Rev. Biol. Trop., 27(1): 111-118, 1979

Responses by a stingless bee to a subtropical environment

by

H. G. Fowler*

(Received for publication November 13, 1978)

Abstract: The stingless bee, *Trigona angulata fribrigi* Schwartz, predominantly nested in radical cavities of at least 28 tree species in central Paraguay, but were more prone to predation by humans than nests located in trunk cavities. Colonies were randomly dispersed and occured at a density of 3.7 ± 4.3 colonies/ha. Multiple regression analysis revealed that temperature, time of day, and relative humidity explained a significant amount of seasonal colony foraging intensity ($R^2 = 0.66$). Over seasons, colony foraging intensity and the number of flowering herbs and trees were canonically correlated with mean temperature, relative humidity, month and hours of available sunlight.

One of the most common eusocial insects of central Paraguay is the small stingless bee, *Trigona angulata fribrigi* Schwartz. Colonies of this bee are readily found in forests, and are commonly pillaged by local inhabitants for their highly regarded honey. Due to their numerical abundance and their exploitation by humans, I elected to examine the nesting and seasonal foraging patterns of *T. angulata* in light of the physical constraints of their environment.

Evidence suggests that stingless bees do not discriminate among tree species for nesting sites (Hubbell and Johnson, 1977), but only Wille and Orozco (1975) have published information on the effect of environment on the foraging of stingless bees, in contrast to the many studies which have been done on *Apis* (Ribbands, 1953). Stingless bees would seem to be ideal candidates for such investigations as they tend to be generalized in their flower visitation behaviors (Heithaus, 1974), thus minimizing the effects of specialized behavioral modifications. Seasonal environment must also play a major role in the foraging behavior of subtropical bees.

MATERIAL & METHODS

Nesting: During a period of 2 years (1974-1976), whenever possible I made field trips through principally the following political departments: Central, Cordillera, Paraguari, and Misiones. When I encountered nests of *T. angulata,* I

---

* Instituto de Ciencias Básicas Universidad Nacional de Asunción, Ciudad Universitaria, Paraguay. Present address: Department of Biology, New Mexico State University, Las Cruces, NM 88003, U.S.A.

noted the tree species with which it was associated, whether the nest was located in the root system or the trunk. and whether the nest had been abandoned or predated. Nest identification was facilitated by the characteristic entrance.

Colony densities were estimated in March, 1976, in 25 1 ha plots in semideciduous woodlands near San Lorenzo, Paraguay (25° 22' 23"S, 57° 33' 36" W). Colonies were tallied as they were found. Dispersions of colonies were studied by Morisita's (1962) index:

$$I = N \frac{\Sigma x^2 - \Sigma x}{(\Sigma x)^2 - \Sigma x}$$

where N is the number of samples, and x the number of colonies. Significance of a departure from random dispersion is given by:

$$F = \frac{I(\Sigma x - 1) + N - \Sigma x}{N - 1}$$

with the appropriate values of F at the significance level desired given in F tables, where n_1 is N − 1 and n_2 is infinity.

Foraging intensity and environment: I selected 2 colonies of *T. angulata* in radical cavities of tipa trees, *Tipuana tipa* Hubbl. et Rheed, in a woodland near San Lorenzo, Paraguay, to examine the effects of environment on the intensity of foraging. For a period of 2 days per month, for the months November and December, 1976, and January, February, March, May and June, 1976, I hourly counted the number of bees entering and leaving the nest per 2 minutes. I took simultaneous readings of nest entrance temperature and relative humidity near ground level with a Grant's recording thermometer and psychrometer assembly. The actual and potential hours of unobstructed sunlight were obtained from the University weather station, about 1 km away.

During the same days that foraging intensity was monitored, I recorded the number of flowering herbaceous species in each of 15 1 m^2 quadrants, and the number of flowering trees in a 2500 m^2 plot.

Data were analyzed by the standard multivariate techniques of multiple regression and canonical correlation (Morrison, 1976) with standard SAS computer programs (Barr *et al.*, 1976) at the computer facilities of Rutgers University, New Brunswick, N. J.

