International Research Journal of Biological Sciences ISSN 2278-3202
Vol. **2(2),** 44-50, February **(2013)** *Int. Res. J. Biological Sci.*

Nesting Pattern Preferences of Stingless Bee, *Trigona iridipennis* Smith (Hymenoptera: Apidae) in Jnanabharathi Campus, Karnataka, India

Nayak Pavithra P.[1], Reddy Shankar M. [2] and Jayaprakash[3]
[1]Centre for Applied Genetics, Jnanabharathi Campus, Bangalore University, Bangalore - 560 056, Karnataka, INDIA
[2,3]Department of Zoology, Jnanabharathi Campus, Bangalore University, Bangalore - 560 056, Karnataka, INDIA

Available online at: www.isca.in
Received 21th November 2012, revised 26th November 2012, accepted 14th December 2012

Abstract

The patterning aspects of nests are receiving increased attention in nature, so we have studied it in human-dwelling environments involving repeated spatio-temporal mold of pattern. Different criteria such as nesting sites, orientations, nest characters, longevity and elevation of nests have been selected to check the level of preferences exhibited by an indigenous resident species of stingless bee, Trigona iridipennis Smith at the Jnanabharathi campus in the southern part of Bangalore (Karnataka). Nesting patterns gave a precise measurement of preference level exhibited by testing different paradigms. The deciduous, shrub type of vegetation helped for successful dominance in higher number of nests to thrive well, which in turn helped to look at the varying patterns of nests. Observations on different nests revealed: i. preference for the habitats made of walls, ii. north facing direction for nest opening, iii. different type of nests with oval-shaped opening and medium-sized exposure outside, iv. nests with more accumulation of mud, resin and wax deposits and v. bees preferring middle elevation range of 11-15 feet for nest-building purely depending on the safer strategies such as availability of flora, protection from predators for better and safe survival at the nesting sites.

Key words: Stingless bees, *Trigona iridipennis,* patterns, nest sites, preferences, orientation, substratum, elevation, JB campus.

Introduction

The stingless bees (Hymenoptera: Apidae: Meliponini) are eusocial and corbiculate, showing tropical and southern subtropical distribution[1] with a distinguished character of reduction and weakness of wing venation, presence of the penicillum and vestigial sting[2]. All stingless bees build elaborate nests with structures that are often characteristic for the species or for higher taxa[3, 4]. Meliponini are the tribe, little studied, with two genera: *Lisotrigona* and *Trigona* found to occur in Asia[5]. Asiatic stingless bee *Trigona (Tetragonula) iridipennis* Smith is one of the most primitive honeybee found in India[6]. The Indian subcontinent with a tropical Savanna climate, varying physiographic environment, higher altitudes and luxuriant flora offers an abode for the rich and wide distribution of stingless bee *(T. iridipennis)*.

Social insects co-ordinate many colony-level preferences even though without any evidence of having a central control. Consequently, social insects like *Trigona* build spatio-temporal patterns far beyond their size[3,7]. Patterns in general terms determine the recognizable regularity in the observed data. The patterns built are simple repetition of some basic module being repeatedly present but organized with specific interest and importance. The patterns could also be an outcome of variety of stimuli, which include not only environmental cues but also direct or indirect interactions among nest mates involving pheromones, and stimulus may initially activate nest-building behaviour but pattern formation proceeds. These stimuli become more complex and vigorous thereby inducing new types of behaviour that can lead to morphogenetic process during which past construction sets the stage for new building actions[8].

The whole scenario of study objectives has been put forth to know the preferences implemented, consistency of preferences, their basic history and criteria affecting them through the exploitative behavior exhibited on account of observations of nests of these stingless bees.

