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Nesting behaviour and provisioning in *Bembix merceti* and *Bembix zonata* (Hymenoptera: Crabronidae)

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We studied the nesting behaviour and provisioning of *Bembix merceti* Parker and *Bembix zonata* Klug during three flight seasons (1993–1995). The females of *B. merceti* capture Diptera from seven different families to feed their larvae. Provisioning is progressive. The females provide a greater number of prey over subsequent days during larval growth. This activity begins increasingly earlier and lasts for longer, and prey capture is increasingly faster. Although the activity of the females is greater during the middle hours of the day, towards the end of each day the number of prey per wasp increases slightly and the duration of provisioning flights is reduced. Regarding *Bembix merceti*, we also report on nest structure and excavation as well as about the different natural enemies of these wasps. The data recorded for *B. zonata* refer to nest digging and structure, the wasps' natural enemies and their provisioning strategies, which in general are similar to those seen for the females of *B. merceti*.

KEYWORDS: provisioning, nests, prey, *Bembix*, Diptera.

Introduction

Bembix Fabricius is a cosmopolitan genus with more than 50 species in the Palearctic region (Bohart and Menke, 1976). The females excavate uni- or pluricellular nests in the soil and usually capture adult dipterans to feed their larvae (although various species, especially those from Australia, prey upon other orders of insects). The provisioning is usually progressive (Evans, 1957). The relatively large size of these wasps, high number of species (more than 300, according to Bohart and Menke, 1976) and nesting in aggregations, have made them spectacular. Accordingly, the general aspects of their biology (nest structure, prey preferences, natural enemies...) are fairly well known and several studies have explored such aspects in depth, while others have focused on ethological aspects (e.g. Nielsen, 1945; Tsuneki, 1956, 1957, 1958). Ecological aspects and nesting behaviour were studied by Evans (1957, 1966) for Nearctic species, Evans and Matthews (1973) for the Australian ones, and Grandi (1961) for western Palearctic species. Nevertheless,

the nesting behaviour of many species of *Bembix* remains unknown and data—many of them anecdotal—are only available for 15 Palearctic species.

Here we report on the nesting behaviour of *Bembix merceti* J. Parker, and *Bembix zonata* Klug. The former species, restricted to the Iberian Peninsula, was studied only by Asís *et al.* (1992) who provided data on prey and nests and described the mature larva. *Bembix zonata* is found in the south of Europe and only a few species of prey have been reported (Bernard, 1934; Asís *et al.*, 1992), whereas Asís *et al.* (1997) described the mature larvae.

Methods

Observations were made in the neighbourhood of Rabanera del Campo (Soria, Spain), a region mainly dedicated to growing cereal crops. The nests were found in a small bare area of ca 150 m², with sandy soil, mostly devoid of vegetation and with isolated stands of *Bromus diandrus* Roth, *Artemisia campestris* L., *Scirpus holoschoenus* L. and *Thymus mastichina* L. The data, corresponding to 20 nests of *B. merceti* and four of *B. zonata*, were collected on 9–13 and 23–27 July 1993, 8–11 and 16–22 July 1994, and 11–17 August 1995. Observations started at about 07:30, before the females had begun their activity, and lasted until the females closed their nests for the night (between 16:00 and 18:00). Hours are expressed as GMT.

The females were labelled on their thorax with two dots of different colours using a Pentel[®] marker.

For statistical analysis we used Statistica 4.5[©] (StatSoft Inc.).

Results

Bembix merceti J. Parker

We observed wasps 6 and 7 excavating nests, this activity began at 09:05 and 09:47 and lasted for 6 h 25 min and 5 h 26 min, respectively. Excavation was completed on the same day that it was begun. The method of nest construction was similar to that of other *Bembix* (Evans, 1957, 1966) and also included dispersion of the sand extracted during excavation. One of the females performed the excavation continuously, while the other one interrupted digging, leaving the nest for 35 min. On completing the nest the female levelled the ground around the entrance (7–10 min). No false burrows (see Evans, 1966) were observed.

The nest entrances were covered with temporary closures while females were away for provisioning flights, even when these were occurring at maximum frequency. In one of the nests ($N=8$), the female did not close the nest at the end of excavation, but only before introducing the first prey; from then onwards, the nest remained closed during the female's absence.

