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RESEARCH ARTICLE - WASPS

Trap-nesting solitary wasps (Hymenoptera: Aculeata) in an insular landscape: Mortality rates for immature wasps, parasitism, and sex ratios

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Abstract

The aim of this study was to examine the species composition and the abundance of solitary wasps that nest in preexisting cavities in the Ilha Anchieta State Park, Brazil. Sampling was made during two years utilizing trap-nests. Of the 254 nests obtained, 142 nests were built by 14 species belonging to four genera and four families. In the remaining 112 nests all immatures were dead by unknown causes or had been parasitized by natural enemies. The occupation of trap-nests occurred almost throughout the study period and the wasps nested more frequently during the super-humid season. *Trypoxylon lactitarse, Pachodynerus nasidens, Trypoxylon* sp.2 aff. *nitidum* and *Podium denticulatum* were the most abundant species. The sex ratios of *T. lactitarse* and *Trypoxylon* sp.2 aff. *nitidum* were significantly male-biased, whereas those of *Trypoxylon* sp.5 aff. *nitidum* and *P. nasidens* were significantly female-biased. Sex ratios of *P. denticulatum* and *P. brevithorax* were not significantly different from 1:1. Natural enemies emerging from the nests were identified as belonging to the families Chrysididae, Ichneumonidae and Chalcididae (Hymenoptera), the genus *Melittobia* (Hymenoptera, Eulophidae), and the species *Amobia floridensis* (Townsend, 1892) (Diptera: Sarcophagidae). The number of cells with dead immatures from unknown factors was significantly higher than the number of cells parasitized by insects.

Introduction

There are more than 34,000 described species of aculeate wasps in the world, of which about 14,700 species belong to the families Pompilidae, Crabronidae, Sphecidae, and Vespidae (subfamily Eumeninae) (Morato et al., 2008). For the neotropical region, 1,858 species of Crabronidae and Sphecidae have been recorded (Amarante, 2002; 2005), of which 645 occur in Brazil (Morato et al., 2008). Ninety per cent of the species known have solitary behaviour and diversified nesting habits (O'Neill, 2001). The female captures several insects or spiders to provision the cells, exerting a very significant predation pressure on ecosystems (Krombein, 1967). Around 5% of all species of solitary wasps have the habit of nesting in pre-existing cavities (Krombein, 1967). This characteristic has facilitated the study of these solitary species, because females are attracted to nest in human-made trap-nests.

In studies made with solitary wasp species that nest in pre-existing cavities, the use of trap-nests has provided information not only on the occurrence of species in a given habitat, but also on the wasp community composition and their natural enemies, on the nesting biology of the species, on food sources used to rear the immatures (e.g., Krombein, 1967; Gathmann et al., 1994; Camillo et al., 1995; Camillo & Brescovit, 1999; Zanette et al., 2004; Tylianakis et al., 2006; Buschini et al., 2006; Asís et al., 2007; Buschini, 2007; Santoni & Del Lama, 2007; Buschini & Woiski, 2008; Ribeiro & Garófalo, 2010; Musicante & Salvo, 2010; Loyola & Martins, 2011; Polidori et al., 2011). Habitat quality, the effects of habitat fragmentation and of landscape complexity on community composition and predatory-prey interactions (Tscharntke et al., 1998; Morato, 2001; Steffan-Dewenter, 2002; Kruess & Tscharntke, 2002; Tylianakis et al., 2007; Loyola & Martins, 2008; González et al.,2009; Holzschuh et al., 2009; Schüepp et al., 2011), and how urban environments can support such insects (Zanette et al., 2005) have also been assessed with the use of trap nests.

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Given the important role of solitary wasps in terrestrial ecosystems (LaSalle & Gauld, 1993), any effort to understand them and unsure their survival is fully justified. In this context, biological inventories are the basic tools for the initial survey of biological diversity, as well as for monitoring changes in different components of biodiversity in response to the impacts of both natural processes and human activities (Lewinsohn et al., 2001). The present study reports data on the occupation of trap-nests by solitary wasps from a survey carried out in the Ilha Anchieta State Park, a reserve within the Atlantic Forest domain. Among tropical biomes, the Atlantic Forest is the one that has suffered the most fragmentation and degradation by human intervention, which threatens the high species diversity and the high degree of endemism of this biome (Myers et al., 2000).

Material and Methods

Study Area

The study was conducted within the Ilha Anchieta State Park (45º 02' – 45º 05' W and 23º 31' – 23º 34' S). The park occupies the entire island (828 ha) and has only one perennial stream, which is located in an area of coastal forest (restinga). The topography is rugged and mountainous, with slopes typically greater than 24º. Low-lying level areas (with slopes under 6º) are found at two beaches ('Grande' and 'Presídio'). Areas of intermediate slope are located in the valley bottoms and on the flat hilltops of the island (Rocha-Filho & Garófalo, 2013). The vegetation found on Ilha Anchieta has been described by Guillaumon et al. (1989), following Rizzini (1977), and includes anthropogenic fields, rocky coast, Atlantic Forest, Gleichenial, mangrove, and restinga.