Material and Methods

Study area: The study area, Jnanabharathi campus (12°56´35.58´´N and 77°30´26.92´´E) is at an elevation of 2743 feet in the south-eastern part of Bangalore, encompasses a geographical area of approximately about 449.74 hectare (1100 acres) and lies in the Deccan Plateau with topography mostly of flat to moderate slopes with persistent dry deciduous, shrub type of vegetation that has given room for the stingless bee to flourish well. Natural vegetation (98.38 hectare) of Jnanabharati campus (JB campus), Bangalore University, has been allotted to various institute buildings, such as various departments, hostels, canteens, sports ground, offices, residential quarters, research centers and biodiversity parks, which are all human dwelling places involving both residential and non-residential areas; a sign of urbanized area.

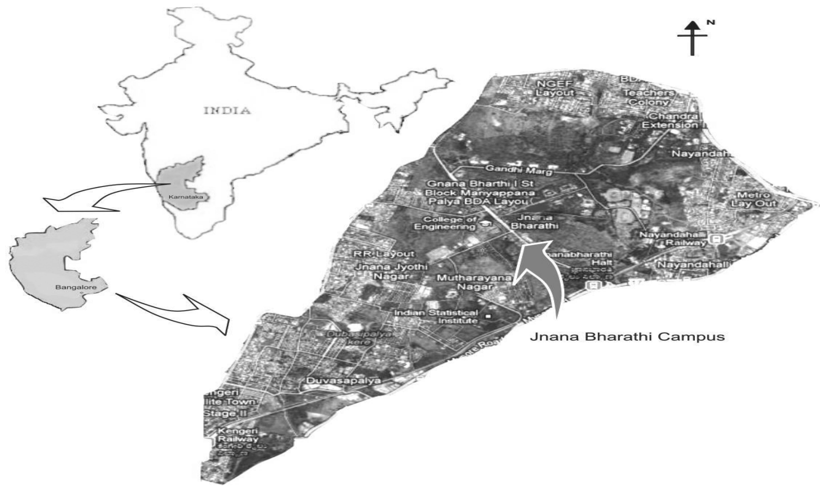

Figure-1
Study area at Jnanabharati campus in Bangalore, Karnataka

Data collection: The observation-based data were collected for a period of 10 months (i.e. May, 2010 – February, 2011) between 0900 and 1700 hours on a weekly basis by following an all out search method through ocular vision. The main task of locating the feral colony was possible by identifying the movements of the bees toward nest entrance. Most of the measurements are taken by using a standard measuring tape on centimeter scale because of its ease of evaluation when compared with other methods. The methods of Sheetal and Basavarajappa[9] have been followed for collecting data on different variables such as nesting sites and their attributes, elevation, orientation of nest and longevity of nest. Nest-site selection, nest orientation and nest architecture are the different modes of passive selections used by social insects to regulate their nest's microclimate. The collected data were compiled using SPSS software V.17 and analyzed with suitable reason. The nests being photographed with Cyber-shot DSC-HX9V digital camera with G lens for future purpose.

Nest sites: A visual based method have been applied to search the nesting sites as mentioned earlier. Consequently, a suitable nesting site is a significant reason for the evaluation of habitats and JB campus is found to be one. A range of habitats or sites been chosen by *T. iridipennis* to build its nest around the man-made structures categorized in a way as human intervention-based regions by distribution, where some sites being used and some unused by humans such as residential, educational areas, road sides parks etc., been taken into consideration. The different substratum like walls made of brick, rock crevices, pillars, metallic sheath; water pipes in the form of iron or cement-based materials; plastic or iron pipes supported for telephone wires; lamp posts; staircases; on ground floor; wooden rim of door and windows got selected for constructing its nest sites. So, a percentage-based graph is plotted (figure-3) for recording which type of natural habitat is being more preferred. Selection can only act on phenotypic variation if it has a genetic basis and the data were available showing genetic origin of habitat assortment, suggesting that habitat preferences do indeed have a genetic basis[10] but, genetic analysis was not carried out to confirm.

