ECOLOGY, BEHAVIOR AND BIONOMICS

Trap-Nest Occupation by Solitary Wasps and Bees (Hymenoptera: Aculeata) in a Forest Urban Remanent

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Ocupação de Ninhos-Armadilha por Espécies de Vespas e Abelhas Solitárias (Hymenoptera: Aculeata) em um Fragmento de Mata Urbano

RESUMO - Avaliou-se a variação temporal das freqüências de nidificação de vespas e abelhas solitárias, a mortalidade e o parasitismo associados às suas espécies em um fragmento de mata em Belo Horizonte, MG. Os Hymenoptera foram coletados por meio de ninhos-armadilha dispostos em três tamanhos de área (25, 100 e 400 m^2). De fevereiro a novembro de 2004, coletou-se o total de 137 ninhos fundados por 11 espécies de abelhas e vespas. A maioria (75%) foi fundada por vespas. As armadilhas apresentaram picos de ocupação nos meses de março (25%) e setembro (26%). O mês em que ocorreu menor ocupação foi junho (2%). Excetuando-se *Trypoxylon* (*Trypargilum*) *lactitarse* Saussure, não foram observadas correlações significativas entre o número de ninhos ocupados e as médias mensais de temperatura e pluviosidade. O total de 48% dos ninhos apresentou mortalidade de imaturos e 13% deles foram parasitados. As taxas de mortalidade e parasitismo foram diferentes para abelhas e vespas, i.e., ninhos de vespas apresentaram maior mortalidade.

PALAVRAS-CHAVE: Nidificação, mortalidade, parasitismo, *Trypoxylon lactitarse*, *Auplopus militaris*

ABSTRACT - Temporal variation of solitary wasps and bees, nesting frequency, mortality, and parasitism were recorded from a remanent forest in Belo Horizonte, MG, Brazil. Wasps and bees were collected in trap-nests placed in areas with 25, 100, and 400 m^2, from February to November 2004. The 137 trap-nests collected contained 11 species of wasps and bees. Wasps occupied most nests (75%). Occupation peaks occurred in March (25%) and September (26%); in June, the lowest occupation (2%) was observed. Except for *Trypoxylon* (*Trypargilum*) *lactitarse* Saussure, no significant correlation was found between number of occupied nests, and temperature and rainfall means. In the nests, 48% of the immature specimens died; 13% of the nests were parasitized. Total death and parasitism rates of wasps and bees differed significantly.

KEY WORDS: Nesting behavior, mortality, parasitism, *Trypoxylon lactitarse*, *Auplopus militaris*

The Hymenoptera order is of utmost importance for environmental conservation. Hymenoptera families are essential ecosystem components that act as pollinators, controllers of herbivorous insect populations and as nutrient cyclers, and can be very sensitive to environmental changes (LaSalle & Gauld 1993).

Wasps belong to the Hymenoptera order and have a wide variety of behaviors and morphological characteristics (O´Neill 2001). To the present, 26,000 species have been described in the world and approximately 90% of them were classified as solitary insects (Evans & Eberhard 1970, Martins & Pimenta 1993). Females of most wasp species build one nest at a time, for laying one or more eggs (O´Neill 2001). Species of several Eumenidae, Pompilidae, and Sphecidae genera build nests within hollow plant stems, in pre-existing cavities of live or dead tree trunks and branches, and often in orifices made by xylophagous beetles and other borer species (Krombein 1967, Evans & Eberhard 1970).

Bees belong to the superfamily Apoidea. An estimated 4,000 genera and 25 to 30,000 species live in different regions of the world (Michener 2000). Approximately 85% of the described species are solitary (Batra 1984). Similar to wasps, bees have a variety of nesting habits. Several species make nests in the ground and others on ground surface, and some can build large aggregations (Batra 1984, Antonini *et al*. 2000); other species (such as those of the families Megachilidae and Apidae) build nests within plant branches and in pre-existing cavities of live or dead tree trunks (Krombein 1967, Roubik 1989). Bee nests are provided with pollen, nectar, and oil collected from flowers (Eickwort & Ginsberg 1980, Roubik 1989).

The Apoidea are the most important pollinating insects in ecosystems (Kevan & Baker 1983, Michener 2000). Bees are essential for the reproduction of several plant species and most bees rely solely on flowers for their supply of pollen, nectar, oils, and other products such as fragrances, resins, and floral trichomes (Simpson & Neff 1981, Macedo & Martins 1999). Due to bee dependence on plant species, several authors have alerted for the consequences of environmental changes, especially the destruction of nesting habitats on decreasing diversity and quantity of pollinating insects, thus reducing the probabilities of cross-pollination among native and cultivated floriferous plants (Kearns & Inouye 1997).

