ECOLOGY OF CRABRONID WASPS FOUND IN TRAP NESTS FROM SPAIN (HYMENOPTERA: SPHECIFORMES)

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Abstract

We report data obtained concerning the occupation of trap nests by xylicolous Crabronidae (*sensu* Melo 1999) in a study carried out in central Spain between 1992 and 1995. In particular, we analyze the data on the occupation of the nests for *Psenulus concolor* (Dahlbom), *Trypoxylon attenuatum* F. Smith, and *Trypoxylon beaumonti* Antropov. All three species use pre-existing cavities of 2-4 mm to establish their nests. The mortality rates varied between 33% and 55%, and of special interest was the variation between the two species of *Trypoxylon* L. and the absence of mortality due to natural enemies in *P. concolor*. In the three species, mortality was similar along the nests, with no increase in the innermost or outermost cells. *Trichrysis cyanea* (L.) was the most abundant natural enemy in the nests analyzed. Sex distribution was not random in any of the species studied: in *P. concolor* and *T. attenuatum*, the males developed in the outermost cells, while in *T. beaumonti* they appeared in the innermost ones. The sex ratio did not deviate from 0.5 in *P. concolor* and *T. attenuaum*, although in *T. beaumonti*, the number of females was significantly higher than that of males.

Key Words: trap-nests, xylicolous, kleptoparasitoids, *Psenulus*, *Trypoxylon*, *Trichrysis*

Resumen

Se presentan los datos obtenidos sobre la ocupación de nidos trampa por Crabronidae (*sensu* Melo 1999) xilícolas, en un estudio llevado a cabo en el centro de España, entre 1992 y 1995. Se analizan específicamente los datos de ocupación y contenido de los nidos para *Psenulus concolor* (Dahlbom), *Trypoxylon attenuatum* F. Smith, y *Trypoxylon beaumonti* Antropov. Las tres especies utilizan cavidades preexistentes de 2-4 mm para establecer sus nidos. Las tasas de mortalidad obtenidas varían entre un 33% y un 55%, destacando la variación observada entre las dos especies de *Trypoxylon* L. y la ausencia de mortalidad ocasionada por enemigos naturales en *P. concolor*. En las tres especies la mortalidad es similar a lo largo del nido, no incrementándose en las celdas más externas o internas. *Trichrysis cyanea* (L.) es el enemigo natural más abundante en los nidos analizados. La distribución de sexos no es aleatoria en ninguna de las tres especies estudiadas: en *P. concolor* y *T. attenuatum*, los machos se desarrollan en las celdas más externas, mientras que en *T. beaumonti* aparecen en las celdas más internas del nido. El sex ratio no se aparta de 0.5 en *P. concolor* y *T. attenuaum*, aunque en *T. beaumonti*, el número de hembras es significativamente mayor que el de machos.

Translation provided by the authors.

The Crabronidae include a large number of xylicolous species. These wasps build their nests either in soft core or hollow stems and even in soft pieces of wood. They may excavate their own nests (such that they function as true constructors) or may occupy pre-existing nests or empty holes.

The nests may be linear, with cells located one after the other, or branched; the latter are never found in hollow stems. In both cases, the cells are divided by a septum of mud, resin, or wood particles. According to Krombein (1967) the septa "serve to protect against parasites, parasitoids, and predators; they ensure the nutrition of the larvae and prevent cannibalism; they serve as orientation for the exit of the adult". In some cases, there is also a plug at the end of the gallery that forms a "vestibular cell" in front of the last provisioned cell.

Here we report data obtained in a study with trap-nests on 9 species of crabronids (*sensu* Melo 1999): *Passaloecus gracilis* (Curtis, 1834), *P. singularis* (Dahlbom, 1844), *Pemphredon lethifer* (Suckard, 1837), *Psenulus concolor* (Dahlbom, 1843), *Spilomena troglodites* (Van der Linden, 1829), *Stigmus solskyi* Morawitz, 1864; *Trypoxylon attenuatum* F. Smith, 1851, *T. beaumonti* Antropov, 1991, and *T. minus* Beaumont, 1945. However, we only analyze the data from those species whose samples can be considered representative: *Psenulus concolor*, *Trypoxylon attenuatum* and *T. beaumonti*.

