

May 2003

Resource partitioning between *Trigona fulviventris* and *Scaptotrigona mexicana* with overlapping flight ranges

Michelle H. Averbeck

Follow this and additional works at: https://digitalcommons.usf.edu/tropical_ecology

Recommended Citation

Averbeck, Michelle H., "Resource partitioning between *Trigona fulviventris* and *Scaptotrigona mexicana* with overlapping flight ranges" (2003). *Tropical Ecology and Conservation [Monteverde Institute]*. 633.
https://digitalcommons.usf.edu/tropical_ecology/633

This Book is brought to you for free and open access by the Monteverde Institute at Digital Commons @ University of South Florida. It has been accepted for inclusion in Tropical Ecology and Conservation [Monteverde Institute] by an authorized administrator of Digital Commons @ University of South Florida. For more information, please contact digitalcommons@usf.edu.

Resource Partitioning Between *Trigona fulviventris* and *Scaptotrigona mexicana* With Overlapping Flight Ranges

Michelle H. Averbeck

Department of Biological Sciences, Ecology, Behavior and Evolution Program,
University of California, San Diego

ABSTRACT

The theory of resource partitioning predicts that congeneric species are allowed to coexist by a division of the available resources. This study looks at the possibility of resource partitioning between *Trigona fulviventris* and *Scaptotrigona mexicana* on fine temporal scales in Cloud Forest habitat, a region in which stingless bee pollen diets has not been extensively studied. Workers from one *T. fulviventris* and one *S. mexicana* nest, located 200 m apart, were studied synchronously over six days. Capture-mark and release experiments verified that the foraging areas of these two nests indeed overlap. Of the 14 morphotypes of pollen brought in by *S. mexicana* and the 16 morphotypes brought in by *T. fulviventris*, seven morphotypes were found in common between the two species (Sørensen index = 0.3).

RESUMEN

La teoría de la división de los recursos predice que los especies similares son permitidos coexistir para una división de los recursos disponibles. Este estudio ve a la posibilidad de la división de los recursos entre de *Trigona fulviventris* y *Scaptotrigona mexicana* a bajo plazo en el hábitat del bosque de los nubes, una región en que las alimentaciones de polen de abejas sin picaduras no hubo estudiado extensamente. Trabajadores de *T. fulviventris* y de *S. mexicana*, con los nidos 200 metros afuera de juntos, estudiaba a el mismo tiempo por seis días. Experimentos de capturar-marcas-y soltar confirmaron que las áreas de vuelo de esos dos nidos traslapan. De los 14 morfotipos de polen trajo al nido de *T. fulviventris* y los 16 de *S. mexicana*, siete morfotipos compartían entre de los dos especies (índice de Sørensen = 0.3).

INTRODUCTION

Stingless bees (Apidae: Meliponinae) are the predominant bees of the tropics (Hanson 1995). In Guanacaste Province, Costa Rica they comprise nearly 30 percent of the insect community (Johnson and Hubbell 1974). In Central America, eusocial tropical stingless bee communities exist in mixed species and conspecific communities (Johnson & Hubbell 1978). Female workers collect pollen to feed to larvae (Hanson 1995). The high diversity of pollen-producing plants in the tropics may favor generalist consumers if the resources are temporally and spatially heterogeneous (Heinrich 1976). Because stingless bees are generalists, they may be afforded to facultatively switch to differing resources. This may decrease competition, allowing similar species to coexist. Generalist pollen gathering in bees may be an adaptation to deal with the toxicity of pollen of some flowering species (Roubik 1989). Stingless bees are usually generalists when examined over time scales of months (Hubbell and Johnson 1977). Additionally, by shifting activity periods to diminish competition, stingless bees may temporally partition resources (De Bruijn 1997).

When foraging for pollen, stingless bees visit the foraging site, pack pollen grains on their hind legs and return to the nest. Foraging occurs in an area surrounding the nest (Hubbell & Johnson 1977). The size of the foraging area is limited by maximum flight range, which is about 1.2 km for stingless

bees in Guanacaste Province, Costa Rica (Roubik 1989). In Brazil, a smaller species of *Trigona* was trained to fly to an attractive scent, then marked, and their return to the nest was observed and recorded. The greatest distance at which individuals were flying to and returning from the sucrose source was 500 m (Juliana Rangel, pers. comm. 2003).

