2004) Pollination ecology of *Citrullus lanatus* at Yatta, Kenya. International Journal of Tropical Insect Science 24:73-77.

Njoroge GN, Gemmill B, Bussmann R, Newton LE, Ngumi VM (2010) Diversity and efficiency of wild pollinators of watermelon (*Citrullus lanatus* (Thunb.) Mansf.) at Yatta (Kenya). Journal of Applied Horticulture 12:35-41.

Ostwald MM, Smith ML, Seeley TD (2016) The behavioral regulation of thirst, water collection and water storage in honeybee colonies. Journal of Experimental Biology 219:2156-2165.

Pereboom JJM, Biesmeijer JC (2003) Thermal constraints for stingless bee foragers: the importance of body size and coloration. Oecologia 137:42-50.

Pinkus-Rendon MA, Parra-Tabla V, Meléndez-Ramírez V (2005) Floral resource use and interactions between *Apis mellifera* and native bees in cucurbit crops in Yucatán, México. The Canadian Entomologist 137:441-449.

Pisanty G, Afik O, Wajnberg E, Mandelik Y (2016) Watermelon pollinators exhibit complementarity in both visitation rate and single-visit pollination efficiency. Journal of Applied Ecology 53:360-370.

Rader R, Reilly J, Bartomeus I, Winfree R (2013) Native bees buffer the negative impact of climate warming on honeybee pollination of watermelon crops. Global change biology 19:3103-3110.

Rasheed S, Harder L (1997) Economic motivation for plant species preferences of pollen-collecting bumble bees. Ecological Entomology 22:209-219.

Rodrigo Gomez S, Ornosa C, Garcia Gila J, Blasco-Aróstegui J, Selfa J, Guara M, Polidori C (2021) Bees and crops in Spain: an update for melon, watermelon and almond. Annales de la Société entomologique de France 57:12-28.

Roubik DW (1983) Nest and colony characteristics of stingless bees from Panama (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 56:327-355.

Roubik DW (1992a) Stingless bees: a guide to Panamanian and Mesoamerican species and their nests (Hymenoptera: Apidae: Meliponinae). In: Quintero D, Aiello A (Eds), Insects of Panama and Mesoamerica, Oxford University Press, Oxford, pp 495-524.

Roubik DW (1992b) Ecology and natural history of tropical bees. Cambridge University Press, Cambridge.

Roubik DW (2006) Stingless bee nesting biology. Apidologie 37:124-143.

Roubik DW (2012) Ecology and Social Organization of Bees. John Wiley and Sons, Chichester.

Schmickl, T, Crailsheim K (2004) Inner nest homeostasis in a changing environment with special emphasis on honeybee brood nursing and pollen supply. Apidologie 35:249-263.

Schwarz HF (1934) The solitary bees of Barro Colorado Island, Canal Zone. American Museum Novitates 722:1-24.

Silva MD, Ramalho M, Monteiro D (2014) Communities of social bees (Apidae: Meliponini) in trap-nests: the spatial dynamics of reproduction in an area of Atlantic Forest. Neotropical Entomology 43:307-313.

Souza FF, Malerbo-Souza DT (2005) Entomofauna visitante e produção de frutos em melancia (*Citrullus lanatus* Thunb.) –Cucurbitaceae. Acta Scientiarum. Agronomy 27:449-454.

Spicer EK (2007) Efficacy of honeybees and native bees as pollen vectors for watermelon (*Citrullus lanatus*) and some ecologic predictors of pollinator abundance. Dissertation, North Carolina State University.

Stanghellini MS, Ambrose JT, Schultheis JR (1998) Seed production in watermelon: a comparison between two commercially available pollinators. HortScience 33:28-30

Stanghellini MS, Schultheis JR, Ambrose JT (2002) Pollen mobilization in selected Cucurbitaceae and the putative effects of pollinator abundance on pollen depletion rates. Journal of the American Society for horticultural Science 127:729-736.

Taha EKA, Bayoumi YA (2009) The value of honeybees (*Apis mellifera*, L.) as pollinators of summer seed watermelon (*Citrullus lanatus colothynthoides* L.) in Egypt. Acta Biologica Szegediensis 53:33-37.

Tepedino VJ (1981) The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honeybee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). Journal of the Kansas Entomological Society 54:359-377.

Tepedino V, Horn LA, Durham S (2016) Pollen removal and deposition by pollen-and nectar-collecting specialist and generalist bee visitors to *lliamna bakeri* (Malvaceae). Journal of Pollination Ecology 19:50-56.

Thomson JD, Thomson BA (1992) Pollen presentation and viability schedules in animal-pollinated plants: consequences for reproductive success. In: Wyatt R (ed) Ecology and evolution of plant reproduction. Chapman and Hall, New York, pp 1-24.

Thomson JD (1986) Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. The Journal of Ecology 74:329-341.

Thomson JD, Goodell K (2001) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. Journal of Applied Ecology 38:1032-1044.

Thomson JD, Plowright RC (1980) Pollen carryover, nectar rewards, and pollinator behavior with special reference to *Diervilla lonicera*. Oecologia 46:68-74.

Thorp RW (1979) Structural, behavioral, and physiological adaptations of bees for collecting pollen. Annals of the Missouri Botanical Garden 66:788–812

Thorp RW (2000) The collection of pollen by bees. Plant Systematics and Evolution 222:211-223.

Uruena A, Martínez-López V, de Jesús May-Itzá W, Quezada-Euán JJG, De la Rúa P (2022). Morphometric and genetic analyses show differentiation of the widely distributed stingless bee *Nannotrigona perilampoides* (Hymenoptera: Meliponini) across geographic regions in Mexico. Journal of Apicultural Research 61:609-618.

Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM (2016) Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. Proceedings of the National Academy of Sciences 113: E4035-E4042.

Velthuis HH (1992) Pollen digestion and the evolution of sociality in bees. Bee world 73:77-89.

Vollet-Neto A, Menezes C, Imperatriz-Fonseca VL (2015) Behavioral and developmental responses of a stingless bee (*Scaptotrigona depilis*) to nest overheating. Apidologie 46:455-464.

Walters SA (2005) Honeybee pollination requirements for triploid watermelon. HortScience 40:1268-1270.

Westerkamp CH (1991) Honeybees are poor pollinators—why? Plant Systematics and Evolution 177:71-75.

Westerkamp CH (1996) Pollen in bee-flower relations some considerations on melittophily. Botanica Acta 109:325-332.

Willmer PG (2011) Pollination and floral ecology. Princeton University Press, Princeton. Willmer PG, Unwin DM (1981) Field analyses of insect heat budgets: reflectance, size, and heating rates. Oecologia 50:250-255.

Wilson P, Thomson JD (1991) Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. Ecology 72:1503-1507.

Young HJ, Dunning DW, von Hasseln KW (2007) Foraging behavior affects pollen removal and deposition in *Impatiens capensis* (Balsaminaceae). American Journal of Botany 94:1267-1271.

Zych M, Goldstein J, Roguz K, Stpiczyńska M (2013) The most effective pollinator revisited: pollen dynamics in a spring-flowering herb. Arthropod-Plant Interactions 7:315-322.