

A solitary mud-daubing wasp, *Brachymenes dyscherus* (Hymenoptera: Vespidae) from Brazil with evidence of a life-cycle polyphenism

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Abstract: Nests (n=60) of a solitary mud-daubing wasp, *Brachymenes dyscherus* were collected at *Fazenda Santa Carlota*, Cajuru, São Paulo, Brazil in 1995 and 1996. The multi-celled mud nests were constructed on the interior walls of abandoned houses in dry and shaded places. Nests were composed of 1 to 4 layers with cells constructed in two parallel series. The number of cells per nest ranged from 3 to 62. Cells containing prey (larvae of Lepidoptera) numbered from 4 to 29. *B. dyscherus* is a univoltine species. Adults emerge from September to December, and nesting takes place at the beginning of the following year; however, the developmental period for some immatures with prolonged diapause lasted up to 596 days. The total duration of immature stages in nests collected in 1996 was less for males than for females. The sex ratio for the total population was 1.5 males: 1 female with males emerging earlier than females. A life table was constructed, and details of the life cycle of the wasps and parasitoids are presented. The most common mortality factors were either endogenous or due to *Melittobia* sp. (Eulophidae).

Key words: Insecta, Eumeninae, wasps, nest structure, natural enemies, polyphenism.

Carpenter (1982) divides Vespidae into the subfamilies Euparagiinae, Masarinae, Eumeninae (solitary or presocial wasps), Stenogastrinae, Polistinae and Vespinae. Most species in the Vespidae belong to the subfamily Eumeninae, with more than 180 genera and 3.000 species (Carpenter 1986) occurring throughout the world. The eumenine female prepares a brood cell, lays an egg, then she quickly makes several foraging trips, storing the gathered food with her egg. When enough food has been placed in the cell for the complete growth of the larva, she seals the cell and begins work on another. The females of a few solitary vespids may oviposit after they have stored the larval food and some are progressive provisioning during the early larval period (eg, see Cowan 1991).

In the eumenines, the genus *Brachymenes* contains two species. *B. dyscherus* is divided in two subspecies: *dyscherus* (Saussure 1852), restricted from Panama to Argentina, and *catarinae* Giordani Soika 1990, collected only in Santa Catarina State, Brazil. The second species is *B. wagnerianus* (Saussure 1875), occurring in Panama, Venezuela, Colombia, Equador and Peru. In Brazil, *B. dyscherus dyscherus* occurs from the State of Pará to Rio Grande do Sul (Giordani Soika 1990). This species, according to Bertoni (1918, in Giordani Soika 1990), builds its nest with mud on the interior walls of man-made structures, natural rock walls, or dead trees. Nest dimensions are 40 x 80 mm, and nests exhibit a rough and irregular surface. In addition to species that construct their nests with mud or

masticated plant material, there are species of Eumeninae that excavate the soil or occupy and modify preexisting cavities (Iwata 1976).

The purpose of this paper is present biological data on *B. dyscherus*, a common, yet poorly understood species.

MATERIAL AND METHODS

Study site: The study was carried out at *Fazenda Santa Carlota*, Cajuru, SP (21° 17' - 18' S, 47° 12' - 18' W), Brazil. The farm, with an area of 6.300 ha and altitudes ranging from 540 to 944 m, is drained by several streams. Approximately 2.200 ha of the total area are covered with isolated patches of native vegetation (semideciduous forests, riparian forests, *cerrados* (*s.l.*) and *cerradões*). In addition there are areas of secondary growth in various stages of ecological succession. Rhodic Ferralsol and Orthic Ferralsol soils predominate on the farm (Oliveira *et al.* 1983). The study area contains some abandoned buildings surrounded by abandoned orchards, pastures and cultivated land (mainly sugar cane).

Two seasons, distinguished by temperature and precipitation, occurs in the study area. From May to August there is a cool, dry season, with mean monthly temperatures ranging from 18 - 22.1°C and precipitation from 0 - 81.7 mm. From September to April there is a hot, wet season with mean monthly temperatures ranging from 19.9 - 26.1°C and precipitation from 35.3 - 422.6 mm.