In Monteverde, Costa Rica, *Trigona fulviventris* and *Scaptotrigona mexicana* nest 200 m within each other, and therefore have access to similar resources. Stingless bees have exhibited an overlapping of the floral species they choose to visit in long-term studies (Johnson and Hubbell 1974). However, two species with overlapping foraging areas and similar foraging strategies, may compete for resources on finer temporal scales. Others have looked at interspecific resource partitioning in *Trigona* (Eltz et al. 2001). Interspecific aggressive foraging behavior was observed by Johnson and Hubbell (1974) suggesting competition. Another study done in Malaysia suggested resource partitioning occurred through preferences in foraging strata (Nagamitsu et al. 1998).

If two similar stingless bee species were competing for a limiting resource, resource partitioning would lessen the eliminating effects sometimes caused by competition. This study looks first to see if *T. fulviventris* and *S. mexicana* exhibit an overlapping foraging area and second to see if they are partitioning their pollen resources on small temporal scales or usurping the same resources.

MATERIALS AND METHODS

Study Site

The study took place at 1450 m on the Pacific slope of the Cordillera de Tilarán at the Estación Biológica, Monteverde, Costa Rica from April 9-May 5, 2003. Two nests were chosen that were 200 m apart and located in open areas within 100 m from lower montane cloud forest (Nadkarni and Wheelwright 2000).

Flight Range Experiment

Sixty-five *Trigona fulviventris* individuals were collected using hand held aspirators or pheromone traps (see Pollen Collection), marked and released at 100m (the midpoint between the two colonies) and 500 m from the nest. Individuals were marked with paint pens on the thorax following fifteen to twenty minutes of refrigeration. Four mark and release events took place, resulting in the release of 65 individuals at each distance. Nests were monitored for one hour, 24 hours and 48 hours after the release, and returning individuals were collected and terminated to avoid recounting individuals.

Pollen Collection

Bees were always collected between 0900 and 1300 hours. If individuals carrying pollen were collected from one nest, collections were made from the other nest within 24 hours. These consecutive days of sampling for both nests are referred to as paired data days. The nests were tested in paired data days three times, resulting in six days of pollen collection total. A seventh day of data collection was used to sample exhaustively for pollen morphotypes and was not included in pair-wise comparisons. For every day of data collection, 30 bees were collected using a hand-held aspirator. Individuals were also collected using a pheromone trap. This involved placing a small plastic funnel over the colony entrance with a mesh bag attached to the funnel stem. Once an individual wandered into the bag, it was perturbed to release an alarm pheromone, hence attracting other individuals into the mesh bag. The bag was then left unattended and observed in 15- minute intervals until enough bees had been collected. The bees were next cooled for 15-20 minutes in a refrigerator. While the bees were experiencing

reduced mobility due to being cold, individuals carrying pollen loads were found, placed in separate glass vials and subsequently frozen. The remaining bees regained mobility within ten minutes and were released 50 m from the nest.

Pollen Analysis

Pollen from every individual collected was identified to morphotype. Frozen bees were scraped for pollen samples, and pollen was placed on a glass slide and swirled in water to separate pollen grains. Samples were viewed under a monocular compound scope with 40-X power. Each sample was catalogued based on size, shape, texture, and color. A library of pollen morphotypes was created with hand drawings and detailed descriptions, and each morphotype was assigned a corresponding letter for reference. Morphotype per sampled individual was recorded and Shannon-Weiner index was used to find species richness, and morphotype-individual curves were constructed. A Sørensen index was used to test for the overall degree of morphotype overlap between *T. fulviventris* and *S. mexicana*, and a Chi-squared test was used to compare the differences between species within paired data days.

RESULTS

Flight distance and return frequency

Trigona fulviventris returned to the nest from both 100m and 500 m. Nineteen of 65 marked *Trigona fulviventris* released at 100 m from the nest returned to the nest within 48 hours. Three of 65 marked *T. fulviventris* released at 500 m from the nest returned to the nest within 48 hours. Bees released at 100 m returned more often than those released at 500 m (Chi-squared test: $X^2 = 14.0007$, $P = 0.0002$) (Table 1).

TABLE 1. Distances from nest at which *Trigona fulviventris* were released and the frequency of the recorded returns in marked individuals.