Due to the importance of wasps and bees as predators and pollinators, we studied these Hymenopteran's guild by assessing the changes in nesting frequency over time, and mortality and associated parasitism in a forest urban remanent.

Materials and Methods

Research site. The research was conducted at the Estação Ecológica da Universidade Federal de Minas Gerais (56 ha), Campus Pampulha, Universidade Federal de Minas Gerais (340 ha) in Belo Horizonte, MG (19°52' S, 43°58' W), from February to November 2004. In the region, two seasons are well defined: the dry (< 50 mm, monthly temperature average 19°C) and the rainy seasons (up to 300 mm, monthly temperature average 24°C) (Martins & Antonini 1994).

Location of trap-nests. Trap-nests were placed in nine 25-400 m^2 sampling square units considered equivalents for the purpose of this study; the squares were located in six hectares of secondary, semi-deciduous remanent forest. Square sizes varied to test hypotheses that are not considered in this study (for details, see Loyola 2005).

Trap-nests were made from processed Cumaru (*Dipteryx alata* Vog.), a compact wood that resists rot and xylophagous insect attacks even under unfavorable conditions (Lorenzi 1992). Wooden pieces measured 25x25x130 mm and had 11 cm-deep canals with 6, 9, and 12 mm diameter. Trap-nest sizes in this study are similar to those in other studies (Morato & Campos 2000, Morato 2001a, Viana *et al.* 2001, and others). Ten wooden pieces of each canal diameter were randomly arranged as trap-nest blocks. Blocks were plastic-covered for protection against excessive insolation or rain. Five blocks were placed in each of the sampling units: one in the center and the others in each square vertex. Trap-nests were placed in a compound structure made of a 1.5 m aboveground pole, to which a nest-sustaining platform was fixed at 1.4 m aboveground (a similar structure was reported by Viana *et al.* 2001). Each trap-nest block was a collecting site. One-hundred and fifty trap-nests were placed in each sampling unit, or 1,350 pieces in the research site.

Trap-nests were inspected biweekly; those occupied by wasps or bees were collected, taken to the laboratory, and replaced by empty ones to keep the number of traps constant. Trap-nest replacements added 13,500 pieces provided during the 10 months of study.

In the laboratory, nests were individually placed in small tulle meshes, keeping adults until hatching. Adults were fixed in entomological pins, identified to the extent allowed by taxonomists and taxonomic keys, and added to the reference collection at the Laboratório de Ecologia e Comportamento de Insetos, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

Statistical analysis. Observed and expected mortality values were tested by Chi-square, to assess the existence of differential death rates in bees and wasps. Mortality was defined as absence of adult emergence in nest cells.

In 2004, climate data were collected by the Plataforma de Coleta de Dados (PCD, location: 19°52'59.9'' S, 43°54'54.5'' W) in Belo Horizonte (Cepetec 2004). Relationships between climate variables and nesting frequency for each species, and for all bees and wasps were analyzed by simple linear regressions.

All continuous data were tested for normality (Kolmogorov-Smirnov) and homogeneity of variances. Data lacking a normal distribution were transformed (Log_n). All statistical analysis were conducted by the program Statistica for Windows 4.3 (StatSoft, Inc. 1995) and based on Zar (1996) and Sokal & Rohlf (1995). For all probability analysis, $\alpha = 0.05$.

Results

Aculeate composition, mortality and parasitism. Four wasp and seven bee species occupied the 137 nests collected. Wasp species were *Auplopus militaris* (Lynch-Arribalzaga) (n = 53), *Trypoxylon* (*Trypargilum*) *lactitarse* Saussure (n = 25), *Trypoxylon* (*Trypargilum*) sp. (n = 21), and Sphecidae sp. (n = 4). Bee species were *Megachile* (*Ptilosarus*) *bertonii* Schrottky (n = 6), *Megachile* (*Austromegachile*) *corona* Mitchell (n = 4), *Megachile* (*Pseudocentron*) sp. (n = 3), *Anthodioctes megachiloides* Holmberg (n = 10), *Centris* (*Hemisiella*) *tarsata* Smith (n = 8), *Xylocopa* sp. (n = 2), and *Tetrapedia* sp. (n = 1) (Table 1). Most nests (n = 103, or 75%) were occupied by wasp species; bee species occupied 34 nests, or 25%.

Trap-nests were occupied throughout the study (Fig. 1), with occupation peaks in March (n = 34, 3%) and September (n = 36, 3%). The lowest occupation occurred in June (n = 3, 2%). The trend toward higher nest occupation started in November.