Nests: A total of 60 nests of *B. dyscherus* (8 on 7/7/95, 28 on 7/13/95, 8 on 8/15/95, 8 on 4/18/96 and 8 on 8/2/96) were collected using a palette knife and taken to the laboratory. In some nests, immatures from the first layer of brood cells (always in contact with the substrate) were exposed, in which case the immatures were collected and placed in labeled individual vials and identified. In the laboratory all nests were placed in plastic boxes (10 x 10 x 3 cm gerbox-type) covered with same material and together with the vials

were kept at room temperature until the adults emerged. After emergence the nests were opened to analyze their cells and structure. The prey from cells in which the immatures did not develop were collected and counted. In some nests the following measurements were taken: length, width and height of the nests and of the cells of the first layer. The thickness of the walls between the cells and rows of cells of the first layer were measured in addition to the distance from the rows to the nest covering (Fig. 1A). The diameter of adult emergence holes and of the orifice left by female for provisioning the cell was also measured (Fig. 1B).

The greatest width of the head (GWH) determined the width of produced individuals. A life table was constructed (for nests collected in 1995 and 1996) showing the various causes of mortality at different stages in the life cycle and the relative number of immature individuals dying from each known cause. Voucher specimens were deposited in the Entomology Collection of the Department of Biology, FFCLRP-USP.

RESULTS

Nest Construction and Architecture:

The nests are constructed with mud of one or more colors on the walls inside abandoned houses, located at least 1 m from the floor in dry locations with little light. Of 60 collected nests, five had a cell in construction, and 15 had finished cells, either empty or in the initial stages of provisioning.

The occurrence of abandoned balls of clay next to or even away from the nests suggests that before starting nest construction, the wasps may sometimes initiate nests and then abandon the site. The nest is constructed with the longer axis perpendicular to the ground with all the cells joined to one another. The three first cells are constructed one beside the other (first layer), and then one or two over the first ones (second layer). After this, two parallel rows of cells are constructed from bottom to top, always starting from the

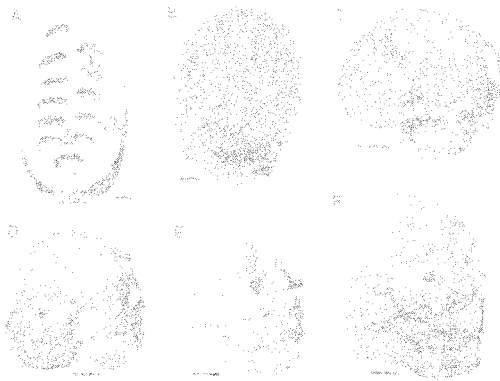


Fig. 1. A - Ventral view of nest with 12 cells in the first layer, illustrating some of the measurements taken: 1 - thickness of the lateral walls between the cells; 2 - between the rows of cells and 3 - between the cells and the nest surface; B - nest with a cell ready for provisioning. The arrow indicates the orifice left by the female; C - Nest with a cell from the first layer, from one of the series, in construction; D - Nest with a cell from the second layer, from one of the series, ready for provisioning; E - Nest with a cell from the third layer, from one of the series, in construction; F - Nest with a cell from the fourth layer, from one of the series, ready for provisioning. The lines correspond to 1.0cm.

substrate surface (Fig. 1C). The second layer is constructed over a cell row in the first layer, and then a third or a fourth as may be the case (Figs. 1D, E, F). (Aquí fig. 1) After this, the female returns to the second row of the first

layer and repeats the process. Of the total number of nests analyzed, 3 had only one layer of cells; 29 had two; 20 had three, and 8 had four layers. The distribution of the brood cells in superimposed layers (cross-section of nest) and in the two parallel series (ventral view of nest) can be observed in Figures 2A and B, respectively.