Psenulus Kohl includes about 160 species, of which 10 have been found in Europe. The biology and ecology of the European species have been described by Freeman (1938); Grandi (1961); Janvier (1962, 1975); Danks (1970, 1971a); Jacob-Remacle

(1976, 1985, 1986); and Bonelli (1988), who provided data concerning nest structure, prey, and parasitoids. Lomholdt (1976); Bohart & Menke (1976); and Dolfuss & Bitsch (2001) compiled data published by other authors, among which the references to natural enemies are outstanding.

Trypoxylon L. is a cosmopolitan genus with around 700 species. The presence of 17 species has been recorded in Europe (Antropov 2001). Many works have addressed the biology of the European species, most of them referring to nest structure, prey identification, and parasitoids. Some works are purely descriptive or just compilations, such as those by Hamm & Richards (1930); Maréchal (1936); Freeman (1938); Bristowe (1948); Binaghi (1956); Grandi (1961); Abraham (1982); and Antropov (2001). Danks (1970, 1971a, b); Jacob-Remacle (1976, 1985, 1986, 1987); and Asís et al. (1994) conducted surveys that, unlike previous works, quantified data obtained about nests, prey, natural enemies, and mortality. Of the species addressed in the present work, *T. attenuatum* has been studied by Danks (1970) and Asís et al. (1994), while *T. beaumonti* biology is almost unknown.

MATERIALS AND METHODS

One thousand and seventeen trap-nests were placed in 19 localities of Burgos, Cuenca, León, Segovia, Soria, Teruel, Valladolid, and Zamora provinces, from central-western Spain, and 931 were collected at the end of the study. The trap-nests, made from stems of *Ailanthus altissima* Swingle (Simaroubaceae) (l = 20-30 cm; d = 2-14 mm) and *Phragmites australis* (Cav.) (Poaceae) (l = 20-30 cm; d = 1-8 mm) (cane) were grouped in sheaves with four stems each. The sheaves represented one of the following models: a) four cane stems of different diameters (≥2 mm); b) two stems of *Ailanthus* and two of cane; c) four stems of cane of 1-2 mm. These sheaves were placed in the field at the beginning of the spring of 1992, 1993, 1994 and 1995, attached to the branches of trees with insulating tape, and were withdrawn in the autumn of each of the above years. Thus, they remained in place for 6-7 months. Once collected, the sheaves were placed in an Iar (model CF 85) refrigerator at 6-8°C. The stems were opened later, any occupation by aculeates was determined, and stems with nests inside were studied.

The data gathered were primarily diameter and length of the built nest, cell numbers and contents, and presence of vestibular cells and septa. The cells were numbered from the exterior to the interior (cell 1 being the outermost one), although chronologically the innermost cell was the one constructed first. The contents of each cell were transferred to glass vials, which were held in a refrigerator (6-8°C) until the following spring, when they were transferred to a Heraeus culture chamber (28°C) to promote the emergence of adults. It was then possible to identify the occupants and some of their parasitoids. The total number of nests studied was 511. Between 15% and 25% of the mature larvae were conserved for a possible later study of the preimaginal stages. This means that the mortalities, calculated as a function of the adults obtained, are slightly overestimated (because mortality affecting immature larvae could not act on mature larvae).

The stems of each class and diameter that were occupied, unoccupied, or abandoned were counted. The calculations regarding occupancy were carried out based on the number of "nesting sites" (approximately double the number of stems) since two nests could have been placed in each of them: one on each side. Possible reoccupation (stems occupied in the first and second generation) was not taken into account in determining global occupation index.

Analyses were limited to the wasps *Psenulus concolor*, *Trypoxylon attenuatum*, and *T. beaumonti* (Crabronidae), and kleptoparasitoid *Trichrysis cyanea* (L., 1758) (Chrysididae). Data refer to individuals of the second generation, because only one collection was made, at the end of the summer. Abandoned nests (i.e., nests occupied during the first generation and abandoned by the adults) were considered to be susceptible to occupation during the second generation.

