

**COMPARATIVE FORAGING OF THE SYMPATRIC STINGLESS BEES  
*TRIGONA NIGRA* AND *PARTAMONA NIGRIOR* (APIDAE:  
MELIPONINI)**

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**Summary**

*Trigona nigra* and *Partamona nigrrior* are stingless bees of very similar size that occur together in abundance in Trinidad, West Indies. We seek to explain this coexistence by comparing two aspects of their foraging behaviour: a) the daily rhythm of foraging, and b) the resource types collected.

**INTRODUCTION**

Stingless bees constitute the tribe Meliponini of the family Apidae (Michener et al. 1994). They are highly social, with several advanced features such as large perennial colonies with well-defined female castes, dependence on swarms for the foundation of new colonies, elaborate nest architecture and often sophisticated communication systems (Michener 1974, Sakagami 1982, Wille 1983). Colonies often amass substantial stores of honey and pollen in the nest.

Stingless bees are a pantropical group of some hundreds of species, with almost no penetration into even the warm temperate zones. The name of the group derives from the secondary loss of stinger.

*Trigona nigra* Cresson and *Partamona nigrrior* (Cockerell) are abundant on the Caribbean island of Trinidad. In the suburban areas in which this study was conducted, both are among the commonest bees. They are shiny black bees of very similar size. The only conspicuous ecological difference between the two species is in their nesting habits. *T. nigra* consistently nests within cavities, typically with very little of the nest wall exposed. *P. nigrrior*, on the other hand, tends to build much more conspicuous nests, typically on tree trunks or branches and often with the greater part of the outer wall exposed. In our experience, *T. nigra* is much less pugnacious, retreating into the nest cavity when disturbed, while it is common for *P. nigrrior* to respond to human provocation with biting attacks of numerous workers.

Roubik (1989) has discussed the wide variety of resources collected by stingless bees for construction and elaboration of the nest, and for food for adults and larvae. These include an array of plant products, such as gums, resins, rotten wood, bark, fruit juices, seeds, leaves, plant hairs, pollen, nectar, oils and sap. It is a fair assumption that the bulk of foraging by *T. nigra* and *P. nigrrior* is for nectar, pollen and resins.

Results of Johnson & Hubbell (1978) on sympatric neotropical stingless bees indicate that their coexistence may depend upon a partitioning of resources based upon timing and spatial dispersion of food resources. Our objective here is to examine the hypothesis that *T. nigra* and *P. nigrrior* can coexist in Trinidad through a tendency to forage at different times and/or on different resources, with an emphasis on species of pollen.

**MATERIALS AND METHOD**

We searched for colonies of *T. nigra* and *P. nigrrior* during August 1997 in north-central Trinidad. By relocating one colony of *T. nigra* and three of *P. nigrrior*, we formed five pairs, each comprising a colony of each species. The members of one pair were about 50 m from each other; in the other four pairs the members were within 5 m of each

other. Three pairs were on the University of the West Indies campus at St Augustine, separated from each other by at least 150 m. The other two were at distances of about 1 km and 8 km from the campus. We chose sites for their accessibility, low levels of disturbance, and shelter from rain.

Relocated colonies were left undisturbed for at least two weeks before testing, in order to allow for home-range orientation and repair of any nest damage.

The study lasted from mid-September to mid-November 1997, during the late rainy season. The daily activity rhythms of the 10 colonies were recorded through observation of flights in and out of the nest. Counts were made for 15 min per hour for each colony, initially from 06:00 to 18:00. This 12-hour period was subsequently shortened to 06:00 to 17:30, as it became too dark for effective observation before 18:00. Both colonies in each pair were studied on the same day during fair weather conditions and not on rainy or overcast days.

A count of workers entering the nest with loaded pollen baskets was also made for each 15-minute period from early to mid-morning, when foraging activity was at its highest. A sample of loaded foragers was caught during this time using a hand-held net. This was done for all colonies, each bee being placed in a separate vial and preserved in a freezer. For examination, each load was scraped off the pollen basket and smeared onto a slide, one drop of Kleermount was added and a coverslip was placed on top.

Pollen loads were compared with reference slides of 26 local species in order to identify the plants from which they came.

This study began on 16 November. Initially, pollen and resin loads could not be distinguished with confidence, so that no distinction was made in the data sets in Figs. 3-6. This involved counting the number of foragers entering the nest with either pollen or resin at the most active pair of nests (Site 2). Sampling was done in a 30-min period of each hour from 07:00 to 11:00. Pollen loads were removed and the workers released. Changes in weather conditions were noted.