	Released from 100m	Released from 500 m
Number of bees released	65	65
Number of bees observed returning	19	3
Return frequency	29.2%	4.6%

OVERALL POLLEN RICHNESS AND OVERLAP

In three sampling periods resulting in 70 total individuals *Scaptotrigona mexicana* brought in 14 morphotypes, mostly of types B and I, and *T. fulviventris* brought in 16 of mostly H and K (Figure 1). Pollen morphotype richness versus individuals sampled curves were similar for both nests (Figure 2). Shannon-Weiner indices for richness of total pollen loads and for paired data days were similar (modified t-tests, $P > 0.05$). Twenty-three morphotypes were catalogued, and the two colonies' pollen load diversity overlapped by seven morphotypes (Sørensen index = 0.3) (Figure 3). Within data sets, differences in morphospecies were more abundant than similarities (Figure 4). The Sørensen index was found to be 0.3, reflecting the seven morphotypes that were in common between the two species.

POLLEN RICHNESS AND OVERLAP FOR PAIRED DATA DAYS

Within the three paired data days, frequency of morphotypes was found to be random for the first paired data days. For paired data days two and three, pollen morphotypes brought in by *T. fulviventris* and *S. mexicana* were found to be significantly different (see Second and Third paired data days).

First paired data days

A total of nine morphotypes of pollen were found on *T. fulviventris* and *S. mexicana*, eight on *T. fulviventris* (three exclusively) and six on *S. mexicana* (one exclusively). Five morphotypes were in common between both species. Significance of frequency of workers carrying the nine morphotypes of pollen was random (Chi-squared test; $X^2 = 10.786$, $P > 0.05$, $n_{T. fulviventris} = 16$, $n_{S. mexicana} = 20$) (Figure 3a).

Second paired data days

Fourteen morphotypes of pollen were recorded for both species. All except for one morphotype of pollen (type K) were found exclusive to either *T. fulviventris* or *S. mexicana*. *T. fulviventris* brought in seven morphotypes, and *S. mexicana* brought in eight. The frequency of the workers carrying the 14 morphotypes of pollen was found to be significantly different between *T. fulviventris* and *S. mexicana* (Chi-squared test; $X^2 = 49.746$, $P < 0.0001$, $n_{T. fulviventris} = 26$, $n_{S. mexicana} = 29$) (Figure 3b).

Third paired data days

T. fulviventris and *S. mexicana* brought in eight morphotypes. Again, all except for one morphotype of pollen (type H) were found to be exclusive. Five morphotypes were found on *T. fulviventris*, and *S. mexicana* brought in four. The frequency of the workers carrying the 14 morphotypes of pollen was found to be significantly different between *T. fulviventris* and *S. mexicana* (Chi-squared test; $X^2 = 27.598$, $P = 0.003$, $n_{T. fulviventris} = 14$, $n_{S. mexicana} = 21$) (Figure 3c).

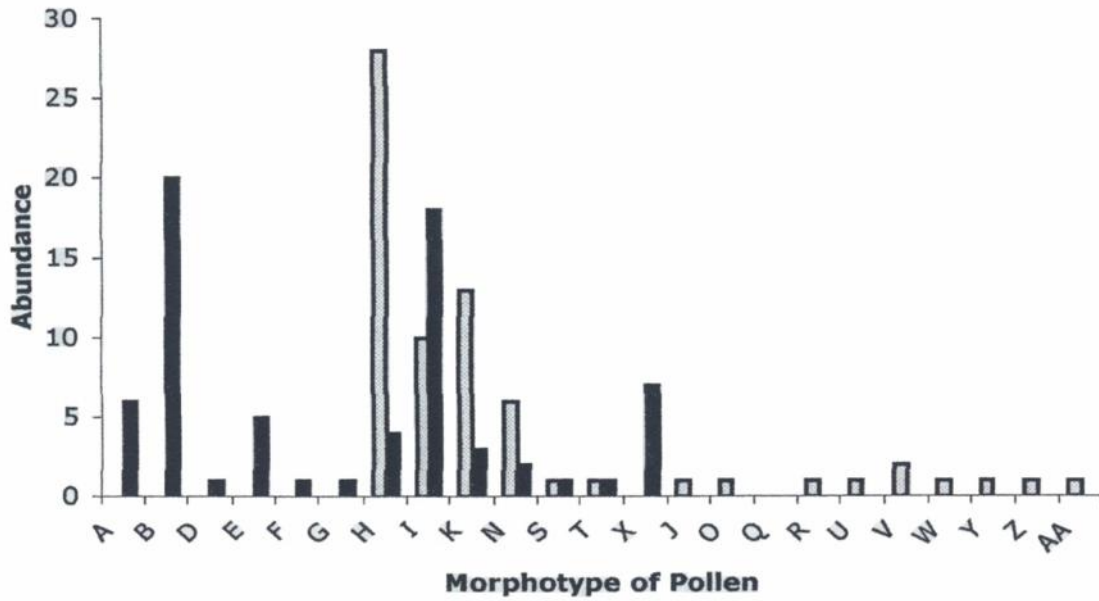


FIGURE 1 Black bars represent pollen morphotypes found on individuals of *Scaptotrigona mexicana*. Gray bars represent pollen morphotypes found on individuals of *Trigona fulviventris*.