The sex ratio was calculated as the "number of males/total number of adults obtained". The following abbreviations are employed: M1 = mortality in the egg stage, including the possible absence of oviposition; M2 = mortality of the different larval stages (with the exception of the mature larva); M3 = mortality due to natural enemies; M4 = mortality in the mature larval stage or in metamorphosis giving rise to the adult.

RESULTS

Trap Nest Occupation

The occupation index was 19.34%, slightly higher for the *Ailanthus* stems (19.75%) as compared with those of cane (19.28%) (Table 1).

In cane stems (Table 1), the differences in occupation, as a function of diameter, were significant ($\chi^2_3 = 31.37$; $P < 0,0001$), those with a diameter of 3-4 mm being the ones most used. This is because these diameters are better adapted to the size of *Trypoxylon attenuatum* and *T. beaumonti*, the species that established the greatest number of nests (Table 2). In *Ailanthus* stems, a preference as a function of diameter was not observed ($\chi^2_3 = 0.57$; $P = 0.90$) (Table 1).

Trypoxylon was the most abundant genus (272 nests, 72.9%), while *Pemphredon* L. (43 nests) and *Psenulus* (12 nests) had much lower percentages

TABLE 1. STEMS COLLECTED AS A FUNCTION OF DIAMETER AND TYPE (A = ABANDONED, NO = NOT OCCUPIED, O = OCCUPIED, T = TOTAL).

Cane	A (%)	NO (%)	O (%)	T
Total	239 (14.1)	1126 (66.6)	326 (19.3)	1691
1 mm	0 (0.0)	107 (99.1)	1 (0.9)	108
2 mm	30 (5.6)	409 (76.9)	93 (17.5)	532
3 mm	183 (20.0)	537 (58.6)	197 (21.5)	917
4 mm	20 (16.5)	69 (57.0)	32 (26.4)	121
5-8 mm	6 (46.2)	4 (30.8)	3 (23.1)	13
Ailanthus				
total	32 (13.4)	159 (66.8)	47 (19.7)	238
2-4 mm	1 (9.1)	8 (72.7)	2 (18.2)	11
5-7 mm	11 (9.3)	82 (69.5)	25 (21.2)	118
8-10 mm	16 (18.2)	55 (62.5)	17 (19.3)	88
12-14 mm	4 (19.0)	14 (66.7)	3 (14.3)	21

of occupation (11.5% and 3.2%, respectively). The presence of *Spilomena* Shuckard, *Passaloecus* Shuckard, and *Stigmus* Panzer was very reduced, with scarcely 2.9% of the nests among the three genera (Table 2).

Differences among the genera were observed in the number of nests employed by each species in the different types of stems (*Ailanthus*—cane). *Trypoxylon* females established their nests exclusively in pre-existing cavities, its reported presence in *Ailanthus* stems (14 nests, 5.1% of the total found for the genus) probably is anecdotal and undoubtedly due to the occupation of pre-existing galleries in stems excavated by various Apoidea or *Pemphredon*. Although data reported for *Psenulus* and *Passaloecus* are scarce, the data also indicate the use of pre-existing cavities. *Pemphredon* spp. (Table 2) occupied both types of stems (22 nests in *Ailanthus*, 21 in cane). Thus, the females excavated their nests in stems with soft cores, or occupied pre-existing cavities. The

data obtained for *Spilomena* and *Stigmus* (Table 2), although also scarce, point towards a preferential use of soft-cored stems.

Wasp Biology

Psenulus concolor. Twelve nests were obtained, 11 in cane stems of 3-4 mm and one in *Ailanthus* (Table 2). The number of cells varied between 2 and 16 ($\bar{x}$ = 9.5 cells). The observed mortality was 48.4%, representing that undergone by mature larvae or 37.7% of those in the process of metamorphosis that gave rise to adults (Table 3). No parasitoids were found attacking this species.

Upon analyzing the mortality in cells as a function of the position they occupied from the exterior, we observed that this was similar in all of them (χ^2_4 = 1.90; NS). The outermost cells did not show a higher mortality index.

The sex ratio obtained was 0.78♂/1♀, not significantly different from 0.5 (binomial test, z =

TABLE 2. CRABRONID NESTS FOUND IN THE DIFFERENT MODELS OF STEMS.