In all three cases observed, the start of provisioning occurred on the day after the nest had been completed; on that day only one prey was brought in. After excavation of one of those nests, we obtained the prey introduced by the female, together with the egg attached to it. Provisioning was progressive, and the number of prey added to the nest increased (figure 1), assumingly with the increasing size of the larva and its need to consume the prey. We excavated nests 6 and 7 between 15 and 17 h after the introduction of the last prey. In both cases we found a mature larva constructing its cocoon. The total numbers of prey provided by females 6 and 7 were 46 and 60, respectively.

The females spent the night within their nests, and began their daily activity

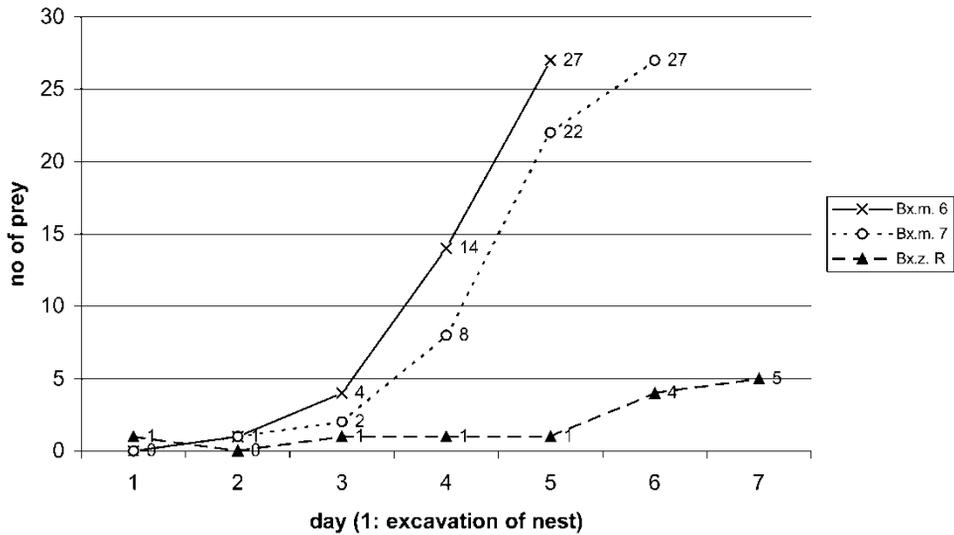


FIG. 1. Number of prey contributed daily by two females of *Bembix merceti* (Bx.m. 6, Bx.m. 7) and one of *Bembix zonata* (Bx.z. R). Day 1 coincides with nest-digging day.

outside between 08:08 and 10:44 (median = 09:31; $N = 10$). A correlation between the time of activity start and the number of prey brought to the nests during the day was observed (Spearman Rank Correlation, $r = -0.854$, $P < 0.001$, $N = 10$): the earlier the activity began, the greater the number of prey. The period of daily activity varied between 62 and 500 min (mean = 305 min, $SD = 131.2$ min, $N = 10$); the longest activity time was observed for the day with the highest number of prey provided (Spearman Rank Correlation, $r = 0.817$, $P < 0.001$, $N = 10$). The number of observed prey (between one and 27) varied, with high probability, as a function of the stage of development of the larva. Nest closure occurred between 11:45 and 17:46 (median 14:11). Final nest closure ($N = 4$) was begun between 07:55 and 09:08, with a duration of 12–62 min (mean = 31 min).

More than 90% (151 out of 165) of the flights observed were for provisioning. A provisioning flight is defined as a tour when the wasp female returns to the nest with a prey. These flights varied in their duration (mean = 18.16 min, range = 1.45–134.5, $N = 151$), being shorter when the number of prey per day increased (Spearman Rank Correlation, $r = -0.787$, $P < 0.001$, $N = 15$). On comparing data for those two females observed during a full nest cycle, the duration of the provisioning flights decreased during successive days with increasing numbers of prey brought to the nests; this was significant for one of these females (*Bembix merceti* 7) (table 1).