Nest orientation: For assessment among un-manipulated nests, orientation with categorical variable has been divided into eight levels: connecting four perfect readings of directions (North, South, East, West), with other four intermediate directions like northeast (0–90º), southeast (91º–180º), southwest (181º–270º), and northwest (271º–360º) was also recorded. The different orientation of the nest been recorded using a GPS inbuilt service from Sony camera and with normal orienteering compass. These categories generally show coordinates in nest orientations with each having its own feature imposed by the azimuth angle of the sun. Therefore, on a percentage basis a graph is plotted with different orientations of the colony to know the most preferred direction of stingless bees (Figure-3) and these plots are built through azimuth orientation; 0-360º.

Nest building: Among the variety of combined activities performed by stingless bees; nest-building is certainly the most amazing activity owing to the difference between single and group levels[11] and where groups often excel in contrast to solitary individual[12]. On the basis of opinions by different pioneers on nest entrance, diverse characters were under consideration such as nest shape, depth, openings, color, resources used, etc., through direct observation and measurements (table-1). The preferential level of most particular character chosen for the building of the nest been examined from the data thought statistics, represented as graphs and results been justified in favor of importance to the nest.

Table -1
Different Nesting attributes of the *Trigona iridipennis* at Jnanabharati campus, Bangalore

Sl. No	Attributes	Observation / criteria's	Most preferred
I	**NEST CHARACTERS**		
1	Size of nest opening	Small, medium, large	Medium sized
2	Shape of nest opening	Circular, oval, irregular	Oval
3	Nest measurements	1. Nest depth (0.1- 35.0) cm 2. Nest opening - circumference (0.15-2.2) cm	0.3 – 4 cm (small projection) 0.8 -1.4cm (medium opening)
4	Nest color of nest	Red, black, grey, brown, cream, light green, orange, yellow (amber), black	Greenish, black
5	Nest orientation	North, south, east, west, northeast, northwest, south east, southwest	North
6	Nest enclosure material	Petroleum products such as grease, resin, wax, wooden pieces, sand, mud, tar, blue paint, pollen, stones, cow dung, animal feces.	Resin, mud , wax
7	Nest height from round	Reading in feet (0 -18 ft)	Middle elevation (11- 15 ft)
8	Surface	Smooth , rough	Rough
II	**NESTING HABITAT**		
1	Places visited	Residential quarters, Educational buildings Hostel , office, road side, parks	Educational buildings
2	Colony Location	Interior , exterior(from the road side)	Interior regions
3	Substratum (Habitat) 1. Wall 2. Water Pipes 3. Electrical pipes 4. Wood 5. Stare cases 6. Floor	 -Stone, mud brick, pillars, metallic sheath -Iron, cemented, plastic -Electric box , lamppost, telephone wires -Wooden : Door rim, Windows rim -Cement plastering's -Mud	 Wall of mud brick

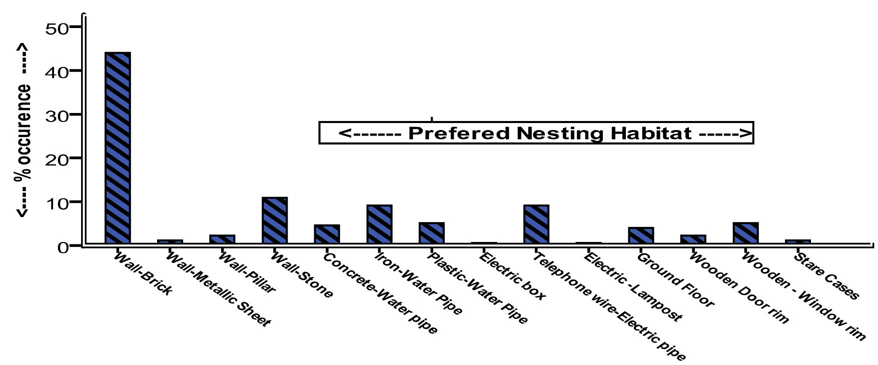

Figure- 2
Preferred nesting habitat of *T. iridipennis* against the percentage occurrences