Temperature and rainfall had similar temporal distributions (Fig. 2). The hottest months were March and November (mean temperature 22.3 ± 3.5°C and 22.7 ± 3.5°C, respectively (mean ± DP). July was the coldest month (mean

Table 1. Solitary wasps and bees captured in trap-nests at the Estação Ecológica, Universidade Federal de Minas Gerais, from February to November 2004.

Group	Family	Species	Sampling unit I	II	III	IV	V	VI	VII	VIII	IX	Total
Wasps	Pompilidae	*Auplopus militaris* (Lynch-Arribalzaga)	3	9	1	2	4	6	16	4	8	53
	Sphecidae	*Trypoxylon* (*Trypargilum*) *lactitarse* Saussure	0	1	2	0	3	2	12	3	2	25
		Trypoxylon (*Trypargilum*) sp.	6	0	1	0	1	3	5	3	2	21
		Sphecidae sp.	1	0	2	0	0	0	1	0	0	4
Bees	Megachilidae	*Anthodioctes megachiloides* Holmberg	2	4	0	1	0	0	2	0	1	10
		Megachile (*Ptilosarus*) *bertonii* Schrottky	0	0	0	1	0	0	1	1	3	6
		Megachile (*Austromegachile*) *corona* Mitchell	0	0	0	0	0	1	0	3	0	4
		Megachile (*Pseudocentron*) sp.	0	0	0	1	0	0	0	0	2	3
	Apidae	*Centris* (*Hemisiella*) *tarsata* Smith	6	0	0	0	0	1	0	0	1	8
		Xylocopa sp.	0	0	0	1	0	0	0	0	1	2
		Tetrapedia sp.	1	0	0	0	0	0	0	0	0	1
Total			19	14	6	6	8	13	37	14	20	137

temperature 16.8 ± 3.7°C). The rainiest month was February (mean rainfall 139.1 ± 116.9 mm) and May was the least rainy (15.7 ± 6.69 mm).

Although climate and nest annual distribution data were similar (peaks approximately in February-March and in September-November, and falls in June-July), correlation between temperature ($R^2 = 0.344$; $P = 0.074$; $n = 10$) and rainfall ($R^2 = 0.035$; $P = 0.605$; $n = 10$) was not significant. A significant correlation was found between number of occupied nests and temperature for *T. lactitarse* ($R^2 = 0.558$; $P = 0.013$; $n = 10$) but none with rainfall ($R^2 = 0.175$; $P = 0.228$; $n = 10$). We observed the same situation for *Trypoxylon* (*Trypargilum*) sp.: a significant correlation with temperature ($R^2 = 0.553$; $P = 0.014$; $n = 10$), not with rain ($R^2 = 0.025$; $P = 0.663$; $n = 10$).

In 48% (n = 66) of the 137 occupied nests, death of

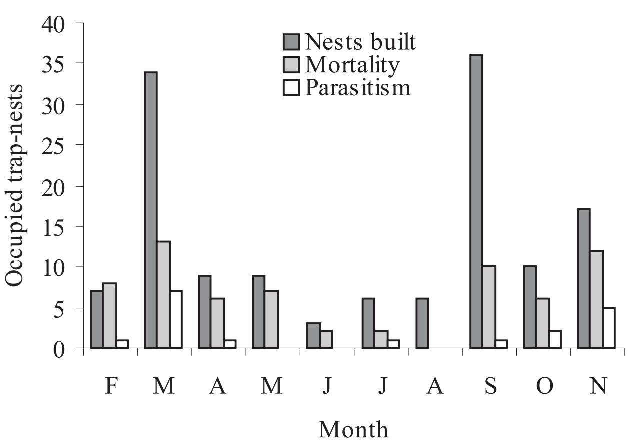

Figure 1. Occupation frequency of trap-nests by solitary wasps and bees, and mortality and parasitism values for the research site (February to November 2004).

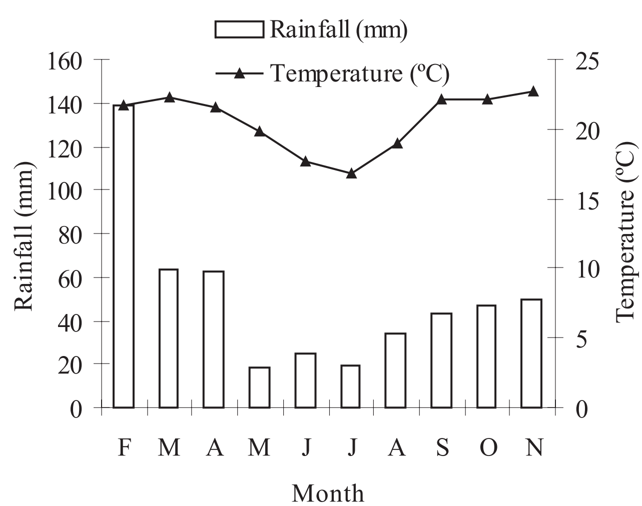

Figure 2. Mean temperature and rainfall in Belo Horizonte, MG (February to November 2004).