RESULTS

Nesting: A total of 149 *T. angulata* nests (Table 1) were encountered in 28 tree species. Of these, 124 (83%) were found in radical cavities, principally in abandoned nest sites of the leafcutting ants *Acromyrmex rugosus* (Fr. Smith) and *Acromyrmex crassispinus* Forel. The remaining 25 nests (17%) were found in cavities located in tree trunks. However, 22% of the nests located in radical cavities had been pillaged by humans, while no trunk nests were observed to have suffered

TABLE 1

Occurrence and state of nests of Trigona angulata
associated with tree species in central Paraguay

	Number of nests				
Tree species	radical	trunk	abandoned	predated	total
Leguminosae					
Enterolobium contortisiliquum	1	—	—	—	1
Epythrina crista	1	1	—	—	2
Gleditsia amorphoides	1	0	—	—	1
Piptadenia rigida	15	2	1	5	17
Pithecellobium guaraniticum	2	—	—	—	2
Pithecellobium multiflorium	4	—	—	—	4
Tipuana tipa	18	3	1	5	21
Anacardiaceae					
Anacardium occidentale	—	1	—	—	1
Astronium fraxnifolium	—	1	1	—	1
Apocynaceae					
Tabernamontana australis	4	—	—	—	4
Pentapanax warmingiana	—	1	1	—	1
Bignoniaceae					
Crecentia alata	1	2	—	—	3
Cybistax antisyphilitica	1	—	—	—	1
Tabebuia argentea	14	2	1	5	16
Tabebuia integra	19	3	—	3	22
Tabebuia ochracea	4	1	—	1	5
Bixaceae					
Bixa orellana	—	1	—	—	1
Bombaceae					
Chorisa speciosa	12	3	1	4	15
Boraginaceae					
Cordia alliodora	1	1	—	1	2
Patagonula americana	3	—	—	1	3
Euphorbiaceae					
Jathropha curcas	4	—	—	—	4
Sapium longifolium	2	—	—	—	2
Sebastiana serrata	1	—	—	—	1
Lauraceae					
Ocotea puberula	3	1	—	1	4
Meliaceae					
Melia azendarch	2	—	1	—	2
Myrtaceae					
Psidium arasa	6	1	—	1	7
Sterculiaceae					
Guazuma ulmifolia	2	—	1	—	2
Tiliaceae					
Heliocarpus americanus	3	1	—	—	4
TOTALS	124	25	8	27	149

this fate. Moreover, 6 of the 8 nests determined to have been abandoned were also located in radical cavities (Table 1).

Censuses of *T. angulata* nests in woodlands near San Lorenzo produced densities of 3.7 ± 4.3 viable colonies/ha. Employing Morisita's index of dispersion, I obtained $I = 1.07$, which gave an F value of 1.26 ($< F_{.05} = 1.52$). Thus, colonies can be assumed to have been randomly dispersed throughout the habitat.

TABLE 2

Correlation matrix of foraging intensity and environmental parameters

	Month	Time of day	Temp.	%R/H.	Colony foraging intensity
Month	1.000	0.119	-0.263	-0.022	-0.187
Time of day	n.s.	1.000	-0.208	0.518	-0.587
Temperature	****	***	1.000	-0.277	0.614
Relative humidity	n.s.	****	****	1.000	0.506
Foraging intensity/colony	**	****	****	****	1.000

TABLE 3

Components of a general multiple regression model of mean colony foraging intensity. Model is in the form of: Mean colony foraging intensity (number of bees/2 min/colony) = parameter 1 + parameter 2, etc.

Parameter	Beta value	Standard error of Beta	F value	T for H_0: Beta = 0
Intercept	30.064	10.748	––	2.80**
Temp. (°C)	2.467	0.196	158.61****	12.59****
%R.H.	-0.507	0.123	16.85****	-4.10****
Hrs from noon	-4.001	0.409	95.44****	-9.77****
Month	-0.330	0.319	1.07	-1.03

Overall F value = 129.85****
$R^2 = 0.657$

** P < 0.05, ****P < 0.0001.

Foraging intensity and environment: Over the study period, monitored environmental parameters were highly correlated with estimates of foraging intensity (Table 2), with temperature being more strongly correlated than relative humidity. A simple model of colony foraging intensity (Table 3) suggests a high dependence on temperature, time of day, and relative humidity, with month showing an insignificant effect on foraging intensity. Thus, even without considering the effects of floral rewards, about 60% of the colony foraging intensity can be explained by simply measured parameters (Table 3). When the effects of floral rewards are incorporated into such a model, it is probable that most of the foraging intensity could be explained.