## RESULTS

### 1. Daily Activity Rhythms

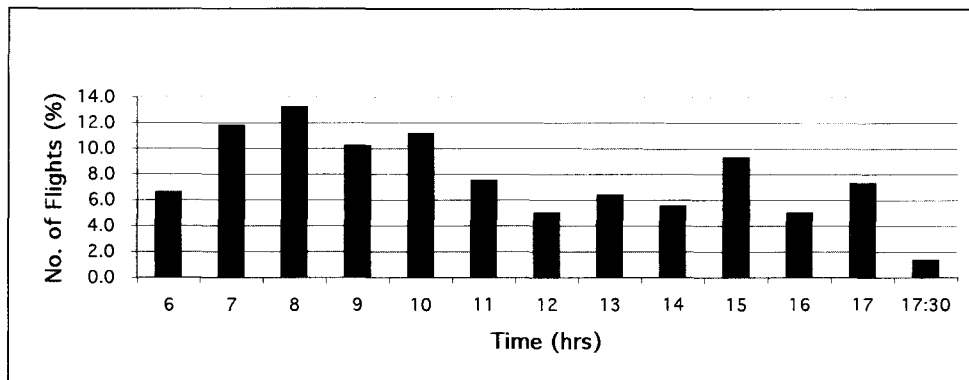


Figure 1: Daily rhythm of flight activity in *Trigona nigra*. Each bar represents the day's percentage of workers flying out or in during a 15-min period that includes the hour or (in the case of 17:30) half-hour marked.

Figs. 1-2 show the daily rhythm of flight activity for *T. nigra* and *P. nigrrior*, respectively. Each species is active throughout the daylight hours, about 06:00 to 17:30. Activity in *T. nigra* (Fig. 1) begins to peak between 07:00 and 08:00 and decreases after 10:00, increasing again from 15:00 to 17:00. Activity in *P. nigrrior* (Fig. 2) peaks around 07:00

and decreases markedly afterwards, increasing moderately again at 16:00-17:00. The secondary peaks in the afternoon are not statistically significant and may be an artefact of mid-afternoon rain on some days.

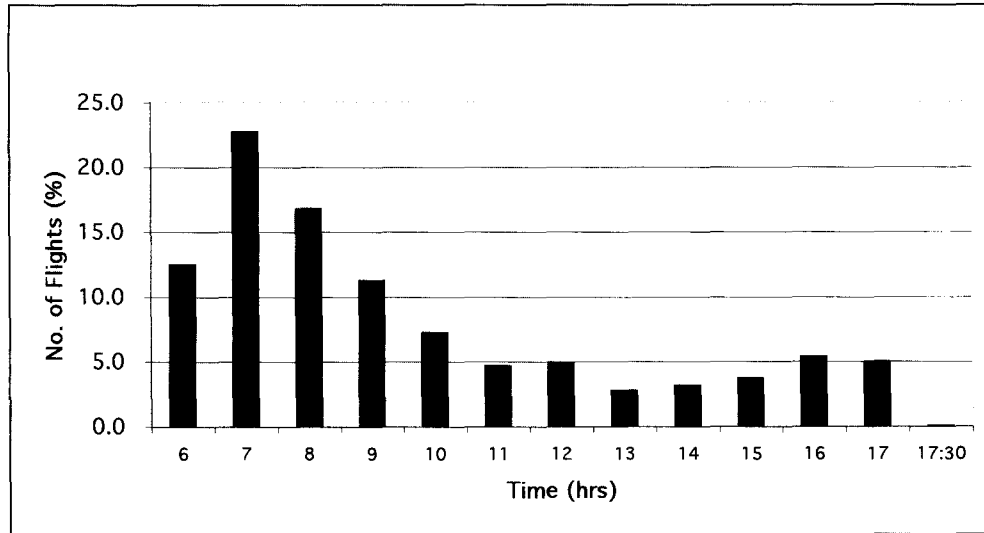


Figure 2: Daily rhythm of flight activity in *Partamona nigrior*. Each bar represents the day's percentage of workers flying out or in during a 15-min period that includes the hour or (in the case of 17:30) half-hour marked.

Figs. 3-4 show the daily rhythm of returning foragers with loads for *T. nigra* and *P. nigrior*, respectively. As with overall flight activity, such foraging occurs throughout the day in each species but is substantially higher in the morning. In *T. nigra* (Fig. 3), the number of incoming foragers peaks at 10:00, while in *P. nigrior* (Fig. 4) the majority of foragers with loads return between 07:00 and 09:00. In the afternoon very few returning bees have loads. The peak at 16:00-17:00 corresponds to the peak seen in Fig. 2.