The climate of Ilha Anchieta is tropical rainy (Koppen, 1948). It has two distinct seasons a year: one super humid, from October to April, with monthly rainfall above 100 mm, and the other less humid, from May to September, when the monthly rainfall is below 100 mm. During the study, from September 2007 to August 2009, the average monthly temperatures ranged from 22.5 °C to 25.8 °C in the super-humid periods and from 18.0 °C to 21.4 °C in the less humid periods. The monthly rainfall totals ranged from 190.3 mm to 488.3 mm in the super-humid periods and from 0 to 220.9 mm in the less humid periods. Temperature and rainfall data of the Ubatuba region were obtained from the Centro Integrado de Informações Agrometereológicas - (http://www.ciiagro.sp.gov.br). The super-humid and less-humid terminology follows Talora and Morellato (2000).

Methods

The design of the trap-nests used in the present study followed Camilo et al. (1995): they consisted of tubes made of black cardboard, with one end closed with the same material. These tubes, with dimensions of 5.8 cm long × 0.6 cm diameter (small tube, ST) and 8.5 cm long × 0.7 cm diameter (large tube, LT) were inserted into holes drilled into wooden plates (length: 30 cm, height: 12 cm, thickness: 5.0 cm). Each wooden plate had a total of 55 holes available, 2.0 cm apart from each other and distributed in five rows. We also used another type of trap-nest made of bamboo canes (BC) which were cut so that a nodal septum closed one end of the cane. The bamboo canes had variable length and their internal diameter ranged from 0.4 to 2.9 cm although all sizes were not equally represented. In order to protect the bamboo canes from the sun and the rain, they were inserted, in bundles of 10-15 units, into a PVC tube, 40 cm long × 12 cm diameter. The plates containing the cardboard tubes and the PVC tubes were arranged on iron stands and placed at the sampling sites. Three sampling sites (site 1: 45° 04' 06.5" W and 23° 32' 22.0" S; site 2: 45° 03' 55.7" W and 23° 32' 24.3" S, and site 3: 45° 03' 52.1" W and 23° 32' 23.6" S) were established on the 'Presídio' beach. Distances between sites ranged from 100 m, between sites 2 and 3, to 308 m, between sites 1 to 3. Sites 1 and 2 were separated by a distance of 220 m. The iron stands were installed behind or next to existing buildings in the area. The geographical coordinates of all three sampling points were recorded with a GPS receiver. The iron stands installed at each sampling site carried 55 large tubes, 55 small tubes, and 90 bamboo canes distributed in three PVC tubes.

The trap-nests were inspected once a month from September 2007 to August 2009. Each inspection was made using a penlight. When traps contained completed nests, they were collected and replaced with empty ones. These nests were taken to the laboratory in Ribeirão Preto, SP, and each trap-nest was placed in a transparent glass or plastic tube, 4.0-5.0 cm longer than the trap and with an internal diameter of 0.9 cm. The nests were kept at room temperature and observed daily until the adults emerged. As the adults emerged into the glass or plastic tube, the trap was removed and the individuals were collected. A few days after the last emergence, the nest was opened and its contents analysed. Cells and nests from which no adult emerged were also opened, and the cause and stage of mortality were recorded. The analysis of the food present in brood cells allowed identification of the genus (or subfamily in the case of Eumeninae) of the breeding species. Voucher specimens of wasps were deposited in the Collection of Bees and Solitary Wasps (Coleção de Abelhas e Vespas Solitárias - CAVES) of the Department of Biology of the Faculty of Philosophy, Science and Letters at Ribeirão Preto –USP.

Statistical Analysis

Statistical tests followed Zar (1999) and were performed using the statistical package SigmaStat for Windows, Version 3.10 (2004 – Systat Software, Inc.). Kruskal-Wallis (H) test was used to verify differences among the diameters of bamboo canes occupied by different species. To isolate the species that differs from the others it was used a multiple comparison procedure (Dunn's Method). Chi-square tests were used to compare mortality rates for immature wasps, parasitism rates, and sex ratios. Pearson correlation analyses were performed to test for the strength of associations between nesting frequency and climatic conditions (average monthly temperature and rainfall). Throughout the text, all means (X) are reported with their associated standard error (SE) as X ± SE.

Results

Occupation of trap-nests by solitary wasps

We collected 150 nests in the first year (September 2007 - August 2008) and 104 nests in the second year (September 2008 - August 2009). Of the nests established in the first year, 78 nests were built by 12 species and of those established in the second year, 64 nests were made by six species. These species belong to four genera (*Trypoxylon, Pachodynerus, Podium,* and *Auplopus*) of four families (Crabonidae, Vespidae, Pompilidae, and Sphecidae). Crabronidae was the family with the highest number of species (nine), followed by Vespidae and Pompilidae, each with two species. Sphecidae was represented by only one species (Table 1). In the 112 remaining nests (72 nests of the first year and 40 of the second one) all immatures were dead from unknown causes or had been parasitized by insects, so that only the genus of the nesting species could be identified.