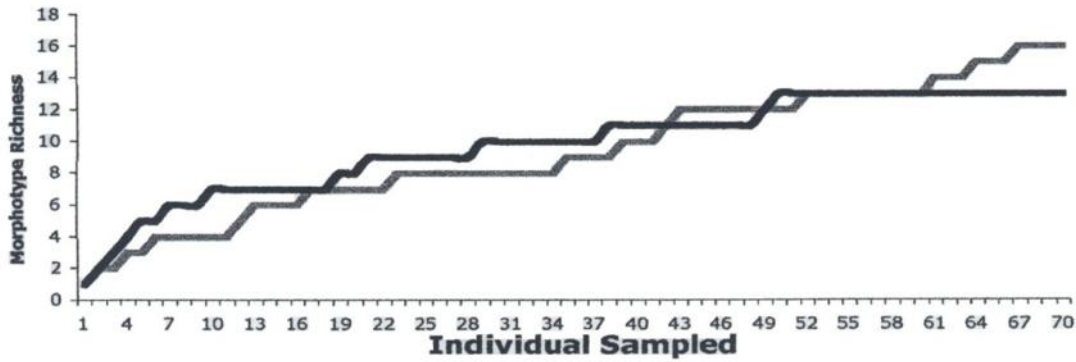
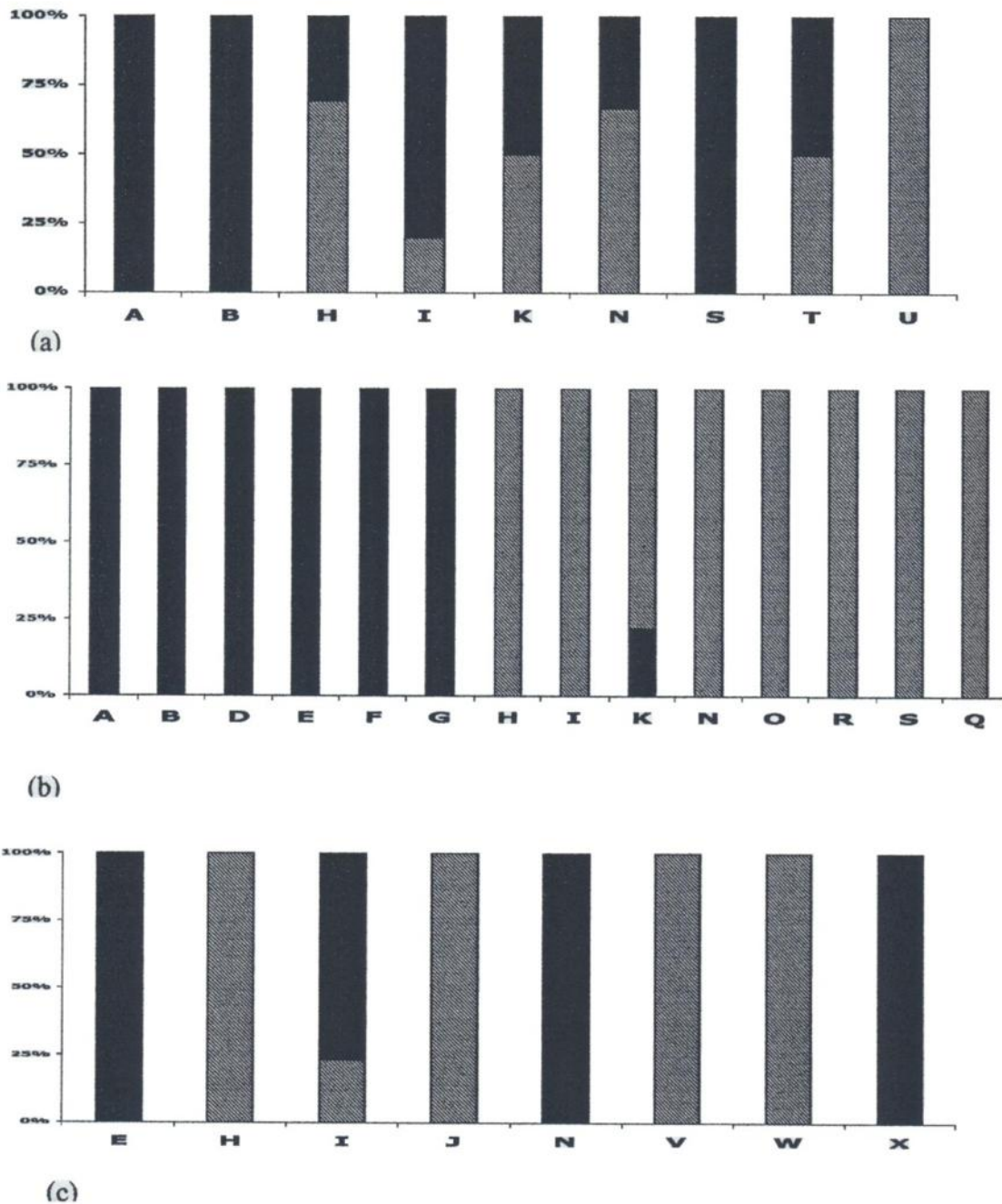