Figs. 5-6 show the total number of foragers returning to the nest and the proportion of these with loads in *T. nigra* and *P. nigrior*, respectively. In the first, the number peaks around 08:00, while in *P. nigrior* the peak is more pronounced and occurs about an hour earlier. The number of workers returning with loads shows a very diffuse peak around 10:00 in *T. nigra* and a more distinct peak around 08:00 in *P. nigrior*. A secondary peak around 15:00 in total returning workers in *T. nigra* may be due to the onset of rain, as the proportion with loads is low. In *P. nigrior* the modest increase in the total number of incoming workers and the number with loads around 16:00 may indicate a resumption of rain-interrupted foraging.

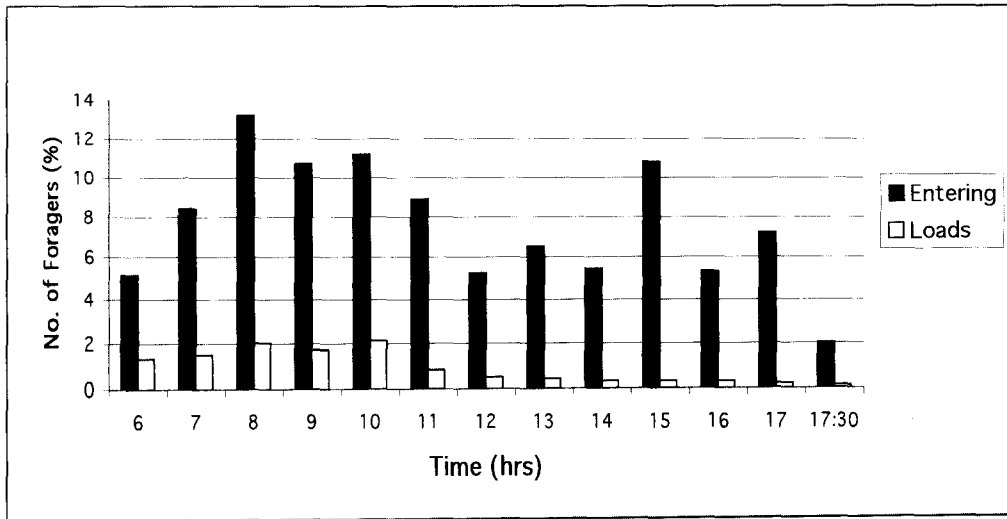


Figure 3: Daily rhythm of incoming foragers with loads in *Trigona nigra*. Computed as in Figs. 1-2.

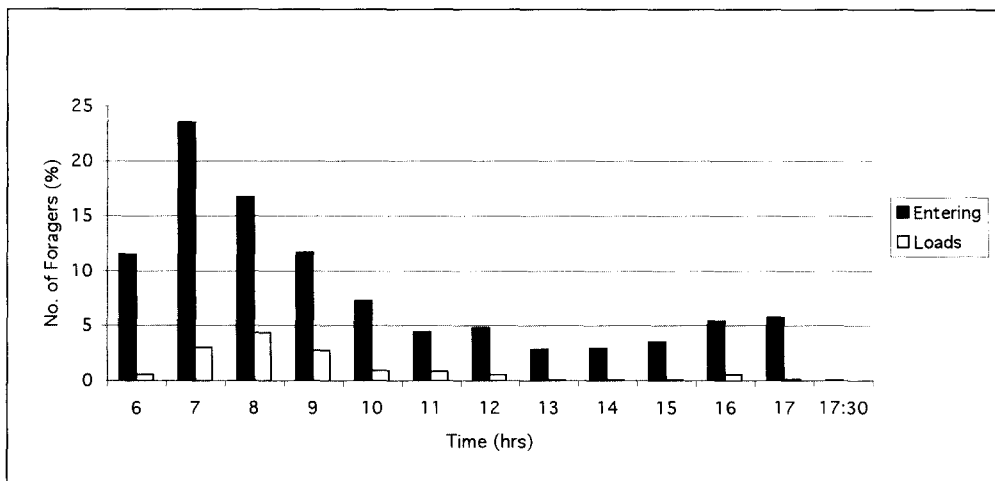


Figure 4: Daily rhythm of incoming foragers with loads in *Partamona nigrior*. Computed as in Figs. 1-2.