Most species (n = 10) nested exclusively in the bamboo cane traps. *Pa. nasidens*, *Pa. brevithorax*, and *Trypoxylon* sp.2 aff. *nitidum* were the only species that used all three types of trap-nest. *Pachodynerus nasidens* nested more frequently in the small and large tubes whereas nests of *Trypoxylon* (n = 75) were found mainly in bamboo canes (n = 69). *Podium denticulatum* occupied only the large tubes and bamboo canes, but most nests were built in bamboo canes (Table 1).

The analysis of the diameters of bamboo canes occupied by *T. lactitarse, Trypoxylon* sp.2 aff. *nitidum, Pa. nasidens* and *Po. denticulatum* revealed significant differences among them (Kruskal-Wallis H = 56.7; df = 3; P < 0.001). The cavities used by *T. lactitarse* were larger than those occupied by *Trypoxylon* sp.2 aff. *nitidum* and *Pa. nasidens,* and those used by *Po. denticulatum* were larger than those used by *Trypoxylon* sp.2 aff. *nitidum.* On the other hand, no significant difference was found among the diameters of bamboo canes used by *Po. denticulatum, T. lactitarse* and *Pa. nasidens* as well as between the canes occupied by *Pa. nasidens* and *Trypoxylon* sp.2 aff. *nitidum* (Table 2).

Phenology of nesting

Trypoxylon lactitarse, Trypoxylon sp.2 aff. *nitidum, Pa. nasidens*, and *Auplopus* sp.1 nested in both years, *Pa. brevithorax* and *Auplopus pratens* nested only in the second year, and the remaining eight species occupied the traps only in the first year (Table 1). The occupation of trap-nests occurred throughout the study period, with the exception of December 2007, when no nests were built. In both years, the wasps nested more frequently during the super-humid season (109 nests in the first year and 76 in the second year) than

Table 1. Species of solitary wasps that nested in the trap-nests in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009, number of nests built and type of trap-nest (ST = small tube; LT = large tube; BC = bamboo cane) occupied.

Species	Number of nests		Frequency of utilization of each type of trap-nest		
	1ST year	2ND year	ST	LT	BC
Trypoxylon lactitarse (Saussure, 1867)	13	21			34
Trypoxylon aurifrons (Shuckard, 1837)	4				4
Trypoxylon punctivertex (Richards, 1934)	2				2
Trypoxylon albitarse (Fabricius, 1804)	1				1
Trypoxylon sp.1 aff. *nitidum*	3				3
Trypoxylon sp.2 aff. *nitidum*	17	11	5	1	22
Trypoxylon sp.5 aff. *nitidum*	5				5
Trypoxylon (*Trypargilum*) sp.1	3				3
Trypoxylon (*Trypargilum*) sp.2	1				1
Pachodynerus nasidens (Latreille, 1812)	7	24	13	11	7
Pachodynerus brevithorax (Saussure, 1852)		5	3	1	1
Podium denticulatum (Smith, 1856)	20			2	18
Auplopus pratens (Dreisbach, 1963)		2			2
Auplopus sp. 1	2	1			3
Total	78	64	21	15	106

Table 2. Diameter of bamboo canes occupied by solitary wasps in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009.

Species	Trap-Nest Diameter (cm)	
	Range	X ± SE (N)
Trypoxylon lactitarse	0.8-1.1	0.96 ± 0.02 (34)
Trypoxylon aurifrons	0.5-0.7	0.6 ± 0.05 (4)
Trypoxylon punctivertex	0.5-0.6	0.55 ±0.07 (2)
Trypoxylon albitarse	1.1	1.1 (1)
Trypoxylon sp.1 aff. *nitidum*	0.6	0.6 (3)
Trypoxylon sp. 2 aff. *nitidum*	0.4 – 0.7	0.5± 0.02 (22)
Trypoxylon sp. 5 aff. *nitidum*	0.6-0.7	0.6 ±0.02 (5)
Trypoxylon (*Trypargilum*) sp.1	0.6	0.6 (3)
Trypoxylon (*Trypargilum*) sp.2	0.9	0.9 (1)
Pachodynerus nasidens	0.6-0.9	0.67± 0.04 (7)
Pachodynerus brevithorax	1.0	1.0 (1)
Podium denticulatum	0.8-1.1	0.93 ±0.02 (18)
Auplopus pratens	1.2-1.5	1.35 ±0.14 (2)
Auplopus sp.1	1.1 -1.5	1.33 ±0.12 (3)

during the less-humid season (31 nests in the first year and 28 in the second year). In both years, the highest frequency of nesting during the hot/super-humid season (average temperature = 23.9 ± 1.1°C) occurred in March. During the cool/less-humid season (average temperature = 19.9 ± 1.06°C), July of the first year and August of the second year were the months with the highest numbers of nests built (Fig 1).