Canonical correlations of seasonal parameters (Tables 4 & 5) underline the strong association of the abiotic and biotic parameters. The statistical tests on the canonical roots are given in Table 4, with the first 2 roots significant. The first pair of canonical variates (Table 4) suggests that the actual hours of available sunlight was the most important factor affecting the biotic response, principally the number of flowering herbaceous species (Table 5). The second pair of canonical variates (Table 4) once again indicates the importance of available sunlight, and to a lesser extent relative humidity and temperature (Table 5), on the number of flowering herbaceous species and the number of flowering trees. For both canonical variates, bee foraging intensity did not enter strongly into the criteria variate.

DISCUSSION

The results of this study confirm previously published reports that stingless bees do not exhibit a great deal of selectivity for tree species as nesting sites (Hubbell & Johnson, 1977), but rather are limited by the availability of cavities, provided the tree is of a suitable diameter (Darchen, 1972; Hubbell and Johnson, 1977). *T. angulata,* however, predominantly nested in radical cavities and was, therefore, less dependent on trunk diameter than true trunk nesting species of *Trigona.* As colonies were generally located in abandoned nesting sites of the leafcutting ant, *A. rugosus, T. angulata* nesting sites were common, due to the elevated colony densities of this ant in the study area. However, the risks of nesting in radical cavities were high when the effects of human activities were considered. Aside from man, the most likely natural predators of subterranean colonies of *T. angulata* in the study site was the army ant, ***Labidus praedator*** (Fr. Smith), which was never observed to raid a colony. In light of this fact, nests located in trunk cavities were less probable of being preyed upon by humans, but it is unlikely that human pillaging of radical nests has produced a preference for nesting in the rarer

TABLE 4

Canonical correlation analysis of biotic and abiotic variates. Chi square tests are given for successive canonical roots

Pair of canonical variates	Canonical roots (R)	Chi-square value	Degree of freedom	Probability of occurrence
1	1.000	999999.937	15	0.0001
2	0.999	67.965	8	0.0001
3	0.780	2.344	3	0.5071

TABLE 5

Canonical vector loadings associated with the first two pairs of canonical variates in Table 4

	Canonical roots	
Variate	1	2
Predictor set:		
Month	-0.0672	-0.1567
Actual hrs sunshine	0.1288	0.8886
Potential hrs sunshine	0.0034	0.0129
Relative humidity (%)	0.0055	-0.3911
Temperature (C)	-0.0327	-0.3196
Criteria set:		
Total bee foraging intensity	0.0004	-0.0007
Number flowering herb spp/m^2	-0.0747	0.2285
Number flowering trees/2500 m^2	0.0038	0.1376

trunk cavities. Human influences have affected the population dynamics of *A. rugosus,* indirectly increasing their colony densities through cultural practices, which in turn increase potential nest site availability of *T. angulata.*

This last speculation may explain why colony densities of *T. angulata* in the study site (3.7 colonies/ha) were higher than those found by Darchen (1972) for savanna-woodland species in the Ivory Coast (≈ 2.5 colonies/ha), and almost a full order of magnitude greater than the value reported by Hubbell and Johnson (1977) for species from Costa Rican forests (0.3 – 0.1 colonies/ha). These higher densities of *T.angulata* colonies in Paraguay may also be attributable to their small size (~ 2 mg/worker), as predicted by Hubbell and Johnson (1977).