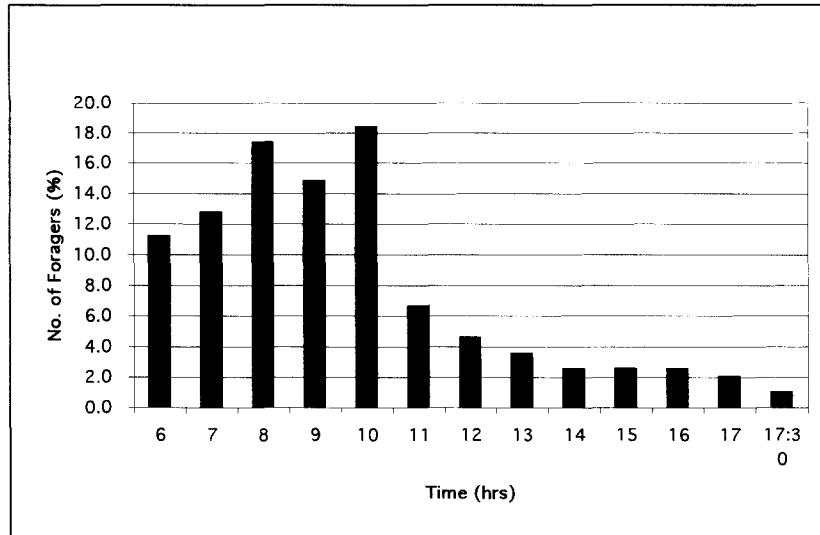


Figure 5: Daily rhythm of total incoming foragers and the fraction of these with loads in *Trigona nigra*. Total incoming foragers computed as in Figs. 1-2.

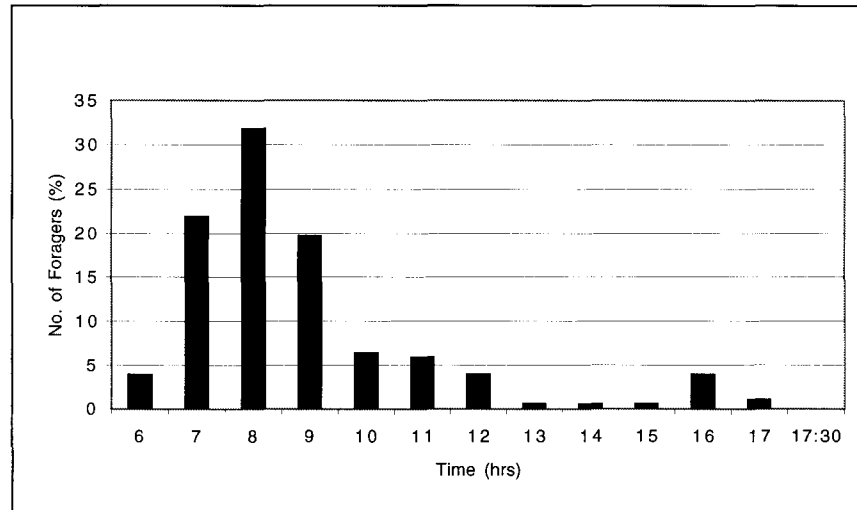


Figure 6: Daily rhythm of total incoming foragers and the fraction of these with loads in *Partamona nigrior*. Total incoming foragers computed as in Figs. 1-2.

## 2. Comparison of Resource Types

Table 1 shows the proportions of pollen loads and resin loads among 84 loads taken from incoming *T. nigra* foragers and 186 from *P. nigrior* foragers. The difference between bee species in proportions of the two resources is not significant (X2 test,  $p > 0.05$ ; Jaccard's Similarity).

Table 1. Resource types in pollen baskets of *Trigona nigra* and *Partamona nigrior* returning foragers.

	<i>T. nigra</i>	<i>P. nigrior</i>
Total loads	84	186
Pollen	55 (63.1%)	104 (56.0%)
Resin	29 (36.9%)	82 (44.0%)

Table 2. Numbers of pollen and resin loads collected by *Trigona nigra* and *Partamona nigrior* foragers at Site 2 from 07:00-11:00 on 11 November 1997.

Time	-- <i>T. nigra</i> --		-- <i>P. nigrior</i> --	
	Pollen	Resin	Pollen	Resin
07:00 - 08:00	3	2	30	38
08:00 - 09:00	18	3	25	14
09:00 - 10:00	5	1	29	19
10:00 - 11:00	5	8	7	3
Total	31	14	91	74

Table 2 is a subset of these same data, according to a timed sampling at the most active pair of colonies (Site 2).

Table 3 lists plants seen to be visited by the two bee species; it does not represent a rigorous survey. Flowers of the three plants seen visited by *P. nigrior* each attract a large array of insects which includes the honey bee *Apis mellifera*. *P. nigrior* and *T. nigra* were found collecting pollen simultaneously at *Veitchia merrilli*. However, while *P. nigrior* foraged at flowers in place on the palm, *T. nigra* was found at fallen flowers on the ground.