	Cane								
	1 mm	2 mm	3 mm	4 mm	5 mm	5 mm	Total	*Ailanthus*	Total
Total (%)	1 (0.3)	93 (28.5)	197 (60.4)	32 (9.8)	1 (0.3)	2 (0.6)	326	47	373
Passaloecus gracilis	0	2 (100)	0	0	0	0	2	0	2
Passaloecus singularis	0	1 (100)	0	0	0	0	1	0	1
Pemphredon lethifer	0	0	5 (83.3)	1 (16.7)	0	0	6	14	20
Pemphredon sp.	0	0	14 (93.3)	1 (6.7)	0	0	15	8	23
Psenulus concolor	0	0	7 (63.6)	4 (36.4)	0	0	11	1	12
Trypoxylon attenuatum	0	67 (37.8)	95 (53.7)	15 (8.5)	0	0	177	4	181
Trypoxylon beaumonti	0	3 (10.7)	20 (71.4)	3 (10.7)	0	2 (7.1)	28	0	28
Trypoxylon minus	0	0	1 (100)	0	0	0	1	0	1
Trypoxylon sp.	0	15 (28.8)	32 (61.5)	4 (10.7)	1 (1.9)	0	52	10	62
Spilomena troglodytes	0	0	0	0	0	0	0	6	6
Stigmus solskyi	0	0	0	0	0	0	0	2	2
Unknown	1 (3.0)	5 (15.2)	23 (69.7)	4 (12.1)	0	0	33	2	35

TABLE 3. CONTENTS OF NESTS OF *PSENULUS CONCOLOR*, *TRYPOXYLON ATTENUATUM*, AND *T. BEAUMONTI*. M1, M2, M3, M4 = TYPE OF MORTALITY.

	P. concolor (%)	*T. attenuatum* (%)	*T. beaumonti* (%)
Preserved	19	153	32
♀♀	27	209	34
♂♂	21	188	10
Adults	48 (51.6)	397 (66.8)	44 (45.4)
Total mortality	45 (48.4)	197 (33.2)	53 (54.6)
M1	3 (3.2)	44 (7.4)	17 (17.5)
M2	6 (6.5)	26 (4.4)	5 (5.2)
M3	0	14 (2.4)	6 (6.2)
M4	36 (38.7)	113 (19.0)	25 (25.8)
Total cells	112	747	129

0.72; NS). The distribution of males and females inside the nests was not similar (χ^2_4 = 15.99; $P <$ 0.01); the sex ratio follows a negative exponential model (sex ratio = -0.396 ln (cell position) + 1.040; R^2 = 0.825) ($F_{1,13}$ = 92.12; $P < 0,0001$), and hence the males are increasingly less abundant towards the innermost cells.

Trypoxylon. At least three species nested in the stems provided (Table 2): *T. attenuatum*, *T. beaumonti* and *T. minus*, a total of 210 nests being counted. Moreover, 62 nests were detected that could not be assigned to any given species with certainty because the larvae had not developed into adults.

Trypoxylon attenuatum. With 181 nests (177 in cane and 4 in *Ailanthus*) *T. attenuatum* was the most abundant species. Occupation is shown in Table 2 as a function of stem diameter. No preference for any specific diameter was observed within the 2-4 mm range (χ^2_2 = 1,82; NS), although no nests in canes of other diameters were found.

The number of cells per nest varied between 1 and 11 ($\bar{x}$ = 4.12). The observed mortality was 33.2%. M4 accounted for the greater part of the mortality (almost 60%), while the incidence of natural enemies was very low, and only 14 cells out of 594 (2.4%) were parasitized (Table 3).

Mortality as a function of the position occupied by the cells from the exterior was found to be quite similar in all of them (χ^2_7 = 11.33; NS). Thus, mortality was not higher in the cells closer to the exterior. Neither were there any significant differences as a function of the number of cells in the nests. Mortality in the nests with few cells was of the same order as in those with more cells (χ^2_6 = 8.55; NS).