The time during which the female remained inside the nest for prey deposition before leaving to capture another one varied between 25 and 247 s (mean = 82.8 s, $SD = 27.3$, $N = 154$). This time decreased when provisioning was more intense (i.e. when the number of prey brought to the nest increased) (table 1). The females ($N = 7$) that brought few prey (<5) over the day spent more time inside the nest (mean = 112.8 s, $SD = 49.1$, $N = 17$) than those females ($N = 8$) that captured more prey (between 8 and 27) (mean = 79.1 s, $SD = 20.7$, $N = 137$) (Mann-Whitney U test, $z = -3.88$, $P < 0.001$).

Table 1. Average duration of provisioning flights and time spent in nests between successive prey contributions for two females of *Bembix merceti*. Also indicated is the number of prey contributed per day by the female, and the values of the Kruskal-Wallis test for differences between days and its associated probability (day 1 coincides with nest-digging day).

	2nd day	3rd day	4th day	5th day	6th day	Kruskal-Wallis test	<i>P</i>
<i>B. merceti</i> 6							
Mean provisioning flight (min)		27.31	24.79	16.4		$H=4.89$	$P=0.087$
Mean inside the nest (s)		110.5	88.1	92.5		$H=3.69$	$P=0.158$
Number of prey		4	14	27		–	–
<i>B. merceti</i> 7							
Mean provisioning flight (min)	50.75	41.75	27.17	14.15	11.27	$H=9.96$	$P<0.05$
Mean inside the nest (s)	185	113	83	65	65.5	$H=19.10$	$P<0.001$
Number of prey	1	2	8	22	27	–	–

In 12 of the 13 cases observed, when foraging had ceased and the last prey had been introduced into the nest, the female performed an additional flight (mean = 44.13 min, range 13.75–120.75, $N=12$), returning to the nest without a prey, and closing it from inside. These flights, performed irrespective of stage of larval development, were longer than the provisioning ones (Mann-Whitney U test, $z = -3.686$, $P < 0.001$).

The number of foraging females was greatest between 10:00 and 14:00, when about 90% of them were active (figure 2). The total number of captured prey was greatest between 11:00 and 13:00. However, the number of captures per active wasp increased later in the day (figure 3), although the variation is not significant (Chi-square test = 5.189, $df=9$, $P=0.818$). The number of prey captured per active female (figure 3) shows a different distribution from that reflecting the number of

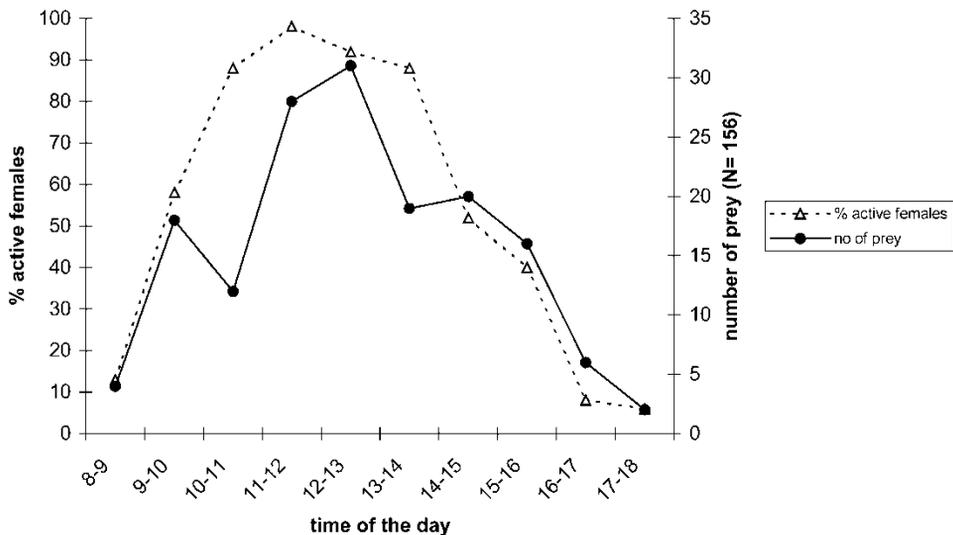


FIG. 2. Percentage of active females of *Bembix merceti* (outside the nests) and number of prey introduced in the nests as a function of the time of day.