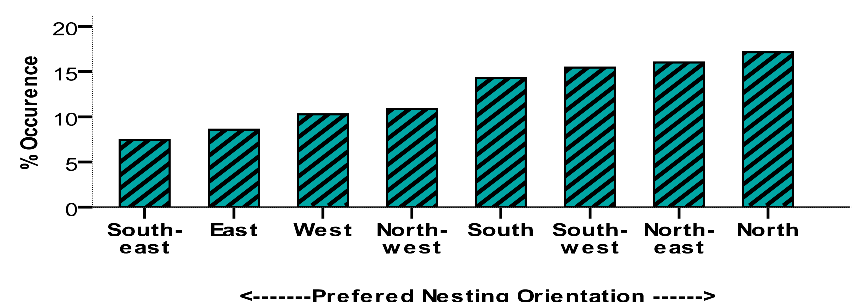

Figure- 3
Nesting orientation of *T. iridipennis* against the percentage occurrences

Longevity and elevation of colonies: It is impractical to make direct clarification about longevity of colonies within a work period of nine months. But, still attempts have been made to monitor the feral colony by periodic visits. A technique of earlier marking process was maintained to ensure live or abandoned state of nests. Elevation as a paramount component of environment, is also been considered for attention and the height of the colony from the ground level been assessed using measuring tape. With little understanding about these bees we tried to make a small attempt to check how both longevity and elevation facility with JB campus is deciding inclination level of these bees.

Results and Discussion

Nests being notable point to the colonial life of social insects play a major role in providing physical protection against environmental perturbations; while in others microclimate of nest provides relatively stable temperature. The nest-site preferences are an adaptive response to fitness cost imposed by variation in nest-site microclimate and among the different nesting attributes chosen. Occurrences of the habitat on the wall made of bricks showed the distinct preference of 43% (table-1), while other substrata acted as the subset or intermediates for the distinct preferences to build nest by *T. iridipennis* (figure-2) and it is not possible to cover all habitats within the area of visit as bees wander over a large area that permits them to access favorability and obviously difficult for a human to reach. The frequency of different nesting habitation depends on proper substrates. However, difference in the food supply toward the nest appears as a principal variable that could meet for the differences in the attractiveness of the habitats. Relating to this, the number of nest in the interior region (83.4%) such as in residential quarters, office buildings and educational buildings counted for higher numbers than colonies at exterior area (16.6%), i.e., nests more exposed toward road side. But, factors influencing the choice of nest sites are difficult to predict, as the bees often spent several hours prospecting most likely places. The habitat preferences are considered as adaptation in nature, such that fitness is higher in preferred habitats causing natural selections to support it - on the basis of genetic factors[10]. An array of environmental factors may also exert selection on preferences[12-15] which could be based on intrinsic and extrinsic factors[16-18]. Therefore, advances in understanding evolution of habitat preferences depend on an individual-level examination of habitat choices and its fitness consequences, examination of the phenotypic traits and mechanisms that underlie habitat-induced variation in fitness components[19].

The nest entrances play a sticking role toward nest characters. The simplest stingless bee nest entrance protrudes slightly from the base of the entrance hole. The nest entrance opening is largest in certain *Trigona species*[20]. The feral colonies measurement of *T. iridipennis* in Jnanabharati campus revealed an average value of 87.7 ± 3.82 (Mean ± SE) nest, with small bee excavating from the nest with a tunnel depth of (mean ± SE, range, N) 1.79 ± 0.27, 0.1–35 cm, 175 and nest opening measurements of 0.76 ± 0.02, 0.15–2.2cm, 175 of the entrance opening from outer surface. The nest entrance revealed bees preferring nest opening of middle range 0.8–1.4 cm over larger and smaller openings and also showed preference, when it came to the shape of the entrance, i.e., oval shape been more preferred to circular and irregular opening (table-1) and there was a null hypothesis acceptance between shape and size of the nest opening that suggested a statistical significance for two variables to be independent ($X^2 = 13.45$; df = 4, $p > 0.05$). A small or unornamented nest entrance is cryptic; only means for potentially defensive adult bees and nest entrance characters such as flexible entrance tube, exposed nest, sticky resin, fecal material, pollen accumulation or scutellum, wax deposit, wood fiber (paper), trash used as nest material are common in the genus - *Trigona*[20]. The wall could serve two functions. The colonies of social insect are compared with factories within fortresses[21]. Here, nest wall has been a barricade against natural enemies and a hostile climate; it can also serve as infrastructure to regulate the factory. The proper arrangement of wall will decide how much space the inhabitants of the colony allocate to themselves which can regulate their density, encounter rates and might also influence task allocation[22, 23, 24].