The number of males and females obtained was similar (0.9♂/1♀), and did not depart significantly from a sex ratio of 0.5 (binomial test, z = 1.42; NS). However, the distribution of males and females within the nests was not the same (χ^2_3 = 46.35; $P < 0.0001$): the males developed in the outermost cells, and the sex ratio follows a negative

exponential model (sex ratio= -0.314 ln (cell position) + 0.743; R^2 = 0.941) ($F_{1,9}$ = 76.80; $P < 0.0001$).

Trypoxylon beaumonti. Twenty-eight nests were obtained, all of them from cane stems (Table 2). Although the data are scarce, there seemed to be a significant preference towards the occupation of galleries of 3-4 mm (χ^2_3= 8.17; $P < 0.05$). The number of cells varied between 2 and 7 ($\bar{x}$ = 4.6).

The observed mortality was 54.6% (Table 3), with six cells attacked by *Trichrysis cyanea*. Mortality varies depending on the position occupied by the cell from the exterior (χ^2_3 = 10.48; $P < 0.01$), being higher for the most exterior cell (80%) and smaller for inner cells (around 40%).

Important differences were seen between the number of males and females obtained (0.29♂/1♀), and the sex ratio departed significantly from 0.5 (binomial test, z = 3,47; $P < 0.001$). Sex distribution inside the nests was not similar (χ^2_4 = 13.96; $P < 0.01$), the males being found in the innermost nests and the females being progressively more abundant towards the exterior.

Trichrysis cyanea. This kleptoparasitoid was found in 32 nests, belonging to different species of *Pemphredon* and *Trypoxylon*, and parasitized 44 (37%) of the cells (Table 4). The mean number of cells parasitized per nest was 1.38. Eleven of the nests affected, with two or more cells, had more than 50% of the cells parasitized. No significant differences were observed as a function of the position of the cell. The outermost cells did not exhibit a greater probability of being parasitized than those located more to the interior of the nest (χ^2_5 = 9.77; NS). In three of the 44 cells the kleptoparasitoid did not complete its development, although the larvae managed to become pupae. Of the 41 adults obtained, 23 were male and 18 female, and the sex ratio (1.27 ♂:1♀) was not significantly different from 0.5 (binomial test, z = 0.63; NS).

DISCUSSION

In *Psenulus concolor*, the mortality value (48.4%) was higher than that reported in Great

TABLE 4. NESTS AND CELLS OF DIFFERENT HOSTS AFFECTED BY *TRICHRYSIS CYANEA*.

	Nests affected	Total number of cells	Parasitized cells	Nests with 2 or more cells parasitized
Pemphredon sp.	2	10	3	1
Trypoxylon attenuatum	4	23	7	2
Trypoxylon beaumonti	8	29	10	3
Trypoxylon sp.	18	57	24	5
Total	32	119	44	11

Britain for the same species by Danks (1970, 1971b) (29.3% and 26%) ($\chi^2_2 = 10.72$; $P < 0.01$). However, the mean number of adults produced per nest was greater in this study (5 adults/nest) than in those of Danks (1970, 1971b) (4.0-4.2 adults/nest), due to the higher number of cells in the nests analyzed (9.3 in this study as compared with 5.4-5.9 in those of Danks 1970, 1971b). It is striking, nevertheless, that no parasitoids were found attacking this species; all mortality derived from the interruption of development during larval and pupal stages. The same observation was reported and attributed to a paucity of data by Danks (1970).

The mortality rates found for European species of *Trypoxylon* vary between 33.2% (for *T. attenuatum* in this study) and 63.8% (for *T. attenuatum* and *T. figulus* in Danks 1971b). The observed differences are significant ($\chi^2_5 = 144.25$; $P < 0.001$). Mortality in *T. attenuatum* is lower, both in this study (33.2%) and in that of Asís et al. (1994) (44.0%). Furthermore, the values reported by Danks (1971b) for *T. attenuatum* and *T. figulus* (63.8%) and by Jacob Remacle (1986) for *T. clavicerum* and *T. minus* (58.2%) are clearly higher, while the value found for *T. beaumonti* (54.6%) and that given by Danks (1970) for *T. attenuatum* and *T. figulus* (54.6%) do not deviate from the mean values. This shows that the populations of these wasps are subject to important fluctuations, although it seems that *T. attenuatum* in the Iberian Peninsula could have appreciably lower rates than the rest of the species or than other populations of this species present in more northern areas.