Trypoxylon lactitarse, Pa. nasidens, Trypoxylon sp.2 aff. *nitidum* and *Po. denticulatum* were the most abundant

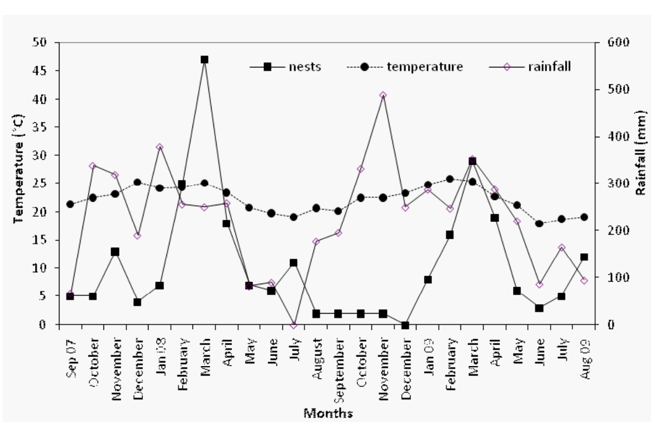

Fig 1. Climatic conditions (average temperature and rainfall) and number of nests established in trap-nests by solitary wasps in the Ilha Anchieta, state of São Paulo, from September 2007 to August 2009.

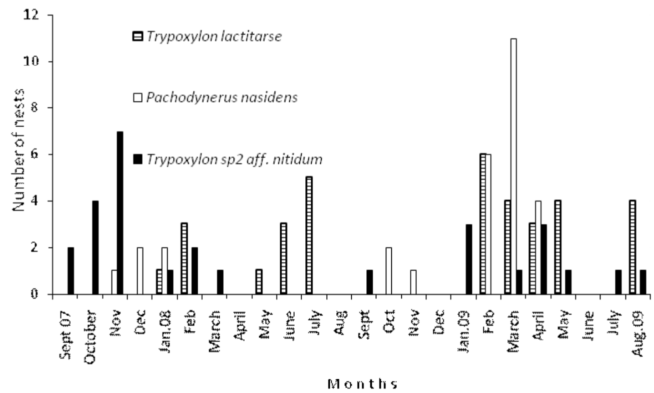

Fig 2. Number of nests built by *Trypoxylon lactitarse*, *Pachodynerus nasidens* and *Trypoxylon* sp.2 aff. *nitidum* in trap-nests in the Ilha Anchieta, Ubatuba, state of São Paulo, from September 2007 to August 2009.

species in terms of number of nests. *Trypoxylon lactitarse* showed an overall higher frequency of nesting in the second year (Table 1). More traps were occupied in the cool/less-humid season in the first year (n= 9 nests), and more traps in the hot/super-humid season in the second year (n = 13 nests). In both years, the females were active for only five months (Fig 2).

Pachodynerus nasidens was the second most abundant species. This species built 7 nests in the first year and 24 in the second one (Table 1). Except for two nests constructed in July of the first year, the nests were constructed in the hot/super-humid season (Fig 2). *Trypoxylon* sp.2 aff. *nitidum* occupied more traps in the first year (17 nests) than in the second year (11 nests) (Table 1). The nesting peak occurred in November of the first year, whereas January and April were the months with the highest number of nests in the second year. Regardless of the total number of nests built the females of *Trypoxylon* sp.2 aff. *nitidum* were active for a longer period than the females of other species (Fig 2). Females of *Po. denticulatum*, the fourth most abundant species, occupied trap-nests only in February, March, and April of the first year. Analysis of the temporal distribution of nesting of the four most abundant species in relation to average monthly temperature and rainfall only revealed a significant correlation between the number of nests and temperature for *Pa. nasidens* ($r = 0.45$; $P = 0.02$; $df = 24$).

Period of development and sex ratio

The total duration from oviposition to adult emergence was not determined. However, the maximum interval between nest collection and adult emergence may provide an estimate. Excepting two males of *T. punctivertex* and one female and six males of *Po. denticulatum*, which emerged from 165 to 192 days after the nests had been removed from the field, other individuals had the maximum interval ranged from 59 to 66 days (Table 3). These figures indicate an egg-to-emergence period about of two months. On the other hand, the results obtained for *T. punctivertex* and *P. denticulatum* indicate the occurrence of diapause in nests established in February (*Po. denticulatum*), March (*T. punctivertex* and *Po. denticulatum*), and April (*Po. denticulatum*).

The sex ratios of *T. lactitarse* and *Trypoxylon* sp.2 aff. *nitidum* were significantly male-biased, whereas those of *Trypoxylon* sp.5 aff. *nitidum* and *Pa. nasidens* were significantly female-biased. Sex ratios of *Po. denticulatum* and *Pa. brevithorax* were not significantly different from 1:1 (Table 4). Females and males of the remaining species were produced in similar numbers from the nests of *A. pratens* and *T. punctivertex*, whereas from the nests of *T. albitarse* and *Trypoxylon* sp.2 only males emerged (Table 4).