The material used for construction of the nest has a definite characteristic function[25] according to its physical properties than its taxonomy, and that proportions of materials of different types used vary not only with availability but also with the requirements of particular substrate and habitat situations. So, we could see some nest entrance found with more deposits of mud, whereas others with the gathering of resin, wood pieces, stones, pollen, etc., table-1. Among the resources, mud and resin accounted the chief components preferred around the nest, as these bees also called Dammer bees[26]. Dammer bees collect dammer a kind of resin for the building of their nest along with the wax produced from their body. The insulation provided by wood, resin, earth, stone or other nest substrates makes it unlikely that colonies overheat and nests are not in full sunlight so that not too many bees engage in fanning during extremely high ambient temperatures. Sand being the another substance seen on the surface acts as an ideal building material because walls built from sand grains are quantified easily and has stiffness[8, 27]. In addition to endogenously produced wax, stingless bees incorporate large amounts of plant material in their nests and wax exhibits intermolecular changes at surprisingly low temperatures, a feature that makes it strong and workable[28]. The nest entrance tube blocked with resin or cerumen, or layered outside with fresh resin through which ants could be halted, immobilize even large beetles [29,30,31] and wood usually helps in providing insulation. Among all the materials used by *T. iridipennis*, accumulation of the mud (40%) was found in higher content around the nests, when compared with other substances used at nest entrance. Nest surfaces found in dry and wet conditions with suitable situation get bound to them, according to the changing seasons. The accumulation of more amount of mud would help them especially in windy spots and more moss in a relatively cold microclimate, i.e., the tight construction helps in effective insulation, as nest opening is the place to have a direct contact with the outer environment. The interactive effects of various colors were visible on the outer surface. As a result to check the preferential level, lists of choices made by bees have been gathered. Interestingly, black colored deposits been seen more often, that could be to have protection against the predators over other colors at the nest surface (table-1).

The crucial signal at each stage of orientation is the sun and nest orientation often influences the amount of solar radiation absorbed and time at which the highest radiation been received by the nest. The different categories chosen for study reflected all biologically real conditions that bees may use in deciding upon the nest orientation. So, some species orientated their nests such that they are warmed by solar radiation in the cool of the morning and while other species orientated the nests so that they offer the smallest possible profile to incident solar radiation during the middle of the day and use magnetic information, as a compass is among the most intriguing mechanisms used by animals to orient and navigate. Hence, the focus on nest orientation in measuring nest-site preferences toward direction of the nest opening having a clear and causal link to nest microclimate and nest orientation determines when and for how long the nest been exposed to direct insolation, thus largely determining temperature within the nest[32]. However, very little is known on nest orientation in tropical and subtropical social insects. *T. iridipennis* being found in the tropical and subtropical regions selected various orientations at nest sites but, there was a particular preference of northward (17%) direction been recorded with in the categorical arc from 91º to 180º over other directions selected at a higher range shown in figure-3. Differing to our results, previous understanding of stingless bees on orientation of nest have reports of preferring southern sector to build nests[33], through emphasis on spontaneous behaviour by magnetic compass.