It is also possible to observe an important variability in mortality due to different agents, and of special interest is the low mortality attributable to the action of natural enemies in the species analyzed here (2.4-6.4%), whereas the rates found in other works are between 15% and 25%.

In *Trypoxylon*, cases have been described in which the distribution of the individuals of each sex in the nest seems to be irregular (see Cross et al. 1975), although in many cases it follows a defined trend. Thus, in some species the males are found in the innermost cells and the females in the outermost ones (IMOF, inner males outer females) while in other species the inner cells harbor females (IFOM). The IMOF model is the main one among species of the subgenus *Trypargilum*, in which the male remains inside the nest during its provisioning, copulating with the female when she returns to it (Krombein 1967; Medler 1967; Coville & Coville 1980; Coville & Griswold 1983, 1984; Camillo et al. 1993, 1994). In wasps of the subgenus *Trypoxylon*, the model seems to be IFOM (Krombein 1967; Asís et al. 1994; Oku & Nishida 1999). *Trypoxylon attenuatum*, as reported by Asís et al. (1994), follows this model. However, the data obtained for *Trypoxylon beaumonti* seem to reflect the IMOF model. This could be due to a lack of data, although it might also be a reflection of differences in the behavior of this species, an aspect that deserves further attention.

In some species of *Psenulus*, sex ratios that clearly deviate towards a greater production of males have been described (0.86 in Krombein 1967, for *Psenulus pallipes* (Panzer), $z = 5.04$, $P < 0,0001$; 0.68 in Matthews 2000, for *P. interstitialis* Cameron, $z = 2.19$, $P < 0.05$). Nevertheless, the data obtained by us and those reported by Danks (1970, 1971b) point to a different situation for *P. concolor*, with a sex ratio that does not depart significantly from 0.5. Regarding the species of *Trypoxylon* studied, the sex ratio does not depart significantly from 0.5 in *T. attenuatum*, while it does deviate from that figure, and towards a greater production of females, in *T. beaumonti*. According to the theory of parental inversion proposed by Fisher (1999), in large randomly breeding populations selection will result in equal investment in sons and daughters (hence a sex ratio of 0.5). Since the males are smaller than the females in most solitary wasps and require a lower investment, one would expect a greater production of males than of females (i.e., a sex ratio >0.5). However, in situations such as those that affect certain wasps, with fragmented populations in which there is local competition for mates among brothers, the females will be selected to produce female-biased sex investment ratios (Hamilton 1967; Cowan 1991). This could explain the deviation, towards the production of females, observed in *T. beaumonti*, whereas *T. attenuatum*, with larger and less isolated populations on the Iberian Peninsula, would show sex ratios close to 0.5.

It is also necessary to take into account the influence that can be exerted by the nesting sub-

strate on the sex ratio since different studies have shown that cavities with smaller diameters shift the sex ratio towards the production of males (Krombein 1967; Charnov et al. 1981). The diameters offered do not seem the limit the nesting possibilities of the species of *Trypoxylon* studied because mainly the cavities with a medium-sized diameter were those occupied. However, if the cavities offered are larger or smaller than those usually available in nature, a bias towards a greater production of one of the sexes could arise, as long as there is sexual dimorphism as regards size (Trivers & Hare 1976). In any case, Oku & Nishida (2001) have demonstrated that the use of small samples could lead to mistaken conclusions concerning the sex ratio, so caution should be exercised on drawing conclusions from few data.

REFERENCES CITED

ABRAHAM, R. 1982. The biology of *Trypoxylon attenuatum* and *T. figulus*. Entomol. Mitt. 114: 137-147.

ASÍS, J. D., J. TORMOS, AND S. F. GAYUBO. 1994. Biological observations on *Trypoxylon attenuatum* and description of its mature larva and of its natural enemy *Trichrysis cyanea* (Hymenoptera: Sphecidae, Chrysididae). J. Kansas Entomol. Soc. 67: 199-207.