immature specimen was due to non-development of eggs and larvae, to parasitism, and to fungi colonization of nests. Death frequency was higher among wasps (n = 42.64%) than among bees (n = 24.36%). The two mortality peaks were in March (n = 13) and November (n = 12). Mortality decreased after March and started increasing again in September (n = 10). Death frequency did not follow any clear temporal distribution trend during the study period (Fig. 1). We observed a mortality differential between bees and wasps ($\chi^2 = 4.545$; $P = 0.033$; gl = 1), wasp nests having significantly higher mortality.

Eighteen (13%) of the occupied trap-nests were parasitized on the field and the adult parasites ecloded in the laboratory. Parasitism was low and apparently did not influence the abundance of species nor their temporal and spatial distribution. All parasitized nests belonged to *T. lactitarse*, *Trypoxylon* sp. and *A. militaris*. The *A. militaris* parasitoids were *Photocryptus* sp. (Ichneumonidae), *Ephuta sapuca* (Mutillidae), and an unidentified Braconidae species. The only *T. lactitarse* and *Trypoxylon* sp. parasitoid was *Melittobia* sp. (Eulophidae). No parasitoids were found in bee nests.

Temporal distribution of trap-nest occupation. *A. militaris* was the most abundant wasp species (53 nests occupied). This species nidified throughout the observation period, with peaks in March (n = 18) and September (n = 8) (Fig. 3). In 25% (n = 13) of the nests occupied by *A. militaris* adults did not eclode and 21% (n = 11) were parasitized by *Photocryptus* sp. (Ichneumonidae). The highest death months were May (n = 5, 100%) and April (n = 3, 60%).

The Sphecid *T. lactitarse* was the second most abundant wasp species (n = 23), followed by *Trypoxylon* (*Trypargilum*) sp. (n = 21). In June, females of this genus did not occupy trap-nests. Nesting frequency of species belonging to the *Trypoxylon* genus did not follow an easily identifiable pattern, in spite of the nidification peaks in March (n = 10) and September (n = 13) (Fig. 3). April and July were the lowest nidification periods for *Trypoxylon* species (n = 1, each month).