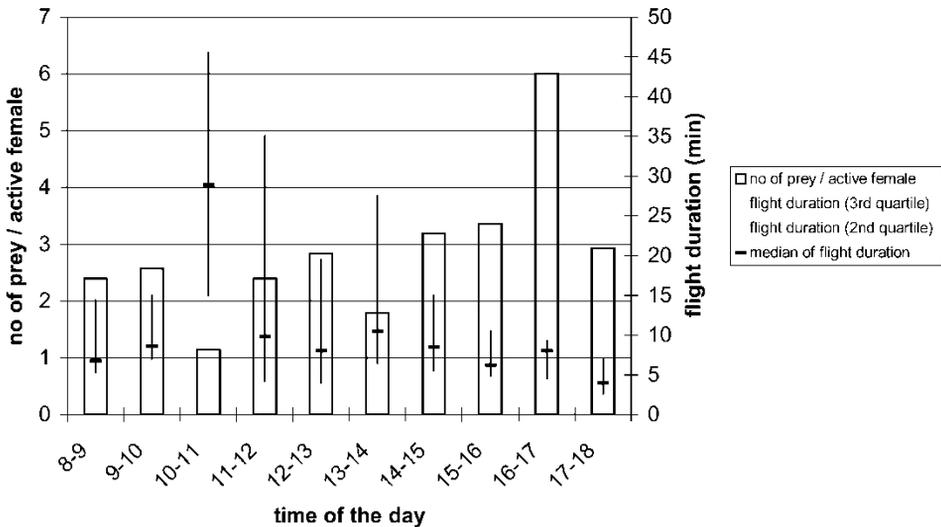


FIG. 3. Number of prey captured per active female (bars) and duration of provisioning flights (lines) as a function of the time of day for females of *Bembix merceti*. The length of the lines indicates the amplitude of the range between the 1st and 4th quartiles and the horizontal mark indicates the median of flight duration.

foraging females (figure 2) (Wald Wolfowitz Runs test, $z = -4.14$, $P < 0.001$). Moreover, flights tended to be slightly shorter during the day, with significant differences between flights at different periods (Chi-square test = 43.20, $P < 0.001$, $df = 9$). Flights were longer between 10:00 and 11:00 and shorter than expected in the last hour of the afternoon, and the range between the 1st and 4th quartiles was particularly broad between 10:00 and 14:00 (figure 3).

We obtained prey from 15 nests, collecting them from provisioning females returning to their nests ($N = 6$) or excavating the nests ($N = 9$). The distribution of specimens by family and year is shown in table 2. The 57 prey identified were as follows:

Bombyliidae

Anastoechus exalbidus (Wiedemann)

Anthrax virgo Egger

Aphoebantus scutellatus Loew

Exoprosopa jacchus (F.)

Hemipentes velutinus (Meigen)

Heteralonia rivularis (Meigen)

Thyridanthrax elegans (Wiedemann)

Usia aenea (Rossi)

Calliphoridae (unident.)

Muscidae

Musca domestica L.

Neomyia cornicina (F.)

Syrphidae (unident.)

Stratiomyidae

Sargus cuprarius (L.)

Tabanidae

Haematopota csikii Szilády

Tachinidae (unident.)

Table 2. Prey of *Bembix merceti* removed from 15 nests in 1993 and 1994.

	1993 (nine nests)	1994 (six nests)	Total
Bombyliidae	21 (88%) (nine nests)	5 (15%) (four nests)	26 (46%)
Calliphoridae	–	6 (18%) (three nests)	6 (10%)
Muscidae	1 (4%)	16 (49%) (three nests)	17 (30%)
Syrphidae	–	3 (9%) (one nest)	3 (5%)
Stratiomyidae	–	1 (3%)	1 (2%)
Tabanidae	–	1 (3%)	1 (2%)
Tachinidae	2 (8%) (two nests)	1 (3%)	3 (5%)
Total	24 (100%)	33 (100%)	57 (100%)

The nests (figure 4a, b) were unicellular and the eight studied displayed a sharp turn (95–140°) in front of the actual cell. Table 3 shows all the characteristics of these nests. During provisioning, the cell was separated from the main burrow by an internal closure. Oviposition was performed on the first prey captured ($N=2$), which was placed with the ventral side upwards. The egg was deposited perpendicular to the prey, adhering at its posterior part to the pleural region of the prey. In one of the cells, the ‘pedestal’ prey had two wasp eggs.

