SALVATORE VICIDOMINI

Dipartimento di Zoologia Università Federico II, Via Mezzocannone, 8 - 80134 Napoli - Italy

Biology of *Xylocopa* (*Xylocopa*) *violacea*, (L., 1758): Giant Nest! (Hymenoptera: Apidae)

ABSTRACT

The present paper aims to find an explanation for the presence of exceptionally long and branched nests in the Xylocopini species. Two giant nests of *Xylocopa violacea* (L., 1758), excavated in a *Prunus persica* trunk, were found in 1994: M94/1 and M94/2. The former was formed by seven tunnels, four of which were ascending and 111 mm in average length, and 3 were descending and 108 mm in average length; the total length of the nest was 795 mm. M94/2 showed 9 tunnels, 7 of them were ascending and 98 mm in average length, and 2 were descending and 66 mm in average length; the total length of the nest was 856 mm. Nests of similar or slightly larger sizes have been reported for *X. frontalis* (social and multivoltine), *X. hirsutissima* (social and multivoltine), *X. subvirescens* and *Lestis bombylans* (communal nesting and multivoltine). Giant nests are common in both social and multivoltine species, since the founder female is helped by the daughters of the 1st generation in the construction of the cells of the 2nd generation, nest lengthening, and even oviposition. Moreover, the nest can be reused for several years and therefore subjected to further lengthening. The explanation for these two giant nests is not simple for the following reasons: 1) *X. violacea* is considered by all the authors as univoltine and solitary without any mother-daughters interaction; 2) the M94 nests were excavated in 1994, and therefore cannot be the result of lengthening due to its reuse; 3) the M94 nests had an entrance each, and therefore cannot be the fortuitous, or otherwise, result of the mergence of two or more nests. Therefore, five hypotheses are here formulated, based on my 10-year observations and literature data on this and other co-generic species. The main conclusion is that it is necessary to reconsider the whole life cycle of *X. violacea*, by carrying out further investigations on the life of the founder female after the nest has been completed, as well as on the fecundity of the Xylocopini species from the evolutionary standpoint.

Key Words: Nest-morphometrics, giant branched-nest, Xylocopini, Southern-Italy, Apidae.

INTRODUCTION

The Xylocopini tribe (Apidae: Xylocopinae) shows remarkable uniformity of nesting behavior and nest morphostructures. *Lestis* (~2 species) and *Xylocopa* (~730) nest by excavating tunnels with their jaws in rotten wood (trunks, branches or artificial substrates as poles, pylons, etc.) or vegetable pre-existing cavities (cane or bamboo internodes, flower stalks and herba-

ceous plants filled with soft pith); for this reason, these species are referred to as "large carpenter bees"; the only exceptions are represented by the *Proxylocopa* species (~23), which only secondarily acquired the habit of hypogean nesting. The energetic cost is very low when the nest is built in a pre-existing cavity (e.g.: MALYSHEV, 1931; HURD & MOURE, 1963; SAKAGAMI & LAROCA, 1971; ROUBIK, 1989; MINCKLEY, 1994; VICIDOMINI, 1995, 1996, in press). Therefore, the Xylocopini species adapt themselves easily to new types of substrate. However, nest morphology of artificial origin is very uniform and simple. In fact, nests in canes or bamboos are always linear (unbranched). The same morphology characterizes the nests excavated in poles and pylons, since their very narrow circumference does not allow branching, and the three-dimensional nest development (e.g.: MAETA *et al.*, 1985; VICIDOMINI, 1996, in press). Conversely, branched nests are widespread among all the species nesting in trunks. In the study area, where almost exclusively poles are present, the *Xylocopa* (*Xylocopa*) *violacea* (L., 1758) typical nest morphology is characterized by one tunnel ascending and the other descending, lying on the same longitudinal axis, parallel to the major pole axis. In 1994, two giant branched nests (M94/1, 2) were found, one with seven tunnels and the other with nine.

The purposes of this paper are the following: a) to describe the morphometry of the *X. violacea* M94 nests, comparing them with those excavated in poles and canes, and with those reported in literature; b) to analyze the most branched nests reported in literature for other Xylocopini species; c) to give a tentative explanation for the occurrence of the exceptionally branched nests reported in literature and by me for *X. violacea* and the other species.