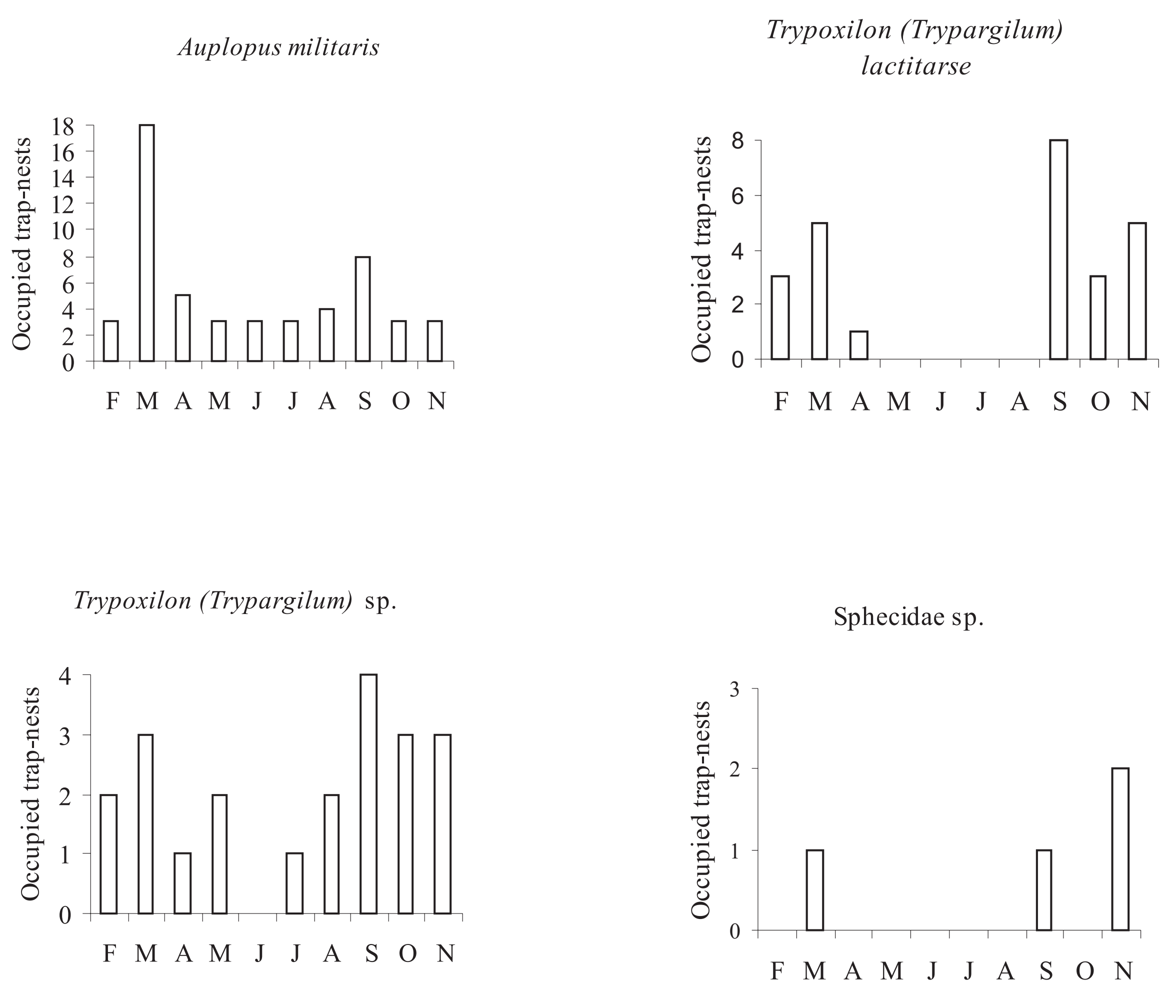

Figure 3. Occupation frequency of trap-nests by some of the most abundant wasp species living in the research site (February to November 2004) (Note: graphs are presented in different scales).