Mortality of immatures

Of 768 brood cells constructed in 254 nests, 240 (31%) contained dead immatures from unknown causes, and 199 (26%) had been parasitized by insects. The number of cells with dead

Table 3. Period (in days) between the collection of the nests of solitary wasps that occupied the trap-nests in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009, and emergence of individuals produced.

Species	Period (in days) between collection date and emergence			
	Males		Females	
	Range	X ± SE(N)	Range	X ± SE(N)
Trypoxylon lactitarse	9-61	39.1±1.30(65)	20-56	37±1.35(30)
Trypoxylon aurifrons	17-20	17.4±0.39(8)	17-20	18±0.98(3)
Trypoxylon punctivertex	177	177(2)	09-12	10.5±1.49(2)
Trypoxylon albitarse	66	66(1)		
Trypoxylon sp. 1 aff. *nitidum*	15-30	24.3±3.6(4)	22	22(1)
Trypoxylon sp. 2 aff *nitidum*	9-35	23.6±0.97(50)	9-37	22.9±1.36(22)
Trypoxylon sp. 5 aff. *nitidum*	26	26(1)	11-26	16.1±1.52(14)
Trypoxylon (*Trypargilum*) sp. 1	28-42	32.2±2.59(5)	30	30(1)
Trypoxylon (*Trypargilum)* sp. 2	24	24(1)		
Pachodynerus nasidens	11-58	22±3.19(28)	5-59	21.5± 1.77(50)
Pachodynerus brevithorax	11-19	17±1.22(6)	11-21	17.3±2.15(4)
Podium denticulatum	11-177	91.1±20.0(14)	10-192	68.7±31.89(7)
Auplopus pratens	17-18	17.5±0.50(2)	21-22	21.5±0.50(2)
Auplopus sp.1	2/20	6.8±3.33(5)	21	21(1)

Table 4. Number of males and females emerged and sex ratio for each species that nested in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009. (Values of χ^2 in bold indicate a sex ratio significantly different at P < 0.05 and df = 1, from 1:1).

Species	Number of males	Number of females	Sex ratio (no. ♂ : no. ♀)
Trypoxylon lactitarse	65	30	2.2♂: 1 ♀ (**χ^2= 12.9**)
Trypoxylon aurifrons	8	3	2.6♂: 1 ♀
Trypoxylon punctivertex	2	2	1♂: 1 ♀
Trypoxylon albitarse	1		
Trypoxylon sp.1 aff. *nitidum*	4	1	4♂: 1 ♀
Trypoxylon sp.2 aff. *nitidum*	50	22	2.3♂: 1♀ (**χ^2= 10.9**)
Trypoxylon sp.5 aff. *nitidum*	1	14	0.1♂: 1 ♀ (**χ^2= 11.3**)
Trypoxylon (*Trypargilum*) sp.1	5	1	5♂: 1 ♀
Trypoxylon (*Trypargilum*) sp.2	1		
Pachodynerus nasidens	28	50	(0.56♂:1♀) (**χ^2= 6.2**)
Pachodynerus brevithorax	6	4	1.5♂: 1 ♀ (χ^2= 0.4)
Podium denticulatum	14	7	(2♂:1♀) (χ^2= 2.33)
Auplopus pratens	2	2	1♂: 1 ♀
Auplopus sp.1	5	1	5♂: 1 ♀

immatures was significantly higher than the number of cells parasitized (χ^2=4.10; P < 0.05; df=1) only in nests of *Trypoxylon* whose species could not be determined (Table 5). For *Trypoxylon* (*Trypargilum*) sp.2 and *A. pratens*, the offspring had a survival rate of 100%. In the case of *T. albitarse*, the only cause of non-emergence was death of the immature from unknown causes, whereas for *Trypoxylon* (*Trypargilum*) sp1 the one cell from which a wasp did not emerge had been parasitized. Although in relatively small numbers all others species had immature mortality due to unknown causes and parasite attack (Table 5).

Natural enemies and hosts

The natural enemies were identified as belonging to the families Chrysididae (Hymenoptera), Ichneumonidae (Hymenoptera), and Chalcididae (Hymenoptera), the genus *Melittobia* (Hymenoptera: Eulophidae), and the species *Amobia floridendis* (Townsend, 1892) (Diptera: Sarcophagidae).

Trypoxylon sp.2 aff. *nitidum* was the species with the highest number of nests attacked (15) and cells parasitized (21), followed by *T. lactitarse, Pa. nasidens*, and *Pa. brevithorax* with 17, 5 and 4 cells parasitized, respectively (Table 6). Among the nests that could not be identified to the level of species due to total mortality of the brood cells from unknown causes or parasitism, the largest number (61 nests) belonged to the genus *Trypoxylon*, followed by *Podium* (10 nests), Eumeninae (3 nests), and *Auplopus* (2 nests)(Table 6). No natural enemy was found in the nests of *A. pratens, T. albitarse*, or *Trypoxylon* (*Trypargilum*) sp.2.