None of the nine cells studied contained parasites. However, females of *Blakeius leopoldina* (Invrea) (Hymenoptera, Mutillidae) and *Holopyga chrysonota* Förster (Hymenoptera, Chrysididae) entered nests of *B. merceti*. Both could act as natural enemies of *Bembix merceti*. Also, a worker ant entered one of the nests being

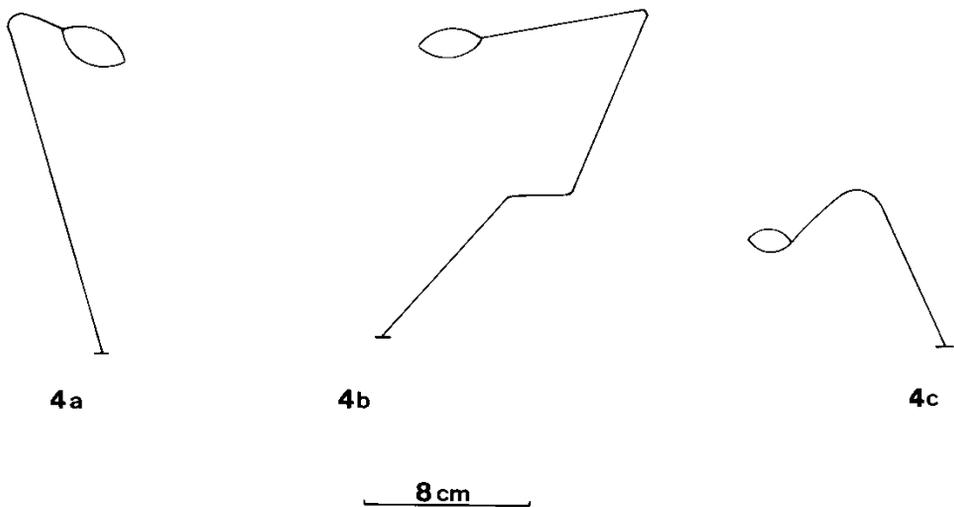


FIG. 4. Nests of *Bembix merceti* (a, b) and *B. zonata* (c) (main burrow and cell in superior view).

Table 3. Characteristics of the nests of *B. merceti* and *B. zonata*.

	Total length (cm)	Cell depth (cm)	Cell (l × d) (cm)
<i>Bembix merceti</i>			
Range	17–30.4	8.2–14.8	2.9–3.8 × 1.3–1.8
Mean	21.0	12.0	3.3 × 1.6
SD	4.4	2.0	0.3 × 0.2
N	8	8	8
<i>Bembix zonata</i>			
Range	13.1–17	8–11.5	2.2–3 × 1.2–1.3
Mean	15.1	9.8	2.6 × 1.3
SD	2.8	2.5	0.6 × 0.1
N	2	2	2

d, diameter; l, length.

provisioned and in which the female had deposited at least three prey. This nest was abandoned by the wasp and upon excavation revealed only one prey.

Bembix zonata Klug

Nest excavation was observed on three occasions, the females spending between 2 h 26 min and 5 h 11 min on this task. Two of the females finished the nest the day it was started, after which provisioning began; the third female excavated the nest over 2 days, the total active time devoted to this activity being 3 h 41 min. This female began provisioning on the fourth day after beginning the excavation. In all three cases, the females levelled the ground (between 6 and 11 min).

The females began their daily activity between 08:45 and 12:03 (median 11:00, $N=8$) and retired into the nests between 10:41 and 14:12 (median = 12:53, $N=9$), the period of their activity ranging between 49 and 127 min (mean = 116 min, $SD=63$, $N=8$). Provisioning was progressive (figure 1) and during the absence of the female, the nests remained closed. One female for which the complete provisioning activity for one larva was observed brought a total of 13 prey to the nest.