MATERIALS AND METHODS

The observations were carried out from 1986 to 1994, for a total of 1200 hours, 800 of them in the first six months of each year. The study area is cultivated with fruit trees and vegetables, and it is located in Nocera Superiore (Agro Nocerino Sarnese Valley: Campania: Italy. U.T.M.: 33TVF70. N 40°44'; E 14°41'. Altitude: 60 m. a.s.l. Extension: 4660 m^2).

In the periods 1986-1992 and 1994-1995 all the nests present in the study area were taken away and studied; sampling for 1993 was incomplete. The following nests were analyzed: 67 in dried canes from *Arundo donax,* placed horizontally to the ground, 8 in vertical poles fixed in the ground, 1 in a dried branch, 1 in a horizontal pole, 1 in a dead and rotten tree (branch), 2 (branched) in a dried and rotten trunk. For canes, the total lengths of the nest-con-

taining cavities that were formed by 1 to 3 internodes were measured. Eight qualitative and quantitative parameters were determined in branched and unbranched nests: wood condition (M: completely rotten. Me: externally rotten. 1/2M: upper half of the substrate length rotten. 1/4M: the upper quarter of the substrate length rotten. B: good conditions); species of the plant containing the nest (C.s.: *Castanea sativa*; P.c.: *Prunus cerasus*); height of the substrate; depth of the entrance (vestibule); length of the ascending (A) and descending (D) branches of the nest (vestibule excluded); diameter and circumference of the substrate at the entrance level. By adding the length of the vestibule to those of the tunnels, the total length of the nest was obtained. Some authors have measured the volume of the tunnels in cm^3 (e.g.: SAKAGAMI & LAROCA, 1971). However, this parameter, as well as in part the entrance diameter, is strongly influenced by the size of the carpenter bee rather than by its fecundity, voltinism, probable reuse of the nest and social interactions, as instead happens for the nest total length and the tunnel numbers. Therefore, I did not determine the volume of the *X. violacea* nests, since it does not come within the scope of present investigation. Additional measurements were performed only for the tunnels of the M94 nests: distances between tunnels; distance between the first (and the last) tunnel and the proximal wall of the trunk; inside diameters. Poles and canes are artificial substrates because they are used by farmers to support and align the plants. All the observations were carried out causing the minimum stress to the nesting individuals.

For bibliographical data collecting, only the papers containing photos, drawings or explanations of nest architecture in several Xylocopini species were used. Papers in which the photos or drawings represented only a part of the nest, those which failed to indicate whether the nest had one or more entrances or did not identify the species which had constructed the nest and the papers that reported less than four branches, were usually omitted (Tab. 3).

RESULTS

GENERAL CONSIDERATION

X. violacea is commonly considered as a solitary and univoltine species. The nest is founded and developed by a single female. In this species, reproduction takes place only once in a year; the individuals mate in February-April; in April-June they nest, and the new generation emerges in June-August. No evidence either of interaction between mother and juveniles or of

Tab. 1 - Morphometry (in mm) of unbranched nests of *X. violacea* excavated in poles and branches (see Materials & Methods for the symbol used).

nest-code	year	wood conditions	sub stratum	height	length (A)	length (D)	circumference	diameter	vestibule	nest total lenght
M1	1986	Me	C.s.	1800	210	63	150	50	42	284
M4	1986	B	C.s.	1112	81	129	108	35	17	222
M7	1986	Me	C.s.	1485	105	160	172	53	22	275
M8	1986	Me	C.s.	1508	154	130	280	86	29	295
M1	1987	1/2M	C.s.	1571	210	110	130	40	25	331
M2	1987	1/4M	C.s.	720	-	245	110	30	19	265
M3	1987	M	P.c.	2360	210	125	210	65	100	344
M4	1988	B	C.s.	1641	42	126	97	30	20	179
M2	1990	Me	C.s.	2147	120	55	290	68	40	187
Mc	1991	M	P.c.	2946	125	180	118	41	21	316
P2	1988	B	C.s.	630	-	300	119	33	-	300

common nesting between mother and daughters has been reported in literature; the new generation will reproduce after winter, in the following summer; as many other co-tribal species, nests are reused (SAKAGAMI & LAROCA, 1971; BONELLI, 1976).