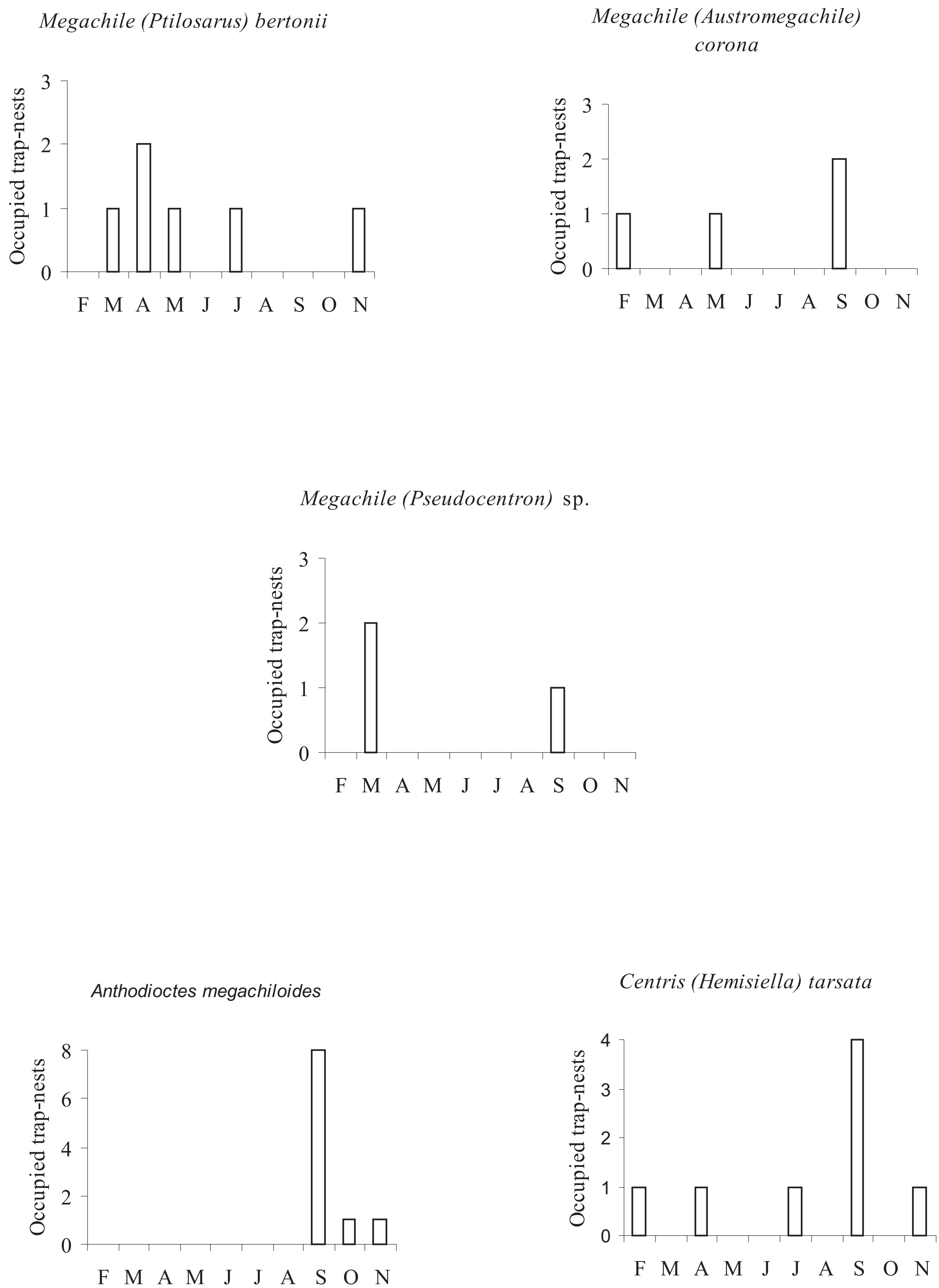

Figure 4. Occupation frequency of trap-nests by some of the most abundant bee species living in the research site (February to November 2004) (Note: graphs are presented in different scales).

Death of immature specimens occurred in 52% (n = 13) of the *T. lactitarse;* November concentrated the highest mortality (n = 5, 100%). Mortality was higher among *Trypoxylon* (*Trypargilum*) sp.: adults did not eclode in 57% (n = 12) of the 21 occupied nests.

The Sphecidae sp. occupied only four nests: one in March, one in September, and two in November (Fig. 3). Death occurred only in the nest occupied in March and the species could not be identified in detail because the immature specimens in all occupied nests died. Nonetheless, the species was identified as Sphecidae belonging to the genus *Podium* or *Penepodium* due to its nest characteristics and particularly, prey types.

The bee species *A. megachiloides* Holmberg built the largest number of nests. Their nidification occurred only in the last three sampling months. The nidification peak was in September (n = 8); one nest was made in October and another in November (Fig. 4). Death of immature specimens did not occur.

In September, *C. tarsata* reached the highest occupation of the eight occupied trap-nests (n = 4) (Fig. 4). This bee species built the second largest in number of nests. Death of immature specimens in their nests occurred in April and July.

Among all bee species belonging to the genus *Megachile, M. bertonii* occupied the largest number of nests (n = 6), followed by *M. corona* (n = 4) and *Megachile* (*Pseudocentron*) sp. (n = 3). *Megachile* females did not nidify in June, August nor October; their nidification peak (n = 3) was in March (Fig. 4). The highest *Megachile* spp. immature specimens' mortality occurred in February, March, and May (n = 1 for all months), although 23% (n = 3) of the nests failed.

Xylocopa sp. was the second least frequent locally, with only two nests occupied in March. Immature specimens did not die but species identification was not possible because adults ecloded in the field, before trap-nest collection. Nonetheless, we were able to determine the genus of the nest occupying species by looking at nest interior characteristics such as architecture and construction material.

Tetrapedia sp. nidified only once in November, being the rarest among all bee species. Similar to *Xylocopa* sp., *Tetrapedia* sp. immature specimens did not die. However, when trap-nests occupied by this species were open for description, well-formed adults that could not leave the nest were found.

Discussion

The number of trap-nests occupied by solitary bees and wasps as found in our study was relatively high compared with data obtained in other studies conducted in Brazil, if we take into consideration that our research was conducted in a forest urban remanent (Aguiar & Garófalo 2004, Silva *et al*. 2001, Viana *et al*. 2001). The high nest-occupancy reveals the importance of forest urban remanents in sheltering species with narrow ecological tolerance (e.g., *A. militaris*) and typical of forest environments (Zanette *et al.* 2004). Therefore, forest urban remanents must be preserved because urban conservation strategies must consider different spatial scales to be effective (Theobald *et al.* 1997, Cane 2001).

More important nest occupation in March and September seem to be indirectly associated with the climate. We know that low temperatures and low humidity have a negative effect on the activities performed by solitary bees and wasps, which have low thermoregulatory capacity (Eickwort & Ginsenberg 1980). Indeed, of all species collected during this study, those belonging to the genus *Trypoxylon* occupied fewer trap-nests when the temperature and rainfall were lower. Aguiar & Garófalo (2004) found significant correlations between number of nests occupied by *Centris* (*Hemisiella*) *tarsata* Smith and monthly precipitation in the State of Bahia. However, in a study done in the Central Amazon region, no significant correlation was found between rainfall and number of nests occupied by *Anthodioctes moratoi* Urban (Morato 2001b). In general, although no significant correlation was found between temperature, rainfall, and nesting frequency of other species in our study, the climate directly influenced environment-related variables such as system productivity (Begon *et al.* 1996) and the resources availability for nest construction and maintenance (mud, preys and pollen). Consequently, climate factors indirectly affect solitary bee and wasp nidification.