FIGURE 2. Richness of pollen morphotypes per individual sampled. Black line is species richness curve for *Scaptotrigona mexicana*. Gray line is species richness curve for *Trigona fulviventris*.



Morphotypes of Pollen

FIGURE 3. Each bar represents a morphotype of pollen brought in by either nest during one of paired data days. Black bars represent percent of pollen morphotype found on individuals of *Scaptotrigona mexicana*. Gray bars represent percent of pollen morphotype found on individuals of *Trigona fulviventris*. A solid black or solid gray bar means that morphotype was only found on that species. (a) Is the first paired data days, (b) second paired data days and (c) third paired data days.

DISCUSSION

Flight distance and return frequency

Trigona fulviventris has a foraging area that overlaps with *S. mexicana*'s nest location. Theoretical flight distributions can be created with a bee's maximum flight range (Hanson 1995). Three *T. fulviventris* individuals returned from a distance of 500 m from the nest, and their ability to return to the nest increased with decreasing distance with 19 individuals returning from a distance of 100m. A flight range experiment in Brazil also showed *Trigona sp*'s maximum flight range to be 500m (Juliana Rangel, pers. comm. 2003). Other extensive flight experiments show the majority of foraging takes place one-third to one-half of the foraging range (Hanson 1995). Therefore, the *T. fulviventris* workers may spend most of their time foraging 250-300m from the nest with a maximum flight range of 500m. These results are interesting because the two nests included in the study were located only 200 m apart, which puts *T. fulviventris* well into *S. mexicana*'s home range. Although this study did not take foraging direction into account, the results point to an overlapping home range between *Trigona* black and *Trigona* yellow, and if each species forages in a different direction they may avoid competition through spatial differentiation.

Pollen richness and overlap

Trigona fulviventris and *Scaptotrigona mexicana* brought in 23 different morphotypes of pollen overall, and seven of 19 morphotypes were shared between them during paired data days. These seven morphotypes in common reveal overlap in resource foraging. However, within the 24 hour time frame of the paired data days, two of the three paired days showed a non-random frequency of workings bring in pollen, and the morphotypes brought in by both species were significantly different (Figure 3b & 3c). This suggests that on finer time frames *T. fulviventris* and *S. mexicana* may avoid resource overlap. For the second and third paired data days morphotype overlap was low with only one morphotype in common in each case. However, resource overlap was higher for the first paired data day with five morphotypes in common (Figure 3a). Flower phenology may have resulted in a temporary abundance of pollen resources, and in the absence of a limiting resource the two species would not be benefited by the decrease in competition associated with resource partitioning. Other studies have also shown that although there is substantial overlap in the type of flowers stingless bees visit in the long-run, resource partitioning indeed exists between eusocial tropical bees on finer temporal scales (Eltz et al. 2001, Sommeijer et al. 1983, Nagamitsu et al. 1999).