ANTROPOV, V. 2001. Tribu des Trypoxylini, pp. 347-384 *In* J. Bitsch [ed.], Faune de France 86—Hyménoptères Sphecidae d'Europe Occidentale—Volumen 3. Fédération Francaise des Sociétes des Sciences Naturelles, Paris. 459 pp.

BOHART, R. M., AND A. S. MENKE. 1976. Sphecid wasps of the world. A generic revisión. University of California Press. Berkeley. 695 pp.

BONELLI, B. 1988. Note sul comportamento di nidificazione di *Psenulus fuscipennis* (Dahlb.), *Tachysphex fulvitarsis erythrogaster* (Costa), *Sphex albisectus* Lep. e Serv. e *Sphex occitanicus* Lep. e Serv. (Hymenoptera-Sphecidae). Boll. Ist. Entomol. "Guido Grandi" (Bologna) 43: 79-88.

BINAGHI, G. 1956. Su di un eccezionale insediamento del nido pedotrofico di *Trypoxylon attenuatum* Smith (Hymenoptera, Sphecidae). Boll. Soc. Entomol. Italiana 86: 8-12.

BRISTOWE, W. S. 1948. Notes on the habits and prey of twenty species of British hunting wasps. Proc. Linn. Soc. London 160: 12-37.

CAMILLO, E., C. A. GARÓFALO, G. MUCCILLO, AND J. C. SERRANO. 1993. Biological observations on *Trypoxylon (Trypargilum) lactitarse* Saussure in southeastern Brazil. Rev. Brasileira Entomol. 37: 769-778.

CAMILLO, E., C. A. GARÓFALO, AND J. C. SERRANO. 1994. Observações sobre a biologia de *Trypoxylon (Trypargilum) rogenhoferi* Kohl (Hymenoptera: Sphecidae). An. Soc. Entomol. Brasil 23: 299-310.

CHARNOV, E. L., R. L. LOS-DEN HARTOGH, W. T. JONES, AND J. VAN DEN ASSEM. 1981. Sex ratio evolution in a variable environment. Nature 289: 27-33.

COVILLE, R. E., AND C. GRISWOLD. 1983. Nesting biology of *Trypoxylon xanthandrum* in Costa Rica with observations on its spider prey (Hymenoptera: Sphecidae; Araneae: Senoculidae). J. Kansas Entomol. Soc. 56: 205-216.

COVILLE, R. E., AND C. GRISWOLD. 1984. Biology of *Trypoxylon (Trypargilum) superbum* (Hymenoptera: Sphecidae), a spider-hunting wasp with extended guarding of the brood by males. J. Kansas Entomol. Soc. 57: 365-376.

COVILLE, R. E., AND P. L. COVILLE. 1980. Nesting biology and male behavior of *Trypoxylon (Trypargilum) tenoctitlan* in Costa Rica (Hymenoptera: Sphecidae). Ann. Entomol. Soc. America 73: 110-119.

COWAN, D. P. 1991. The solitary and presocial vespidae, pp. 33-73 *In* K. G. Ross and R. W. Matthews [eds.], The Social Biology of Wasps. Comstock Publishing Associates, Ithaca, NY. 678 pp.

CROSS, E. A., M. G. STITH, M. G., AND T. R. BAUMAN. 1980. Bionomics of the organ-pipe mud-dauber, *Trypoxylon politum* (Hymenoptera: Sphecidae). Ann. Entomol. Soc. America, 68: 901-916.

DANKS, H. V. 1970. Biology of some stem-nesting aculeate Hymenoptera. Trans. R. Entomol. Soc. London 122: 323-399.

DANKS, H. V. 1971a. Populations and nesting-sites of some aculeate Hymenoptera nesting in Rubus. J. Anim. Ecol. 40: 63-77. Biology of some stem-nesting aculeate Hymenoptera nesting in *Rubus*. J. Anim. Ecol. 40: 63-77.

DANKS, H. V. 1971b. Nest mortality factors in stem-nesting aculeate Hymenoptera. J. Anim. Ecol. 40: 79-82.

DOLLFUSS, H., AND J. BITSCH. 2001. Tribus des Psenini, pp. 14-55 *In* J. Bitsch [ed.], Faune de France 86—Hyménoptères Sphecidae d'Europe Occidentale—Volumen 3. Fédération Francaise des Sociétes des Sciences Naturelles. Paris. 459 pp.