A. militaris was responsible for the temporal nest distribution pattern when all species were analyzed as a group because it was the only Aculeate species occupying trap-nests throughout the year. This species was common in the remanent forest and has narrow ecological tolerance because if nidifies only in the interior of forests (Zanette *et al.* 2004). We indeed expected that species that were common in our research site (*A. militaris* and the wasp species of the genus *Trypoxylon*) would occupy most trap-nests because their populations tend to be larger or have generation superposition. Therefore, specimens would more efficiently spread their nests in space and in time.

The bees' lower nest occupation can be related to the effects of habitat vertical stratification. Bawa *et al.* (1985) reported that bigger bees are more important pollinators when flowers are located in the canopy. In the Central Amazon region, bees occupied more trap-nests located between 15 m and 8 m high than those at 1.5 m (Morato 2001a). This result may be due to a larger availability of floral resources in the canopy (Roubik *et al.* 1982). Other studies have confirmed the relationship. For instance: the number of Euglossina bees in Central Amazon forests was found significantly larger in higher elevations (10-12 m) (Oliveira & Campos 1996); in an experimental assay with flowers of *Cassia biflora* Griseb. (Caesalpinioidea), the bee species Anthophorini and Euglossina foraged more intensively in flowers located higher (Frankie & Coville 1979); in another study, the flight height of butterflies belonging to the subfamily Ithomiinae was positively correlated with the height of its larvae's host plants (Beccaloni 1997).

However, contrasting results were found in other studies

(Roubik *et al.* 1982, Wolda & Roubik 1986, Roubik 1993). In general, pollinators (including bees) move often between layers (Bawa *et al.* 1985). Nonetheless, Roubik (1989, 1993) argues that there seems to be no strong correlation between foraging height and nesting height.

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References

Aguiar, C.M.L. & C.A. Garófalo. 2004. Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Rev. Bras. Zool. 21:477-486.

Alves dos Santos, I. 2003. Trap-nesting bees and wasps on the University Campus in São Paulo, Southeastern Brazil (Hymenoptera: Aculeata). J. Kansas Entomol. Soc. 76: 328-334.

Antonini, Y., C.M. Jacobi & R.P. Martins 2000. Philopatry in the Neotropical ground-nesting solitary digger bee, *Diadasina distincta* (Holmberg, 1903) (Hymenoptera: Apidae) at a nesting site in southern Brazil. Revt. Etol. 2: 111-119.

Batra, S.W. 1984. Solitary bees. Sci. Amer. 250: 86-93.

Bawa, K.S., N.D. S.H. Bullock, D.R. Perry, R.E. Coville & M.H. Grayum. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. Amer. J. Bot. 72: 346-356.

Beccaloni, G.W. 1997. Vertical stratification of ithomiinae butterfly (Nymphalidae: Ithomiinae) mimicry complexes: The relationships between adult flight height and larval host-plant height. Biol. J. Linnean Soc. 62: 313-341.

Begon, M., J.L. Harper & C.R. Townsend. 1996. Ecology: Individuals, populations and communities. Blackwell Science, Oxford, 945p.

Cane, J.H. 2001. Habitat fragmentation and native bees: A premature verdict? Conserv. Ecol. 5: 1-12.

Cepetec 2004. Centro de Previsão de Tempo e Estudos Climáticos, Instituto Nacional de Pesquisas Espaciais (INPE), Ministério da Ciência e Tecnologia, Governo Federal (http://canela.cptec.inpe.br:8080/BDPCD/consulta_pcdm.jsp). Acessed in 07/0I/2005.

Eickwort, G.C. & H.S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. Ann. Rev. Entomol. 25: 421-446.

Evans, H.E. & M.J.W. Eberhard. 1970. The wasps. Ann. Arbor., The University of Michigan Press, Michigan, 265p.

Frankie, G.W. & R.E. Coville. 1979. An experimental study on the foraging behavior of selected solitary bee species in the Costa Rican dry forest (Hymenoptera: Apoidea). J. Kansas Entomol. Soc. 52: 591-602.

Kearns, C.A. & D.W. Inouye. 1997. Pollinators, flowering plants and conservation biology. Bioscience 47: 297-307

Kevan, P.G. & H.G. Baker. 1983. Insects as flower visitors and pollinators. Ann. Rev. Entomol. 28: 407-453.