A significant amount of variation in colony foraging intensity could be explained by several abiotic factors. These factors may affect the heat and water budgets of the bees directly, and consequently limit activity periods, which in the extremes of temperature and humidity is quite probable. Under less extreme conditions, the importance of these factors may be indirect. For example, nectar flow in flowers is known to fluctuate on an hourly and daily basis (Park, 1929; Vansell *et al.,* 1942; Corbet, 1978), and also to respond to temperature and humidity (Park, 1929), which may affect the visitation patterns of pollinators (Vansell *et al.,* 1942; Corbet, 1978). If nectar flow and pollen availability were taken into account, a much better predictive model of foraging intensity should be produced, even though extremely small stingless bees, such as *T. angulata,* tend to forage individually or in small groups on highly dispersed resources (Johnson & Hubbell, 1974).

Finally, the high dependence of seasonal flowering of trees and herbs on environmental conditions adds further support to these conclusions. As flowering phenology should be linked to the coevolutionary predictability of pollinator availability, we should expect proportionally more flowering species to be present at times favorable for pollinator service. During cooler periods, environmental factors probably limit the physiological activity of foraging, and proportionally fewer flowers were available. These conditions were reversed during the summer, when plant flowering was highly linked with available sunlight. Although these conclusions are very general, and do not take into account diel patterns of nectar secretion, which may make different flowering species available for pollination at different hours of the day, nor do they take into account the effect of pollinator specialization, they do seem to explain the data at a basic level, especially since stingless bees are generalized in their flower visitation patterns (Heithaus, 1974).

ACKNOWLEDGEMENTS

I gladly acknowledge the prompt species identification by Dr. J. M. Camargo, and the support to carry out this study provided by the U. S. Peace Corps and the Instituto de Ciencias Básicas, and its director Dr. N. Gonzáles Romero. I thank R. B. Roberts and E. Rajotte for their comments on earlier drafts and their constant encouragement. Computer facilities were provided by Rutgers University.

RESUMEN

La abeja, *Trigona angulata fribrigi,* construye sus nidos con preferencia en cavidades radicales de por lo menos 28 especies de árboles en Paraguay central, y también en cavidades en los troncos. Los primeros están más expuestos a la depredación humana. Las colonias se dispersaron al azar a densidades de 3,7 ± 4,3 colonias/ha. Los análisis de regresión múltiple indican que la temperatura, la hora, y la humedad relativa afectan la intensidad forrajera de las colonias de *T. angulata* (R^2 = 0,66). A lo largo de las estaciones, la intensidad de búsqueda de alimentos y el número de plantas y árboles florescentes se correlacionaron con los factores abióticos.

LITERATURE CITED

Barr, A. J., J. H. Goodnight, J. P. Sall, & J. T. Helwig
1976. A user's guide to SAS 76. SAS Institute. Raleigh, North Carolina.

Corbet, S. A.
1978. Bee visits and the nectar of *Echium vulgare* L. and *Sinapis alba* L. Ecol. Ent., 3: 25-37.

Darchen, R.
1972. Ecologie des quelques trigones *(Trigona* sp.) de la savane de Lamoto (Cote d'Ivoire). Apidologie, 3: 341-367.

Heithaus, E. R.
1974. The role of plant-pollinator interactions in determining community structure. Ann. Mo. Bot. Gard., 61: 675-691.

Hubbell, S. P., & L. K. Johnson
1977. Competition and nest spacing in a tropical stingless bee community. Ecology, 58: 949-963.

Johnson, L. K., & S. P. Hubbell
1974. Aggression and competition among stingless bees: field studies. Ecology, 55: 120-127.

Morisita, M.
1962. I_δ -index, a measure of dispersion of individuals. Res. Pop. Ecol., 4: 1-7.

Morrison, D. F.
1976. Multivariate statistical methods. 2d ed. McGraw Hill, New York. 415 p.

Park, O. W.
1929. The influence of humidity upon sugar concentration in the nectar of various plants. J. Econ. Ent., 22: 534-544.

Ribbands, C. R.
1953. The behavior and social life of honey bees. Bee Res. Assn. Ltd., London.

Vansell, G. H., W. G. Watkins, & R. K. Bishop
1942. Orange nectar and pollen in relation to bee activity. J. Econ. Ent., 35: 321-323.

Wille, A., & E. Orozco
1975. Observations on the founding of a new colony by *Trigona cupira* (Hymenoptera: Apidae) in Costa Rica. Rev. Biol. Trop., 22: 253-287.