Nests collected on 4/18/96 were observed in construction on 3/27/96. On this day, I never observed more than one female per nest. Some of the females were collecting mud nearby for nest construction. This behavior consisted of two distinct procedures. Initially, the female leaves the nest toward a small puddle of water, flying soon after to a place with loose earth (approximately 2 m away). The second procedure entails the female regurgitating the water, mixing it with the earth and later returning to the nest with a ball of mud. Evidently females can construct more than one cell per day. A nest with five cells that was observed on 3/27/96 being constructed by one female, had 41 closed cells when it was observed a second time on 4/18/96. Females fully construct and provision a cell before working on another.

Once completed, the nests are totally covered with mud, resulting in a distinctive

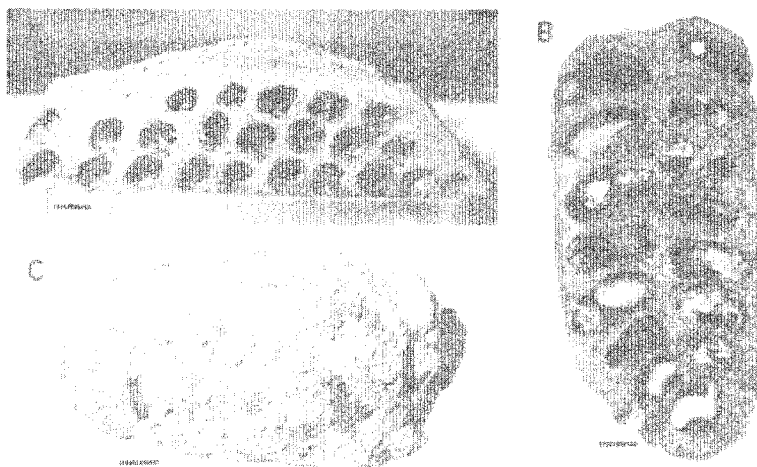


Fig. 2. A - Nest cross-section showing the position of the cell layers; B - Ventral view of a nest with 14 completed cells and one ready for provisioning (abandoned). In addition, it is possible to distinguish some prepupae and remnants of cocoons; C - Dorsal view of nests. Note the balls of mud placed on the covering. The lines correspond to 1.0 cm.

TABLE 1

Dimensions (mm) of nests of Brachymenes dyscherus in relation to the number of layers

No. of layers	No. of nests	Length		Width		Height	
		Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
1	2	32.0-44.0	38.0±8.4	22.0-40.0	31.0±12.7	14.9-17.0	15.9±1.4
2	26	36.6-154.6	73.0±30.1	33.5-75.4	51.1±11.4	17.8-41.6	27.4±5.9
3	18	58.6-149.0	92.3±26.8	46.0-65.4	56.4±5.7	29.7-50.1	36.6±4.8
4	8	57.8-153.2	104.1±33.5	42.4-58.3	51.4±6.2	33.2-53.8	41.1±7.2
Total	54	32.0-154.6	82.7±32.1	22.0-75.4	52.2±10.2	14.9-53.8	32.1±8.4

shape. The surface is rough, and in some cases it is possible to distinguish the balls of mud. The width of this covering, 0.96 cm, was measured in one nest. Generally, this covering made it impossible to distinguish individual cells (Fig. 2C). During nest construction, a group of closed cells may or may not be covered, because some of the nests collected with cells that were abandoned, partially constructed, or those being provisioned were almost completely covered. Fifty-four nests had varying dimensions depending on the number of cell layers present. The maximum mean nest length increased with the number of layers. The same occurred with respect to maximum mean nest height and number of layers (Table 1).

The number of cells per nest varied from 3 to 62, with most nests having from 3 to 25 (Fig. 3); in nests with 4 layers, the maximum number of cells counted was 23 for the first layer, 20 for the second, 16 for the third, and 5 for the fourth (Table 2). With respect to the first cell layer (the one in contact with the substrate), the thickness of the dividing walls between two contiguous cells (lateral walls) varied from 1.1 to 8.3 mm ($\bar{x} = 2.6 \pm 1.2$ mm, n=146); the thickness of the walls between the cells and the nest surface (external walls) varied from 1.6 to 13.8 mm ($\bar{x} = 6.7 \pm 2.4$ mm, n=148); the thickness of the walls between the two rows of cells (internal walls) varied from 1.5 to 9.1 mm ($\bar{x} = 3.5 \pm 1.4$ mm, n=83). The cells had a maximum length varying from 13.0 to 23.8 mm ($\bar{x} = 17.8 \pm 2.2$ mm, n=121), maximum height from 6.3 to 11.5 mm ($\bar{x} = 8.9$