In terms of longevity few nests were identified as abandoned, as no bees were visible with the successive trip conducted for confirming persistence of colony life, and it is noteworthy to mention that some nest colony got shifted to new spot with unknown earlier history and made settlement in a new place by abandoning the existing one and their abandoned nests were never dismantled. As a consequence, the number of live (168 ± 4.2) to deserted nests: 4.4 ± 0.66 showed a drastic variation among themselves but statistically it was found as a matter of change, i.e., null being rejected (X^2 = 27.0; df = 24, p > 0.05). Figure-5 shows a graph of the number of live and deserted colonies on the monthly basis. The colonies with bees showing deserted nature are very less compared to the colonies with live ones, perhaps could be due to accessibility of flora in the surroundings and this consistency toward longevity of feral colonies were on account of stingless bees apparently preferring living in perennial colony[1].

The earlier work on *T. iridipennis* highlights that; these small bees build their nests at a height within reach, up to 1m from ground level[34]. But, the nests observed at different elevation planes at JB campus varied from ground level up to 20 feet in height. A collective distance of opening of nest from the ground level accounted to 9.36 ± 0.36 (mean ± SE) in feet. The nesting elevations offered by *Trigona* above ground level showed very distinct preference of 47% between an elevation range of 11–15 ft from the ground point but, between 0–5 ft and 6–10 ft of ranges only 28% of nests were found which means that they demonstrate moderate preference for lower elevation (figure-4). The higher elevation been not opted for nesting; however, preferring middle elevation revealed a statistical significance (X^2 =12.694, df = 15, P > 0.05). Similar observations also been reported by Janzen[35, 36] i.e. species richness peaks at middle elevations and not at lower elevations which explains mid-elevation peaks being more favorable. The basic instinct of any insects would always prefer for a safer zone. The reasons behind decline of species richness or reduction in colony number at higher elevation probably due to reduced habitat area reduced resource diversity, increasingly unfavorably environments and reduced primary productivity and different elevation gradients met by ecologically variable insects could be essential to them[37]. The specific nests found to different faces of habitats at particular elevations provide protection against predators, wind, sun, parasites and symbionts that are part of micro-environment[20]. So, the role of adaptive adjustment with respect to height modulation been observed in colony construction.

Conclusion

Eventually, at a fixed point of departure we can bring in with a notion that stingless bees as a group display all degrees of preferences and patterns. Preferences are being molded with geographical expediency, ecological variability and seasonal cycles. It seemed likely that a range of alternatives though existed, the individual bee exhibited behaviour of building consecutive nests in very different ways and situations, with distinct preferences for some and shared preferences being extreme as possible. Among the different range and factors considered for analysis of nest variance, evolution has fine-tuned the functional properties of the material and structure to fit the demands placed on the nest by the bees and their environment into a dynamic equilibrium between changing systems.

Acknowledgement
The authors are thankful to the Chairpersons of Centre for Applied Genetics and Department of Zoology, for the facility extended and Mr. Srinivas Raghavan for his help on statistical analysis of the data, during the research work.

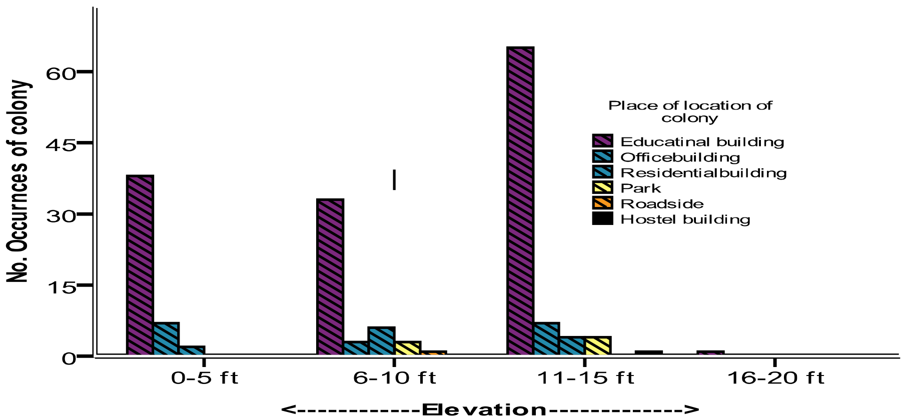

Figure-4
Preferred nesting elevations of *T. iridipennis* under different habitats zones