Krombein, K.V. 1967. Trap-nesting wasps and bees: Life histories, nests and associates. Smithsonian Press, Washington, 570p.

Lasalle, J. & I.D. Gauld. 1993. Hymenoptera and biodiversity. CAB International, Wallingford, 348p.

Lorenzi, H. 1992. Árvores brasileiras – manual de identificação e cultivo de plantas arbóreas nativas do Brasil, v I, Ed. Plantarum Ltda., 352p.

Loyola, R.D. 2005. Efeitos de área e estrutura de habitat sobre a riqueza e nidificação de vespas e abelhas solitárias (Hymenoptera: Aculeata). Dissertação de Mestrado. Universidade Federal de Minas Gerais, Belo Horizonte, 89p.

Macedo, J.F. & R.P. Martins. 1999. A estrutura da guilda de abelhas e vespas visitantes florais de *Waltheria americana* L. (Sterculiaceae). Anais. Soc. Entomol. Brasil 28: 617-633.

Martins, R.P. & H.R. Pimenta. 1993. Ecologia e comportamento de vespas solitárias predadoras. Ciência Hoje 15: 14-19.

Martins, R.P. & Y. Antonini. 1994. The biology of *Diadasina distincta* (Holmberg, 1903) (Hymenoptera: Anthophoridae). Proc. Entomol. Soc. Wash. 96: 553-560.

Michener, C.D. 2000. The Bees of the World. The Johns Hopkins University Press. Baltimore and London, 913p.

Morato, E.F. 2001a. Efeitos da fragmentação florestal sobre vespas e abelhas solitárias na Amazônia Central. II. Estratificação vertical. Rev. Bras. Zool. 18: 737-747.

Morato, E.F. 2001b. Biologia e ecologia de *Anthodioctes moratoi* Urban (Hymenoptera, Anthidiini) em matas contínuas e fragmentos na Amazônia Central, Brasil. Rev. Bras. Zool. 18: 729-736.

Morato, E.F. & L.A.O. Campos. 2000. Efeitos da fragmentação florestal sobre vespas e abelhas solitárias em uma área da Amazônia Central. Rev. Bras. Zool. 17: 429-444.

Oliveira, M.L. & L.A.O. Campos. 1996. Preferência por estratos florestais e por substâncias odoríferas em abelhas Euglossinae (Hymenoptera: Apidae). Revta. Bras. Zool. 13:1075-1085.

O´Neill, K.M. 2001. Solitary wasps: Behavior and natural history. Comstock Publishing Associates, New York, 406p.

Roubik, D.W. 1989. Ecology and natural history of tropical bees. Cambridge University. New York, 514p.

Roubik, D.W. 1993. Tropical pollinators in the canopy and understory: Field data and theory for stratum "preferences". J. Insect Behav. 6: 659-673.

Roubik, D.W., J.D. Ackerman, C. Copenhaver & B.H. Smith. 1982. Stratum, tree, and flower selection by tropical bees: Implications for the reproductive biology outcrossing *Cochlospermum vitifolium* in Panama. Ecology 63: 712-720.

Silva, F.O., B.F. Viana & E.L. Neves. 2001. Biology and architecture of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera: Apidae: Centridini) nests. Neotrop. Entomol. 30: 541-545.

Simpson, B.B. & J.L. Neff. 1981. Floral rewards: Alternatives for pollen and nectar. Ann. Miss. Bot. Gard. 68: 301-322.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research. 3 ed. W. H. Freeman and Company, New York, 889p.

StatSoft, Inc. 1995. STATISTICA for Windows [Computer program manual]. Tulsa, OK.

Theobald, D.M., J.R. Miller & T.N. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape Urban Plann. 39: 25-36.

Viana, B.F., F.O. Silva & A.M.P. Kleinert. 2001. Diversidade e sazonalidade de abelhas solitárias (Hymenoptera: Apoidea) em dunas litorâneas no nordeste do Brasil. Neotrop. Entomol. 30: 245-251.

Wolda, H. & D.W. Roubik. 1986. Nocturnal bee abundance and seasonal activity in a Panamanian Forest. Ecology 67: 426-433.

Zanette, L.R.S., R.P. Martins, L.A. Soares & H.R. Pimenta. 2004. Nesting biology and sex ratios of *Auplopus militaris* (Lynch-Arribalzaga 1873) (Hymenoptera: Pomplidae). Trop. Zool. 17: 145-154.

Zar, J.H. 1996. Biostatistical analysis. 3a ed., Prentice-Hall, Inc., Englewood Cliffs.

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