Table 3. Sight records of visits to flowers by *Trigona nigra* and *Partamona nigrior*.

Plant	<i>T. nigra</i>	<i>P. nigrior</i>
Antigonon leptopus	+	+
Citrus aurantifolia	+	
Cocos nucifera	+	+
Ixora coccinea	+	
Jatropha multifida	+	
Jatropha pandurifolia	+	
Rosa sp.	+	
Veitchia merrilli	+	+

Table 4. Pollen loads collected from *Trigona nigra* and *Partamona nigrior* returning foragers. Species A1 through N are unidentified.

Species	Family	<i>T. nigra</i>	<i>P. nigrior</i>
<i>Antigonon leptopus</i>	Polygonaceae	5	
<i>Citrus aurantifolia</i>	Rutaceae	6	2
<i>Cocos nucifera</i>	Palmae	3	3
<i>Ixora coccinea</i>	Rubiaceae	9	1
<i>Lantana camara</i>	Verbenaceae	1	
<i>Mangifera indica</i>	Anacardiaceae	5	1
<i>Mimosa pudica</i>	Mimosaceae	12	
<i>Phthirusa adunca</i>	Loranthaceae	2	3
<i>Veitchia merrilli</i>	Palmae	11	13
<i>Plumbago capensis</i>	Plumbaginaceae	4	1
Sp. A1		1	4
Sp. H		1	
Sp. K		1	
Sp. L		1	
Sp. M		1	
Sp. N			7
Sp. R		2	
Total		65	35

Table 4 shows pollen species identified in incoming loads on worker bees. Under light-microscope examination, all loads appeared to be pure or very nearly so. If we set aside the six species of which fewer than five loads were collected by *T. nigra* and *P. nigrior* together, we find 10 species collected by *T. nigra* and nine by *P. nigrior*. The two bee species show a significantly different taxonomic pattern of pollen collection (X<sup>2</sup> test,  $p < 0.05$ ). Further restricting attention to pollen species represented by at least 10 loads yields the same statistical result.

Table 5 shows the pollen species represented in loads during the timed sampling at Site 2.

Table 5. Pollen species collected by *Trigona nigra* and *Partamona nigrior* at Site 2 from 07:00-11:00 on 11 November 1997.

Species	Family	<i>T. nigra</i>	<i>P. nigrior</i>
<i>Antigonon leptopus</i>	Polygonaceae	+	
<i>Cocos nucifera</i>	Palmae	+	
<i>Ixora coccinea</i>	Rubiaceae	+	
<i>Phthirusa adunca</i>	Loranthaceae		+
<i>Veitchia merrilli</i>	Palmae	+	+
Sp. R		+	

## DISCUSSION

Roubik (1989: Fig. 2.35-2.37) presented data on the daily timing of foraging in 13 species of stingless bees. Our results are consistent with the general pattern of peak pollen collecting in early to mid morning. Insofar as incoming bees without externally

visible loads can be considered nectar foragers, our results likewise fit the general pattern of a more even distribution of nectar foraging throughout the day.

Comparative data between *T. nigra* and *P. nigrior* corroborate less quantitative observations by B. de Dijn (pers. comm.) that the former forages at a steadier rate throughout the day, while the latter mainly forages in the morning. In *T. nigra* 50% of flight activity occurs from 06:00–10:00, while in *P. nigrior* the same fraction occurs between 06:00–08:00. Foraging activity of the two species thus overlaps considerably but is more time-concentrated in *P. nigrior*.

The proportion of pollen:resin loads brought to the nest was about 3:2 in each species.

Although *P. nigrior* builds a much more exposed nest, with presumed greater expenditure of building materials, its pollen:resin load ratio was not significantly below that of *T. nigra*, which nests almost entirely inside cavities.

Each species collects pollen from an array of plant species, with moderate overlap between the two.

Sharing of resources between similar species can be facilitated by their stratification into different zones of space or time (Pontin, 1982). This can arise through various means: a) adaptation to a particular part of available conditions, b) differential habitat selection, and/or c) range restriction of one species through interference by another.

The second and third of these are not relevant to present results, but the first (a) is certainly in evidence. *T. nigra* and *P. nigrior* overlap broadly in their foraging times and resources collected, but with significant biases in both aspects. Furthermore, there is reason to believe that the competitive relationship between the two species is asymmetrical. The overall pattern of differences -and especially the intriguing observations of bees foraging at *Veitchia merrilli* - suggests that *P. nigrior* is the superior competitor, so that *T. nigra* is partially marginalized from preferred foraging times and resources.

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