The duration of the provisioning flights ranged between 3.5 and 141.75 min (mean = 41.2 min, $SD=34.9$, $N=15$). The females that captured more prey in 1 day (between four and five per day) performed faster flights (mean = 34.3 min, $SD=25.8$, $N=9$) than those that captured only one prey (mean = 51.6 min, $SD=46.1$, $N=6$), although the differences were not significant (Kolmogorov-Smirnov test, $D=0.389$, $P>0.05$, $N_1=6$, $N_2=9$). The time spent by the female in the nest after introducing a prey varied between 57 and 279 s (mean = 139 s, $SD=89.4$, $N=11$).

In all cases observed, when daily provisioning had been completed and before entering the nest to spend the night, the females left for 6.25–93.25 min (mean = 31.4 min, $SD=29.8$, $N=8$). The duration of these final flights was not different from that of the provisioning ones (Mann-Whitney U test, $z=-0.645$, $P>0.05$, $N_1=15$, $N_2=8$).

The nests were unicellular (figure 4c) and their characteristics are shown in table 3. While one female was inside the nest after arriving with a prey, a female of *Parnopes grandior* (Pallas) (Hymenoptera, Chrysididae) entered and then left the nest rapidly, followed by the host. Although the wasp spent the night inside the nest, she abandoned the burrow the following day.

Discussion

In *Bembix merceti*, as provisioning progresses and as the requirements of the larvae for prey increases, the females begin their activity earlier in the morning, continue to be active for longer times, and capture their prey faster. The fact that their activity begins earlier suggests that, before leaving the nest, the female knows the needs of the larva for that day, adjusting the start of provisioning to the stage of larval development. Additionally, the fact that the provisioning flights become increasingly shorter over successive days indicate that the duration of provisioning tours are not determined by varying difficulties in finding and catching prey. If prey availability were the only factor determining flight duration, this would be more or less the same on the different days of provisioning a given nest. The 'acceleration' in provisioning even seems to affect the time that the females remained in the nest to deposit their prey, which is reduced when provisioning occurs faster. Tengö *et al.* (1996), studying a different pattern of behaviour in *Bembix rostrata* L., also reported a greater speed in homing time as a function of the day of the provisioning cycle. Although in the case of *B. zonata* the data about provisioning are insufficient, the results obtained do suggest a situation similar to that reported for *B. rostrata*.

The number of prey captured per active female is smaller during the morning, and increases slightly (but not significantly) towards the afternoon; this is paralleled by a decrease in the duration of the provisioning flights (figure 3). Nevertheless, since the number of foraging females is greater between 10:00 and 14:00, the total number of prey contributed during this period is higher, and this could explain the conclusion of Nielsen (1945) (and other earlier authors), who reported that in *Bembix rostrata*, prey capture mainly takes place during the morning.

An interesting aspect is the fact that the females of both species carried out a final daily flight that was not related to provisioning. Perhaps when they have finished contributing the daily quota of prey, and before closing the nests, they spend some time feeding. Also, the existence of long foraging flights, which were especially abundant between 10:00 and 14:00, suggests that the wasps may also feed when on provisioning flights, mainly within that 4-h period. For other sphecid species, different authors (Evans and O'Neill, 1988; Asís *et al.*, 1996) have reported feeding flights or especially long flights at the beginning and end of each day.

Tengö *et al.* (1996) found that in *Bembix rostrata* the females perform many visits to the nest without contributing prey, in contrast with *B. merceti* and *B. zonata*, where most flights are for provisioning. This discrepancy could be due to the fact that the females of *B. rostrata* (like other species of the genus—see Evans, 1966) periodically remove the remains of prey (Nielsen, 1945; Tengö *et al.*, 1996), whereas this does not seem to be the case in either of the two species studied here. It would be logical to assume that in species that carry out nest cleaning the female would visit the nest on a regular basis.