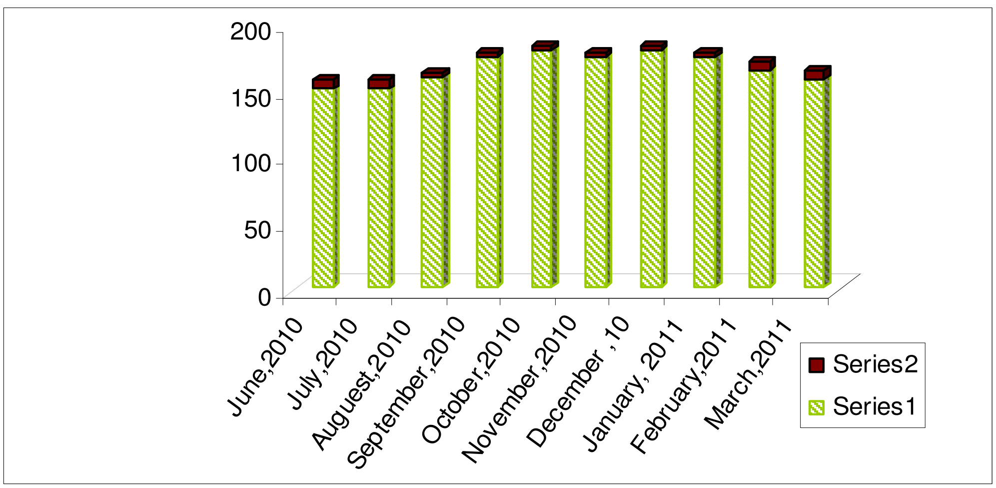

Figure- 5
No. of live verses deserted colony of *T. iridipennis* nest on the monthly scale

References

1. Leonhardt S.D., Kworschak K., Eltz T. and Bluthgen N., Foraging loads of stingless bees and utilization of stored nectar for pollen harvesting, *Apidologie*, **38**, 125-137 **(2007)**

2. Wille A., Biology of the stingless bees. *Ann. Rev. Entomol.,* **28**, 41-64 **(1983)**

3. Michener C.D., The social behavior of bees: A comparative study. Cambridge, Mass, Harvard University press, 404 **(1974)**

4. Sakagami S.F., Stingless bees, in: Herman H.H. (Ed.), Social insects, Academic Press, New York, **3**, 361-423 **(1982)**

5. Michener C.D., The Bees of the World. Johns Hopkins University Press, Baltimore, Maryland, **14 (1),** 913 **(2000)**

6. Lindauer M., Über die Verständigung bei indischen Bienen. *Z. F. vergl. Physiol*., **38**, 521–557 **(1956)**

7. Tschinkel W.R., The nest architecture of the Florida harvester ant, *Pogonomyrmex badius. J. Insect Sci*., **4**, 19 **(2004)**

8. Franks N.R., Wilby A., Silverman, B. W. and Tofts, C., Self-organizing nest construction in ants: sophisticated building by blind bulldozing, *Animal Behaviour*, **44**, 357-375 **(1992)**

9. Sheetal V.K. and Basavarajappa S., Spatial distribution of stingless bee, *Trigona iridipennis* Smith in Manasagangotri, Mysore, Karnataka. *Hexapoda*, **16(2),** 136-140 **(2009)**

10. Jaenike J.J. and Holt R.D., Genetic variation for habitat preference: Evidence and explanations, *American Naturalist*, **137**, S67-S90 **(1991)**

11. Hansel M., Animal architecture and building behavior. Longman, London, **(1984)**

12. Dawkins R., The Extended Phenotype: The long reach of the gene. Oxford University Press, **(1999)**

13. Werner E.E., Gilliam J.F., Hall D.J. and Mittelbach G.G., An experimental test of the effects of predation risk on habitat use in fish, *Ecology*, **64**, 1540-1548 **(1983)**

14. Lima S.L. and Dill L.M., Behavioral decisions made under the risk of predation: A review and prospectus, *Can. J. Zool*., **68**, 619-640 **(1990)**