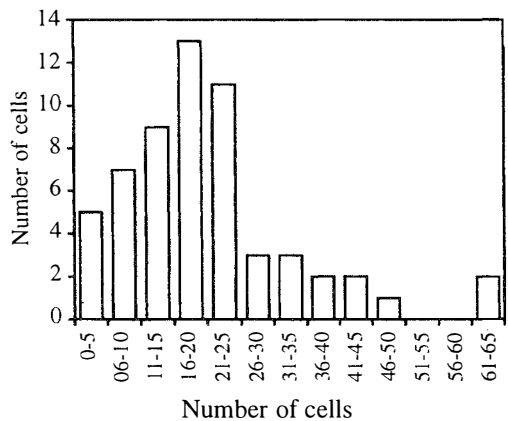


Fig. 3. Frequency distribution of the number of cells per nest of *Brachymenes dyscherus*.

± 1.2 mm, n=120) and maximum width from 6.0 to 12.1 mm ($\bar{x} = 9.1 \pm 1.2$ mm, n=120). In cells that were abandoned during cell provisioning, the diameter of the orifice present in the center of the top part of the cell varied from 2.7 to 4.3 mm ($\bar{x} = 3.3 \pm 0.4$ mm, n=14). The diameter of the orifice of adult emergence varied from 3.8 to 5.1 mm ($\bar{x} = 4.4 \pm 0.4$ mm, n=40) for males and from 4.8 to 6.7 mm ($\bar{x} = 5.6 \pm 0.5$ mm, n=40) for females.

Cells were provisioned with paralyzed caterpillars of Lepidoptera, and the number of these per cell varied from 4 to 29 ($\bar{x} = 9.6 \pm 4.8$, n=93). Most cells contained from 4 to 13 prey (Fig. 4). The cocoons, milkish white and more or less transparent, were affixed to the cell walls (Fig. 2 B). Whole prey or parts of prey, together with larval feces, were found adhered to the external surface of the cocoons.

TABLE 2

Number of cells built by *Brachymenes dyscherus* in each nest layer

No. of nests	No. of Cells	Layer			
		1	2	3	4
3	Range	3	-	-	-
	Mean±SD	3	-	-	-
29	Range	3 - 18	1 - 11	-	-
	Mean±SD	9.34± 4.45	5.03 ± 2.80	-	-
20	Range	6 - 19	5 - 16	1 - 12	-
	Mean±SD	11.75± 3.16	9.55 ± 2.91	4.55 ± 2.43	-
8	Range	8 - 23	6 - 20	3 - 16	1 - 5
	Mean±SD	15.62 ± 5.28	12.12 ± 6.51	9.12 ± 4.79	3.12 ± 1.88
Total 60	Range	-	4 - 29	14 - 43	18 - 62
	Mean±SD	-	13.75 ± 6.41	25.60 ± 7.75	40.87 ± 16.48

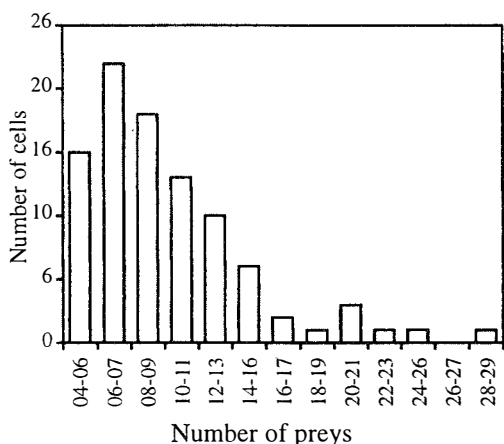


Fig. 4. Frequency distribution of the number of prey per cell of *Brachymenes dyscherus*.