Among the natural enemies associated with the nests, *Amobia floridensis* (Diptera: Sarcophagidae) was the main enemy, attacking the nests of six species and responsible for 58.3% of all parasitized cells. *Melittobia* sp. (Hymenoptera: Eulophidae) caused 23.6% of the combined mortalities of *T. punctivertex, Trypoxylon* sp.2 aff. *nitidum, Pa. nasidens*, and *Po. denticulatum*. Individuals of the family Chrysididae were reared exclusively in the nests of *Trypoxylon*, parasitizing 22 cells (11.1%) in 17 nests. Individuals of Ichneumonidae attacked more often nests of *T. lactitarse*, parasitizing 6 cells in 6 nests. In addition to this host, nests (n = 2) of two other species of *Trypoxylon* also had cells parasitized (one in each nest), and a cell of *Auplopus* sp. was also attacked by this enemy. Individuals of Chalcididae attacked exclusively nests of *Auplopus*, and parasitized two cells in two nests (Table 6).

Discussion

Although there are tendencies to make a comparative analysis between the number of species occupying trap-nests and/or their abundances obtained in inventories carried out

Table 5. Numbers of brood cells, individuals produced, cells with dead immatures and parasitized cells in nests of solitary wasps that occupied trap-nests in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009. (* Nests of unidentified species) **(Value in bold indicates a statistically significant, at P <0.05 and df = 1, difference between the number of immature wasps mortalities due to unknown causes compared to parasite attack).

Species	No. of brood cells	No. individuals produced	No. of cells with dead immatures	No. of parasitized cells	χ^2**
Trypoxylon lactitarse	133	95	21	17	χ^2 = 0.42
Trypoxylon aurifrons	16	11	2	3	
Trypoxylon punctivertex	9	4	2	3	
Trypoxylon albitarse	3	1	2		
Trypoxylon sp. 1 aff. *nitidum*	10	5	2	3	
Trypoxylon sp. 2 aff. *nitidum*	109	72	16	21	χ^2 = 0.67
Trypoxylon sp. 5 aff. *nitidum*	21	15	5	1	
Trypoxylon (*Trypargilum*) sp. 1	7	6		1	
Trypoxylon (*Trypargilum*) sp. 2	1	1			
Pachodynerus nasidens	91	78	8	5	
Pachodynerus brevithorax	17	10	3	4	
Podium denticulatum	27	21	4	2	
Auplopus pratens	4	4			
Auplopus sp.1	9	6	2	1	
Subtotal	457	329	67	61	
*Trypoxylon**	265	0	149	116	**χ^2 = 4.10**
*Podium**	29	0	16	13	χ^2 = 0.31
Eumeninae*	11	0	5	6	
*Auplopus**	6	0	3	3	
Subtotal	311	0	173	138	
Total	768(100%)	329 (43%)	240 (31%)	199 (26%)	

Table 6. Host species, number of nests and brood cells attacked by natural enemies of trap-nesting solitary wasps in the Ilha Anchieta State Park, Ubatuba, state of São Paulo, from September 2007 to August 2009. (* Nests of unidentified species).

Host Species	Natural Enemies				
	Number of nests attacked and (number of brood cells attacked = c)				
	Amobia floridensis	*Melittobia sp.*	Chrysididae	Ichneumonidae	Chalcididae
Trypoxylon lactitarse	7(11c)			6(6 c)	
Trypoxylon aurifrons	1(1c)		1(2c)		
Trypoxylon punctivertex		1(2c)	1(1c)		
Trypoxylon sp. 1 aff. *nitidum*			2(3c)		
Trypoxylon sp. 2 aff. *nitidum*	3(5c)	4(7c)	7(8c)	1(1c)	
Trypoxylon sp. 5 aff. *nitidum*			1(1c)		
Trypoxylon (*Trypargylum)* sp. 1				1(1c)	
Pachodynerus nasidens	3(3c)	1(2c)			
Pachodynerus brevithorax	2(4c)				
Podium denticulatum	1(1c)	1(1c)			
Auplopus sp.1					1(1c)
Subtotal	17(25c)	7(12c)	12 (15 c)	8(8c)	1(1c)
*Trypoxylon**	42(79c)	11(27c)	5 (7c)	3(3 c)	
Podium *	9(12c)	1(1c)			
Eumeninae*		2(6c)			
*Auplopus**		1(1c)		1(1c)	1(1c)
Subtotal	51(91c)	15(35c)	5(7c)	4(4c)	1(1c)
Total	68(116c)	22(47c)	17(22c)	12(12c)	2(2c)