15. Martin, T.E., Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology*, **82**, 175-188 **(2001)**

16. Mccomb, W.C. and Noble R.E., Invertebrate use of natural tree cavities and vertebrate nest boxes. *Am. Midl. Nat*., **107**, 163-172 **(1982)**

17. Roubik D.W., Ecology and natural history of tropical bees. Cambridge, Cambridge University Press, 514 **(1989)**

18. Gibbons P. and Lindenmayer D.B., Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production, *For. Ecol. Manage*., **83**, 245-279 **(1996)**

19. Martin T.E., Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, **79(2)**, 656-670 **(1998)**

20. Roubik D.W., Stingless bee nesting biology, *Apidologie,* **37**, 124-143 **(2006)**

21. Oster G.F. and Wilson E.O., Caste and Ecology in the Social Insects. Princeton, New Jersey: Princeton University Press, **(1978)**

22. Gordon D.M., The organization of work in social insect societies. *Nature*, **380**, 121-124 **(1996)**

23. Boi S., Cousin I., Del-Buono N., Franks N.R. and Britton N., Coupled oscillators and activity waves in ant colonies. *Proc. Royal Soc. London, Series B*., **1417,** 371-378 **(1999)**

24. Brown M.J.F. and Gordon D.M., How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant, *Behavioral Ecology and Sociobiology*, **47**, 195-203 **(2000)**

25. Horvath O., Contributions to nesting ecology of forest birds. Master of Forestry Thesis. Univ. Brit. Columbia, **(1963)**

26. Batra S.W.T., Bees of India (Apoidea) their behaviour, management and a key to the genera. *Oriental Insects*. **11**, 289-324 **(1977)**

27. Franks N.R. and Deneubourg J.L., Self-organizing nest construction in ants: Individual worker behaviour and the nest's dynamics. *Animal Behaviour*. **54,** 779-796 **(1997)**

28. Buchwald R., Alan R.G. and Michael D.B., A Biomechanical Perspective on Bees wax. *American Entomologist,* **51(1)**, **(2005)**

29. Wittmann, D., Nest architecture, nest site preferences and distribution of *Plebeia wittmanni* (Moure and Camargo, 1989) in Rio Grande do Sul, Brazil (Apidae: Meliponinae), *Stud. Neotrop. Fauna Environ,* **24 (1),** 17-23 (**1989)**

30. Camargo J.M.F., Notas sobre habitos de nidificação de *Scaura* (*Scaura*) *latitarsis* (Friese) (Hymenoptera, Apidae, Meliponinae), *Bol. Mus. Paraense E. Goeldi*, **1**, 89-95 **(1984)**

31. Nogueira N.P., Vida e criaçao de abelhas indigenas sem ferrao, Editora Nogueirapis, Sao Paulo, **(1997)**

32. Walsberg G.E., Nest-site selection and the radiative environment of the Warbling Vireo. Condor **83**, 86-88 **(1981)**

33. Marhold S., Wiltschko W. and Burda H., A magnetic polarity compass for direction finding in a subterranean mammal, *Naturwissen-schaften*, **84**, 421-423 **(1997)** (doi:10.1007/ s001140050422)

34. Solomon Raju A.J., Nesting behaviour and foraging ecology of the dammar bee, *Trigona Iridipennis* Smith (Apidae: Meliponinae). Deutsch Nationalbibliothek, German, 12 (**2009)**

35. Janzen D.H., Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity, *Ecology*, **54**, 687-708 **(1973)**

36. Janzen D.H., Ataroff M., Farinas M., Reyes S., Rincon N., Soler A., Soriano P. and Vera M., Changes in the arthropod community along an elevational transect in the Vene-zuelan Andes. *Biotropica,* **8**, 193-203 **(1976)**

37. Lawton J.H., MacGarvin M. and Heads P.A., Effects of altitude on the abundance and species richness of insect herbivores on bracken, *J. Anim. Ecol*. **56**, 147-160 **(1987)**