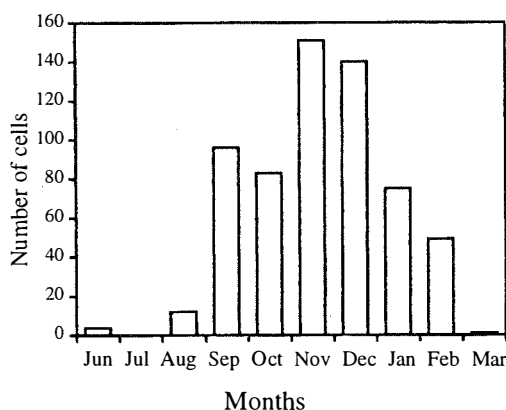


Fig. 5. Number of emerged adults of *Brachymenes dyscherus* obtained monthly.

Development period: Irrespective of the collection date of the nests, the duration of the pupal stage varied from 16 to 25 days for males ($\bar{x} = 20.2 \pm 4.0$ days, $n=107$) and from 19 to 28 ($\bar{x} = 21.5 \pm 3.5$ days, $n=121$) days for females, a statistically significant difference (Mann-Whitney, $Z=4.05$; $p<0.05$). The total duration of the immature stages was estimated from the time lapsed between the nest collection date (recently completed nests collected in April/96) and the emergence of the individuals. This time varied depending on sex. For males it was 158 to 309

days ($\bar{x} = 233.3 \pm 44.1$ days, $n=50$), and for females it was 167 to 320 days ($\bar{x} = 263.9 \pm 56.9$ days, $n=51$), again significantly different (Mann-Whitney, $Z=-4.41$; $p<0.05$).

B. dyscherus is a univoltine species. Most larvae develop into adults during the same year of nest construction, with the greatest number of emergencies occurring from September to December (Fig. 5). However, in one nest collected on 7/7/95, and in five nests collected on 7/13/95, some individuals had much longer development

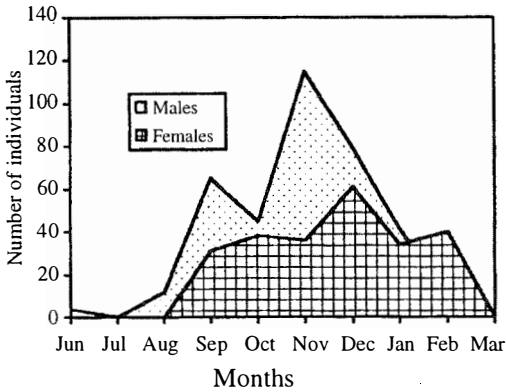


Fig. 6. Number of emerged males and females of *Brachymeres dyscherus* obtained monthly.

periods, evidencing polyphenism. The length of this period, calculated between the nest collection date and the emergence of the adults, varied from 343 to 596 days ($n=17$). In addition to these cases, two others should be pointed out: a prepupa from one nest collected on 7/13/95 died in July/98, and a prepupa from another nest collected on the same day pupated in January/98. Soon after, this pupa died. Moreover, in all of these nests there were emergencies with normal immature stage durations. If we take into consideration that the nests may have been completed months before the collection (in 1996 the nests were completed before the cold season, or in other words, April), the duration of these immature stages may be even longer. The emergence of males began before females (Fig. 6).

Adults size, sex ratio and mortality:

Although there was some overlap in size distribution, the females with the GWH ranging from 3.01 to 4.29 mm ($n=30$) were significantly larger than males whose GWH ranged from 2.72 to 3.94 mm ($n=30$) (Mann-Whitney, $Z=5.82$; $p<0.05$).

The sex ratio determined for the total population produced from the nests was 1.5 males to 1 female which is significantly different from 1:1 ($X^2= 31.19$; $df=1$; $p<0.05$) (Tab. 3). For the 44 nests collected in 1995 and the 16 in 1996, the sex ratios were 1.7 males to 1 female and 1.3 males to 1 female, respectively, which are all significantly different from 1:1 ($X^2= 28.02$ and $X^2= 4.32$, respectively; $df=1$; $p<0.05$). Mortality from developmental failure and parasitoids was observed in 40.7% of the provisioned cells being more accentuated in the first layer. Lost samples, cells accidentally damaged and empty cells corresponded to 4.4% of the cells (Table 3).