at different geographical locations, the results of these analyses should be interpreted with caution. Differences in sampling methods, the type and arrangement of the trap-nests in the study area, the arrangement of natural cavities, and the sampling periods may hinder the formulation of reliable comparisons (Aguiar et al., 2005). Among the 14 species collected from the trap-nests set up on Ilha Anchieta, seven: *T. lactitarse, T. albitarse* (Coville, 1981), *T. aurifrons* (Amarante, 2002), *T. punctivertex, Po. denticulatum* (Bohart & Menke, 1976), *Pa. brevithorax* and *Pa. nasidens* (Willink & Roig-Alsina, 1998), have in common a broad geographic distribution. Within Brazil these species have been reported for three farmland habitats (Santa Carlota Farm, Cajuru, SP, Camillo et al., 1995), a riparian forest area surrounded by crops and pastures (Ituiutaba, MG, Assis & Camillo, 1997), an urban forest (Belo Horizonte, MG, Loyola & Martins, 2006), three habitats in a municipal park (Araucárias Municipal Park, Gurarapuava, PR, Buschini & Woiski, 2008), and tropical savanna and riparian forest areas (Ingai, MG, Pires et al., 2012). They have also been observed in a region of temperate deciduous forest in (Ontario, Canada, Taki et al., 2008) and forest fragments covered by Chaco Serrano vegetation (Córdoba, Argentina, Musicante & Salvo, 2010). Of the seven remaining species, *A. pratens* has been recorded only in Brazil (Fernandez, 2000), *Trypoxylon* sp.1 aff. *nitidum* and *Trypoxylon* sp.2 aff. *nitidum* had occurrences reported by Assis and Camillo (1997), and for the other four species, there is no information available.

Trypoxylon lactitarse, the species that occupied the highest number of trap-nests on Ilha Anchieta, was also the dominant species in the studies by Camillo et al. (1995), Assis and Camillo (1997), Buschini and Woiski (2008), and Musicante and Salvo (2010), which evidences a great plasticity to adapt to different environments. When compared to these studies, *T. lactitarse* on Ilha Anchieta showed significantly elevated reproductive activity, occupying a large number of trap-nests. The only exception was the study by Musicante and Salvo (2010), carried out in forest fragments dispersed in an agricultural matrix strongly dominated by wheat in winter and soya beans or corn in summer, in which the number of *T. lactitarse* nests was smaller than observed on Ilha Anchieta. *Trypoxylon* sp.2 aff. *nitidum* built a larger number of nests on Ilha Anchieta than reported for the habitats studied by Assis and Camillo (1997). Likewise, *Po. denticulatum* nested more frequently on Ilha Anchieta than in the areas studied by Camillo et al. (1996) and Assis and Camillo (1997), who used sampling periods similar to those used in the present study. Although most nests on Ilha Anchieta were built during the hottest and rainiest period of the year, individual analyses for the four most abundant species showed an association between temperature and nesting activity only for *Pa. nasidens*. The relatively small number of occupied trap-nests hinders a more robust analysis of the action of the climatic factors on the phenology of these species.

Krombein (1967) and Fricke (1991) have suggested that the diameter of the cavity used by a given species is not only related to the size of the female, but also to its prey. These parameters may explain the lack of overlap in the diameters of the bamboo canes used by *T. lactitarse* and other species of the same genus. The exceptions were *T. albitarse* and *T.* (*Tripargilum*) sp.2, which presented marginal overlap with *T. lactitarse*, due to the larger size of the individuals of the latter species compared to the other species (Assis & Camillo, 1997) and/or the larger size of the spiders used to provision the cells. *Auplopus* species occupied the bamboo canes with the largest diameters. This is certainly related to the fact that cells are built with material (clay) taken into the cavity, inside which the female needs space to work on the construction. It's interesting to observe that among the most abundant species *T. lactitarse, Po. denticulatum* and *Pa. nasidens* nested in cavities with similar diameters. This could suggest the occurrence of competition among those species depending up of the availability of cavities with those diameters. Considering all the variables that may contribute to the selection of a cavity for nesting, any project aimed at the preservation of species with the characteristic of nesting in pre-existing cavities should provide a large number of options in terms of diameters of the cavities offered.

The method used in the present study does not directly yield data about the duration of the development period of immature wasps (from oviposition to emergence). However, by combining the time intervals between nest collection and the emergence of individuals with information on the distribution of nesting activities throughout the year, it is possible to affirm that species such as *T. lactitarse*, *T.* sp.2 aff. *nitidum, Pa. nasidens*, and *Po. denticulatum*, have more than one generation a year. For species such as *T. lactitarse* and *Pa. nasidens*, the maximum periods observed between nest collection and emergence reflect mainly the influence of a lower temperature resulting in a longer development period. The exceedingly long periods observed for *Po. denticulatum* indicate the occurrence of diapause in some immature wasps of this species, as also reported by Ribeiro and Garófalo (2010), based on studies carried out on the campus of the University of São Paulo at Ribeirão Preto, state of São Paulo. Only two nests of *T. punctivertex* were collected, both in March 2008; from one nest a female rapidly emerged followed much later by two males that had evidently undergone diapause, from the other nest a female rapidly emerged. Considering that diapause acts as a protection mechanism against unfavourable seasons, thereby reducing the extinction risk (Martins et al., 2001), the prepupal diapause observed in *Po. denticulatum* and *T. punctivertex* nests could be a survival strategy against adverse conditions. The occurrence of nests from which some wasps emerge with and others without diapause, as observed with *T. punctivertex*, shows that some adults should pass through an adverse season by sheltering somewhere.