FISHER, R. A. 1999. The genetical theory of natural selection. A Complete Variorum edition. Oxford University Press. New York. 318 pp.

FREEMAN, P. 1938. Notes on the nesting of five species of solitary wasps (Hymenoptera, Sphecoidea). Proc. R. Entomol. Soc. London 13: 1-6.

GRANDI, G. 1961. Studi di un Entomologo sugli Imenotteri superiori. Boll. Ist. Entomol. (Bologna) 25: i-xv, 1-659.

HAMILTON, W. D. 1967. Extraordinary sex ratios. Science 156: 477-488.

HAMM, A. H., AND O. W. RICHARDS. 1930. The biology of the british fossorial wasps of the families Mellinidae, Gorytidae, Philanthidae, Oxybelidae and Trypoxylonidae. Trans. Entomol. Soc. London 78: 95-131.

JACOB-REMACLE, A. 1976. Une opération nichoirs artificiels pour Hyménoptères dans trois jardins de Liège. Bull. Ann. Soc. Entomol. Belgique 112: 219-242.

JACOB-REMACLE, A. 1985. L'occupation plurispécifique des rameaux constituant des nichoirs-pièges pour Hyménoptères Aculéates solitaires et son incidence sur la mortalité des occupants. Bull. Ann. Soc. Roy. Belge Entomol. 121: 396-408.

JACOB-REMACLE, A. 1986. Mortalité de quelques hyménoptéres aculéates nidifiant dans des nichoirs-pièges. Bull. Ann. Soc. Roy. Belge Entomol. 122: 107-118.

JACOB-REMACLE, A. 1987. Influence de l'urbanisation sur les populations d'hyménoptères aculéates xylicoles: étude effectuée à Liège par la méthode des nichoirs-pièges. Natura Mosana 40(1): 3-18.

JANVIER, H. 1962. Recherches sur les Hyménoptères nidifiants aphidivores. IV. Le genre *Diodontus* (Curtis). Ann. Sci. Nat. Zool. Biol. Anim. (Série 12) 4: 489-515.

JANVIER, H. 1975. Nidificación de *Psenulus concolor* (Dahlbom, 1843) (Hymenoptera). Graellsia 29: 117-142.

KROMBEIN, K. V. 1967. Trap nesting wasps and bees. Life histories, nests and associates. Smithsonian Institution, Washington. 570 pp.

LOMHOLDT, O. 1976. The Sphecidae (Hymenoptera) of Fennoscandia and Denmark *in* Fauna Entomologica Scandinavica. 4, part 1:1-224 (1975), part 2:225-452 (1976). Scandinavian Science Press, Klampenborg, Denmark.

MARECHAL, P. 1936. Ethologie des *Trypoxylon* (Hym. Spheg) et observations sur *T. attenuatum* Sm. Bull. Ann. Soc. Entomol. Belgique 76: 373-396.

MATTHEWS, R. W. 2000. Nesting biology of the stem-nesting wasp *Psenulus interstitialis* Cameron (Hymenoptera: Crabronidae: Pemphredoninae) on Magnetic Island, Queensland. Australian J. Entomol. 39: 25-28.

MEDLER, J. T. 1967. Biology of *Trypoxylon* in trap nests in Wisconsin (Hymenoptera: Sphecidae). American Mid. Natur. 78: 344-358.

MELO, G. A. R. 1999. Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. Sci. Pap. Nat. Hist. Mus., Univ. Kansas 14: 1-55.

OKU, S., AND T. NISHIDA. 1999. Factors affecting female-biased sex ratio in a trap-nesting wasp, *Trypoxylon malaisei*. Res. Popul. Ecol. 41: 169-175.

OKU, S., AND T. NISHIDA. 2001. Presence of single-sex broods under local mate competition in *Trypoxylon malaisei* (Hymenoptera: Sphecidae): adaptation or maladaptation? Ann. Entomol. Soc. America 94: 550-554.

TRIVERS, R. L., AND H. HARE. 1976. Haplodiploidy and the evolution of social insects. Science 191: 249-263.