Life table and mortality factors:

Life tables were constructed for *B. dyscherus* on the basis of 1177 cells from the nests (750 in 1995 (Table 4) and 427 in 1996 (Table 5). Unidentified parasitoids (11 cells) and lost samples (27 cells) were not included in the total. When the exact cause of death was indeterminate, it was classified as endogenous mortality. The endogenous causes are probably the result

TABLE 3

Adults produced, parasitoids and dead imatures, lost samples and cells accidentally damaged, and empty cells in each layer in nests of *Brachymeres dyscherus*

	Layers				Total	%
	1	2	3	4		
Males	123	187	82	13	405	33.3
Females	151	94	18	-	263	21.6
Parasitoids and dead imatures	295	142	48	9	494	40.7
Lost samples and Accident	32	4	6	-	42	3.5
Empty cells	6	4	1	-	11	0.9
Total	606	427	150	22	1215	

TABLE 4

Life table for Brachymenes dyscherus (nests collected in 1995) showing the percentage mortality and its causes at different stages of the life cycle

Stages of Development	Number entering each x	Mortality factors	Number Dying in each x	(dx) as a % of (lx)	1-(qx)
	(lx)	(dx F)	(dx)	(100 qx)	(Sx)
Eggs	750	fungi	7	0.93	0.990
		Chrysididae	4	0.53	0.994
		endogenous	20	2.66	0.973
		no eggs	7	0.93	0.990
		TOTAL	38	5.06	0.949
Larvae	712	Ichneumonidae	12	1.68	0.983
		Tachinidae	3	0.42	0.996
		endogenous	74	10.40	0.896
		TOTAL	89	12.50	0.875
Prepupae	623	<i>Melittobia</i> sp.	110	17.65	0.823
		Endogenous	75	12.03	0.879
		Accident	2	0.32	0.996
		TOTAL	187	30.01	0.699
Pupae	436	Endogenous	42	9.63	0.903
Adults in cell	394	Endogenous	10	2.53	0.974
Emerged adults	384				*

TABLE 5

Life table for Brachymenes dyscherus (nests collected in 1996) showing the percentage mortality and its causes at different stages of the life cycle

Stages of Development	Number entering each x	Mortality factors	Number Dying in each x	(dx) as a % of (lx)	1-(qx)
	(lx)	(dx F)	(dx)	(100 qx)	(Sx)
Eggs	427	Chrysididae	2	0.46	0.995
		endogenous	22	5.15	0.948
		no eggs	4	0.93	0.990
		TOTAL	28	6.55	0.934
Larvae	399	Ichneumonidae	2	0.50	0.995
		Endogenous	10	2.50	0.975
		TOTAL	12	3.00	0.970
Prepupae	387	<i>Melittobia</i> sp.	47	12.14	0.878
		Endogenous	46	11.88	0.881
		Accident	3	0.77	0.992
		TOTAL	96	24.80	0.752
Pupae	291	Endogenous	7	2.40	0.976
Adults in cell	284	Endogenous	13	4.57	0.954
Emerged adults	271				

of developmental failure or infection by pathogens and fungi. Endogenous mortality was very high at all stages, accounting for 221 of the 366 deaths, or 60.4%, in 1995 and 98 of the 156 deaths, or 62.8%, in 1996.

Death due to parasitic wasps, *Melittobia* sp. (Eulophidae), was the next most common mortality factor, accounting for 110 deaths, or 30.0%, in 1995 and 47, or 30.1%, in 1996. (Here tables 4 and 5).