In general, the nests of many species of *Bembix* do not appear to display a well-defined structure; the changes in tunnel direction are usually determined by the nature of the soil and by the presence in it of stones, roots, etc. However, in certain species, such as *Bembix belfragei* Cresson, *B. occidentalis* Fox, *B. pallidipicta* Smith (Evans, 1957, 1966) and *Bembix variabilis* Smith (Evans and Matthews, 1973), the nests show peculiar characteristics. The sharp turn observed in all the nests of *B. merceti* seems to be well established and could be considered as a specialization; even in nest 7 (figure 4B), in which the main gallery showed a curve constructed to circumvent a stone, the usual turn was also conserved; Evans (1957, 1966) reported

the existence of similar nests in a Nearctic species, *Bembix texana* Cresson. Both in *B. merceti* and in *B. zonata*, the nests are fairly shallow (9–12 cm); this situation is also seen in the rest of the European species studied, with the exception of *Bembix olivacea*, whose females excavate deeper (20–22 cm) nests (Grandi, 1961).

Abandonment of the nest in response to the entry of worker ants has been reported in *Bembix multipicta* Smith (Cane and Miyamoto, 1979). These authors also detected aggressive behaviour in the wasps against ants, accompanied by closure of the entrance, although in *B. merceti* only abandonment of the nest was observed. In *B. zonata* we also observed abandonment of the nest during an early stage of provisioning, as a result of the entry of a chrysidid female in the gallery.

Both chrysidids and mutillids are frequently cited as natural enemies of species of *Bembix* (Bohart and MacSwain, 1940; Evans, 1957, 1966, 1976; Grandi, 1961; Evans and Matthews, 1973; Evans *et al.*, 1982; Asís *et al.*, 1992). However, the presence of miltogramine larvae in the nests analysed was not observed. The larvae of these Diptera are relatively frequent in the cells of *Bembix* and have been found in all European species studied in detail (Nielsen, 1945; Grandi, 1961; Larsson, 1986; Asís *et al.*, 1992), as well as in several Nearctic (Evans, 1957, 1966, 1970; McCorquodale, 1986; Spofford *et al.*, 1989), Neotropical (Genaro, 1995) and Australian species (Evans and Matthews, 1973). In many cases, perhaps due to the progressive type of provisioning, they do not prevent the larvae from completing their development. However, they doubtless make the female contribute more prey (delaying the end of the cycle) or reduce the food available for the larva, with the corresponding costs.

In general, females of *Bembix* show little specificity with regard to the prey they capture within a fairly broad range (generally between 7 and 12 different families; Evans, 1957, 1966, Evans and Matthews, 1973, Lane *et al.*, 1986). Analysis of the prey captured in two different years by females of *Bembix merceti* seems to confirm the opportunistic nature of prey selection since whereas in 1993 nearly 90% of the prey were bombylids, in 1994 the prey from this family fell to only 15% of the total.

Judging by the data obtained in the present study and those provided by Asís *et al.* (1992), both *B. merceti* and *B. zonata* nest in small or 'diffuse' aggregations. This situation, among European species, would be similar to that observed for *Bembix flavescens bolivari* Handlirsch, *B. oculata* Panzer, and perhaps *B. sinuata* Panzer (Asís *et al.*, 1992), and would be in contrast to species nesting in denser aggregations usually observed for *Bembix rostrata* (Nielsen, 1945; Larsson, 1986; Tengö *et al.*, 1996).

Nest excavation can apparently be completed in a single day by both species (although in one female of *Bembix zonata* it lasted for 2 days), generally starting during the morning hours. This situation is also seen in *B. sinuata* (Asís *et al.*, 1992), *B. tarsata* (Grandi, 1961) and in different American species (Evans, 1966; Alcock and Gamboa, 1975). Nevertheless, this apparently contrasts with what is seen for *B. rostrata*, whose females take several days to construct a nest and mainly carry out this task during the afternoon (Nielsen, 1945: 63, 94).

On considering the table of character states proposed by Evans (1957: 219), *B. merceti* shows many primitive characters (six out of the eight evaluated). Only the observed levelling behaviour and perhaps the final closure of the nest also seem to occur in *B. zonata*. In general, European species of the genus show many primitive characters in comparison with the apparently more specialized Nearctic ones. Only *B. rostrata* and *B. olivacea* show several specialized traits, nest cleaning being

outstanding in the former species and oviposition in empty cells in the latter. However, it should be stressed that the nesting behaviour of European species is much less known than that of Nearctic species. More data, above all concerning levelling and nest closure, the possible failure to perform temporary closures and the variety of nesting sites, would be necessary to obtain reliable conclusions in this respect.

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