Trap-nest diameter (Buschini, 2007) and food availability (Polidori et al., 2011) are two factors that may affect the sex ratio of the offspring of species that nest in pre-existing cavities. Considering the four most abundant species sampled on Ilha Anchieta, *T. lactitarse* and *T.* sp.2 aff. *nitidum* showed a male-biased sex ratio, *Pa. nasidens* a female-biased sex ratio, whereas the sex ratio of *Po. denticulatum* was not significantly different from 1:1. Analogous results have been reported by Borges and Blochtein (2001) for *T. lactitarse*, whereas Buschini (2007) reported similar proportions for the two sexes for the two generations of *T. lactitarse* collected during a study in the state of Paraná. Ribeiro and Garófalo (2010) found a sex ratio of 1:1 for *Po. denticulatum*, as observed in the present study. It is important to highlight that there are multiple factors that may affect the sex ratio of a population. A first step towards evaluating these factors will be the acquisition of more extensive data sets, based on larger sample of nests and to assess the food resources availability in the study area.

Several studies carried out with solitary wasps occupying trap-nests have shown wide variations in the mortality rates of immatures. The loss rate for immatures reported by some authors is typically close to 50% (Krombein, 1967; Freeman & Jayasingh, 1975; Jayasingh & Freeman, 1980; Camillo et al., 1996; Buschini & Wolf, 2006), but some species have reported much lower and others much higher mortality rates (Danks, 1971; Camillo et al., 1993; Gathmann et al., 1994; Assis & Camillo, 1997; Tormos et al., 2005). In the present study, the brood mortality rate based on the total set of collected nests was around 57%, but analysing separately each of the seven species that produced the largest number of brood cells (*T. aurifrons*, 16 brood cells to *T. lactitarse*, 133 brood cells), the loss rate for immatures ranged from 14.3% (*Pa. nasidens*) to 41.2% (*P. brevithorax*). Curiously, the two extremes were represented by Eumeninae species. Except for *Pa. brevithorax*, the other six species that utilized more frequently the trap-nests showed loss rates for immatures that are much lower than the values reported by other authors.

Unknown factors and natural enemies caused brood mortalities in similar proportions in nests built by identified species. Among the natural enemies that attacked the trap-nests, parasitization by individuals of the family Chrysididae was restricted to species of *Trypoxylon* as the host, whereas individuals of the family Chalcididae only attacked the nests of *Auplopus*. Considering the other identified enemies associated with the nests collected on Ilha Anchieta, *Amobia floridensis* was the agent that caused the highest brood mortality, attacking the nests of *Trypoxylon, Pachodynerus*, and *Podium*. With a distribution from the United States to Brazil (Pape et al., 2004), the associations between species of Eumeninae and *Trypoxylon* are well known through reports by Krombein (1967), Freeman and Jayasingh (1975), and but the association between *A. floridensis* and *Podium* is described here for the first time. According to Krombein (1967), the *Amobia* female follows the host female back to its nest, lands, and remains close to the nest entrance. When the host female leaves its nest to forage in the field, the fly enters the nest and larviposits. *Amobia floridensis* larvae compete with the host species larvae for caterpillars and spiders placed in the cells of Eumeninae and *Trypoxylon*, respectively, and according to the results obtained in the present study, they also compete for the cockroaches stored in the cells of *Podium*.

The dispersal ability of flying arthropods is usually determined by body size, as larger species have a better flight capacity (Gathmann et al., 1994; Steffan-Dewenter & Tscharntke, 1999). There is no information available on the flight capacity of the wasp species sampled on Ilha Anchieta, but it is reasonable to propose that the colonization of the island may have occurred through the transportation of adult individuals on the vessels that daily cross the 600 m channel that separates the island from the mainland. Another means by which cavity-nesting wasp species may cross water barriers is within pieces of floating wood, a process known to occur for solitary bees (Michener, 2000). Regardless of the colonization process for Ilha Anchieta, the number of nests collected in the present study may be considered relatively small, given the area of the island and the number of wasp species sampled. However, the number of trap-nests occupied by females may be related to the availability of natural cavities within the study area. One of the tourist attractions on Ilha Anchieta are the ruins of a prison with several buildings constructed in masonry, whose current dilapidated state affords many nesting opportunities for wasps. This fact together with the decline of 30.9% in the number of trap-nests occupied and 50% of species nesting in the second year compared to the first suggests that the populations of solitary wasps on Ilha Anchieta may be dependent on the mainland populations for the permanent occupation of the island.

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