DISCUSSION

The major behavioral change of many aculeate Hymenoptera relative to their parasitoid origin was the evolution of nesting behavior is thought to play an important role in reducing immature mortality (Evans 1977). Iwata (1976) classified solitary Vespidae into three categories with respect to nesting habits: (1) burrowers - excavate nests in soil, (2) renters - occupy and modify preexisting cavities and (3) builders - construct their entire nest from materials such as mud or masticated plant material. The construction material and form of nests are influenced by the availability of nest sites and construction materials, as well as the ability of particular designs to thwart nest parasites and predators (Cowan 1991).

As observed here in *B. dyscherus*, most mud-daubing vespids obtain their mortar for nest construction by drinking water at one place and then flying to a site of dry, clayey soil where they bite at the ground, regurgitate water, and mix the resulting mud to the proper consistency (Iwata 1938, 1939). They then fly to the nest with the globule of mud and incorporate it into the nest structure (Cowan 1991). Because the exposed mud nests of some solitary vespids are quite durable and do not wash away in rain, it may be that saliva is added to the water and soil to strengthen the nest (Isely 1913). Often nests are located near a source of water (Isely 1913, Markin and Gittins 1967, Freeman and Jayasingh 1975), and Gess (1981) has argued that some wasps may be limited geographically and seasonally

by lack of water for mud. Thus, mud nests are commonly found around human habitations because these areas generally provide an abundance of suitable nesting and mud collecting sites (Smith 1979).

Like *B. dyscherus*, other eumenine species apply additional material to the outside surface of the nest after nest construction and provisioning (Williams 1919, Jayakar and Spurway 1965). In the case of the sphecid wasp *Sceliphron laetum* (F. Smith 1856) (similar to *B. dyscherus*), the entire nest is plastered over with a thick layer of mud and raised ridges up to 8 mm thick, once a certain number of cells have been completed (Smith 1979).

According to Brooke (1981) the females of eumenine provide cells with many prey items when prey are small, but females provide only a few when the prey are large. This may explain the great variability in the number of prey collected by *B. dyscherus* in the present study.

In solitary vespids, the pupal stage can last 9-22 days, depending on the species and sex. Females require more time (Krombein 1967). I also observed this variation in males (16-25 days) and females (19-28 days). The occurrence of prepupal diapause (leading to a very prolonged total development period for immatures) observed in nests of *Monobia angulosa* Saussure 1852 (Camillo *et al.* 1997) collected in the same area as the current study, was also observed in *B. dyscherus*. These authors showed that those species have two different strategies in response to adverse climatic conditions. One of the strategies is to remain for a long period of time in the prepupa stage, and the other, in the adult stage. This can be proven because new nesting was only observed in the following year, although emergencies had occurred after the month of August. Jayakar and Spurway (1965) observed that some wasps tolerate weather adverse seasonal conditions in the tropics with a prepupal diapause similar to that of temperate-zone species, but individuals of other species simply seem to disappear during such unfavorable times. Maybe they migrate to more favorable

habitats or seek shelter as adults and remain inactive (Cowan 1991).

B. dyscherus is a univoltine species, but in other tropical wasp species that enter diapause during the dry season (Jayakar and Spurway 1965), the numerically male-biased sex ratio in the diapausing generations (Jayakar and Spurway 1966) is a hint of the existence of partial bivoltinism (Cowan 1991).

Parasitoids of the families Chrysididae, Eulophidae, Ichneumonidae and Tachinidae attack various immature stages of *B. dyscherus*. Species of Chrysididae attack solitary wasps and lay eggs in the stocked cells of his host just before the cells are closed off. *Melittobia* (Eulophidae) have been commonly reared from the nests eumenines, vespids and sphecids, boring its way into closed mud cells and laying large numbers of eggs on fully-grown prepupae inside. Ichneumonidae are parasitoids that consume their host from the outside, or they may develop within the body of the immature stages of other arthropods (Clausen 1940, in Gauld 1987). Tachinidae are parasites of the larvae of Lepidoptera and Hymenoptera, among others. They lay their eggs over the body of the host and the larvae perforate the body wall and feed on the body interior (Borror and DeLong 1969).