Evidence for resource partitioning

This study suggests pollen resources are being partitioned as a way for similar stingless bee species to coexist. Long-term studies have shown resource overlap, but my results show that resources are partitioned on fine time frames. Many speculations can be made about the selection force that resulted in this pattern of resource partitioning. Past studies have suggested spatial or temporal differences in flower search behavior or foraging strategy may lead to a division of resources. (Eltz et al. 2001) Johnson and Hubbell (1974) observed aggressiveness as evidence of competition between species of stingless bees in Costa Rica. The aggressiveness of one species over another determined which species has access to the most coveted floral resources. According to the original resource partitioning theory, it is indeed the partitioning of resources that allows species to coexist and prohibits the competitive elimination of all but one species (MacArthur 1958).

Other hypotheses for differential resource use between bee species have included that different morphological structures (e.g. proboscis length) allow some species to obtain resources from those flowering species with complementary floral structures (Johnson R. 1986). However, *T. fulviventris* and *S. mexicana* have similar body sizes, and the purpose of this study was to verify resource partitioning, not the selective forces behind it.

Due to the substantial evidence pointing towards the existence of resource partitioning in stingless tropical bees, the mechanisms of resource partitioning among stingless bees should be examined. While long-term studies have found that there is resource overlap, this study suggests in the short-term, they are partitioning their pollen resources. Because *T. fulviventris* and *S. mexicana* are visiting different flowers on fine temporal scales (Figure 3b & 3c), they are allowed to coexist. With the experimentally derived overlapping foraging range and the mapped and recorded differences in the pollen diets of *T. fulviventris* and *S. mexicana* it can be concluded that interspecific resource partitioning is maintaining these populations by reducing competition.

ACKNOWLEDGEMENTS

I would like to thank Karen Masters for her support and guidance and her ever-encouraging advice of “Just do it!” I also thank Chrissi Murphy, Frank Joyce, Juliana Rangel, Tracy Rogers and Ramon Amores Campos for their help in formulating this study. Special appreciation goes to Paul Hanson for identifying my stingless bees.

LITERATURE CITED

- De Bruijn, L.L.M. and M.J. Sommeijer. 1997. Colony foraging in different species of stingless bees (Apidae, Meliponinae) and the regulation of individual nectar foraging. *Insects soc.* 44: 35-47.
- Eltz, T.A., C.A. Brühl, S. van de Kaars, V.K. Chey and K.E. Linsenmair. 2001. Pollen Foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. *Insects soc.* 48: 273-279.
- Hanson, P.E. and I.D. Gould. 1995. *The Hymenoptera of Costa Rica*, Oxford University Press, Oxford
- Heinrich, B. 1976. Resource partitioning among some eusocial insects: Bumblebees. *Ecology* 57: 874-889.
- Hubbell, S.P. and L.K. Johnson. 1978. Comparative foraging behavior of six stingless bees exploiting a standardized resource. *Ecology* 59: 1123-1136.
- _____, and L.K. Johnson. 1977. Competition and nest spacing in a tropical stingless bee community. *Ecology* 58: 949-963.
- Nagamitsu, T., K. Momose, T. Inoue and D.W. Roubik. 1999. Preference in flower visits and partitioning in pollen diets of stingless bees in an Asian tropical rainforest. *Res. Popul. Ecol.* 41: 195 – 202.
- _____, K. Momose, T. Inoue. 1998. Interspecific morphological variation in stingless bees (Hymenoptera: Apidae, Meliponinae) associated with floral shape and location in an Asian tropical rainforest. *Entomological Science* 1: 189-194.
- Sommeijer, M.J., G.a. de Rooy, W. Punt, and L.L.M. De Bruijn. 1983. A comparative study of foraging behavior and pollen resources of various stingless bees (Hym., Meliponinae) and honeybees (Hym., Apinae) in Trinidad, West Indies. *Apidologie* 14: 205-224.
- Johnson, L.K. and S.P. Hubbell. 1974. Aggression and competition among stingless bees: Field studies. *Ecology* 55: 120-127.
- Johnson, R.A. 1986. Intraspecific resource partitioning in the bumble bees *Bombus ternarius* and *B. Pennsylvanicus*. *Ecology* 67: 133-138.
- Mac Arthur, R.A. 1958. Population ecology of some warblers of Northeastern coniferous forests. *Ecology* 39: 599-619. In *Foundations of Ecology*. Edited by L.A. Real and J.H. Brown. *Foundations of Ecology*. 1991. The University of Chicago, Chicago.
- Nadkarni, N.M. and Wheelwright N.T. (Ed.) 2000. *Monteverde: Ecology and conservation of a tropical cloud forest*. Oxford University Press, New York, New York.
- Roubik, D.W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, New York.