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REFERENCES

- Borror, D.J. & D.M. DeLong. 1969. Introdução ao estudo dos insetos. EDUSP e Edgar Blucher, São Paulo, 635p.
- Brooke, M. de L. 1981. The nesting biology and population dynamics of the Seychelles potter wasp *Eumenes alluaudi* Perez. Ecol. Entomol. 6: 365-377.
- Camillo, E., C.A. Garófalo & J.C. Serrano. 1997. Biologia de *Monobia angulosa* Saussure em ninhos armadilhas (Hymenoptera: Vespidae: Eumeninae). An. Soc. Entomol. Brasil 26: 169-175.
- Carpenter, J.M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Syst. Entomol. 7: 11-38.
- Carpenter J.M. 1986. A synonymic generic checklist of the Eumeninae (Hymenoptera: Vespidae). Psyche 93:61-90.
- Cowan, D.P. 1991. The solitary and presocial Vespidae, p. 33-73. In K.G. Ross and R.W. Matthews (eds.). The social biology of wasps, Cornell Univ., Cornell.
- Evans, H. E. 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. Bioscience 27: 613-617.
- Freeman, B.E. & D.B. Jayasingh. 1975. Factors controlling the distribution in Jamaica of *Pachodynerus nasidens* (Latr.) (Hymenoptera: Eumenidae). Biol. J. Linn. Soc. (London) 7: 231-241.
- Gauld, I.D. 1987. Some factors affecting the composition of tropical ichneumonid faunas. Biol. J. Linn. Soc. (London) 30: 299-312.
- Gess, F.W. 1981. Some aspects of an ethological study of the aculeate wasps and bees of a Karroid area in the vicinity of Grahamstown, South Africa. Ann. Cape Prov. Mus. Nat. Hist. 14: 1-80.
- Giordani Soika, A. 1990. Revisione degli Euminidi neotropici appartenenti ai generi *Pachymenes* Sauss., *Santamenes* n. gen., *Brachymenes* G.S., *Pseudacaromenes* G.S., *Stenosigma* G.S. e *Gamma* Zav. (Hymenoptera). Boll. Mus. civ. St. Nat. Venezia. 39: 71-172.
- Isely, D. 1913. The biology of some Kansas Eumenidae. Univ. Kansas Sci. Bull. 8: 235-309.
- Iwata, K. 1938. Habits of four species of *Odynerus* (*Ancistrocerus*) in Japan. Tenthredo 2:19-32.
- Iwata, K. 1939. Habits of a paper making potter wasp (*Eumenes architectus* Smith) in Japan. Mushi 12: 83-85.
- Iwata, K. 1976. Evolution of instinct: Comparative ethology of Hymenoptera. Amerind, New Delhi, 235p.
- Jayakar, S.D. & H. Spurway .1965. Winter diapause in the squatter wasps *Antodynerus flavescens* (Fabr.) and *Chalybion bengalense* (Dahlb.) (Vespoidea and Sphecoidea). J. Bombay Nat. Hist. Soc. 61: 662-667.

- Jayakar, S.D. & H. Spurway. 1966. Sex ratios of some mason wasps (Vespoidea and Sphecoidea). *Nature* 212: 306-307.
- Krombein, K.V. 1967. Trap-nesting wasps and bees: Life histories, and associates. Smithsonian Institution, Washington D.C., 269p.
- Markin, G.P. & A.R. Gittins. 1967. Biology of *Stenodynerus claremontensis* (Cameron) (Hymenoptera: Vespidae). Univ. Idaho Coll. Agric. Res. Bull. 74: 1-25.
- Oliveira, V., A.M. Costa & W.P. Azevedo. 1983. Pedologia, folhas SF 23/24. In Projeto RADAMBRASIL, Levantamento de Recursos Naturais 32: 385-552.
- Smith, A. 1979. Life strategy and mortality factors of *Sceliphron laetum* (Smith) (Hymenoptera: Sphecidae) in Australia. *Austr. J. Ecol.* 4: 181-186.
- Williams, F.X. 1919. Philippine wasp studies. II. Descriptions of new species and life history studies. *Bull. Exp. Sta. Hawaii Sugar Planter's Assoc. (Entomol.)* 14: 19-186.