UNBRANCHED NESTS: POLES AND BRANCHES

The average length of the whole nest (tunnels+vestibule) was 272.50 mm (St. Dev. 55.21. Var. 3048.67). The average (A) length was 139.7 mm (St. Dev. 61.06. Var. 3728.75), and that of the (D) was 132.3 mm (St. Dev. 54.90. Var. 3014.23). As you can see, the (A)-(D) difference is negligible. The average circumference of the pole or branch was 162.2 mm (St. Dev. 68.93. Var. 4750.96). The maximum number of tunnels observed was 2, exactly lined up (Tab. 1).

CANES

The average length of the internode/s containing the nest (nest chamber) was 237.85 (St. Dev. 78.06. Var. 6092.92).

BRANCHED NESTS

M94/1 and 2 were found in September 1994 in a *Prunus persica* tree which had died in 1989. Up to that moment, the trunk had not harbored any nest of *X. violacea*, since all the dead trees in this area were continuously inspected during and after the nesting period. The nests total lengths was huge if compared to that of unbranched nests, being three times as long (Tab. 2). The

Tab. 2 - Complete biometry of the two M94-branched (giant) nests (Fig. 1).

Substrate (Trunk Condition; Trunk height)	*PRUNUS PERSICA* (M; 2111)	
Nest code	M94/1	M94/2
Hole diameter (Entrance depth = nest vestibule lenght)	11 (26)	11 (35)
Trunk circumference (Trunk diameter)	260 (65)	285 (97)
Length of (A) tunnel I (inner tunnel-diameter)	94 (14)	92 (14)
Length of (A) tunnel II (inner tunnel-diameter)	150 (14)	101 (14)
Length of (A) tunnel III (inner tunnel-diameter)	100 (14)	112 (14)
Length of (A) tunnel IV (inner tunnel-diameter)	100 (14)	121 (14)
Length of (A) tunnel V (inner tunnel-diameter)	Absent	108 (14)
Length of (A) tunnel VI (inner tunnel-diameter)	Absent	100 (14)
Length of (A) tunnel VII (inner tunnel-diameter)	Absent	55 (14)
Length of (D) tunnel I (inner tunnel-diameter)	155 (14)	43 (14)
Length of (D) tunnel II (inner tunnel-diameter)	75 (14)	89 (14)
Length of (D) tunnel III (inner tunnel-diameter)	95 (14)	Absent
Tunnels total lenght (nest total lenght: tunnels+vestibule)	769 (795)	821 (856)
Average length of (A) tunnels for each nest (D-tunnels)	111 (108)	98 (66)
Average length of (A) tunnels for both nests	103.0 (St. Dev. 22.75. Var. 517.6)	
Average length of (D) tunnels for both nests	91.4 (St. Dev. 40.85. Var. 1668.8)	
Distance between (A) tunnels I and II	2	1
Distance between (A) tunnels II and III	4	2
Distance between (A) tunnels III and IV	5	5
Distance between (A) tunnels IV and V		3
Distance between (A) tunnels V and VI		4
Distance between (A) tunnels VI and VII		1
Distance between (A) tunnel I and the trunk wall	110	108
Distance between the last (A) tunnel and the trunk wall	100	70
Distance between (D) tunnels I and II	3	4
Distance between the (D) tunnels II and III	4	
Distance between (D) tunnel I and the trunk wall	121	150
Distance between the last (D) tunnel and the trunk wall	106	105

trunks circumference was much larger than that of the poles. The (A) and (D) tunnels were much longer in unbranched nests (poles and branches) than in the branched ones (>36 mm). The depth of the entrance or vestibule did not show any differences between the two substrates. The M94 entrances had been excavated under two mushrooms which formed a kind of roof: those two sites were probably made particularly soft by the chemical action of the mushrooms. The number of tunnels was very large, 7 in M94/1 and 9 in M94/2. Each tunnel started from the vestibule, which was therefore very large but very short; the tunnels were not connected with one another; in addition, the nest was developed on several floors, as in a hemisphere, rather than on a single floor, as in a candelabrum (Fig. 1). The distances between tunnels are reported in Table 2.
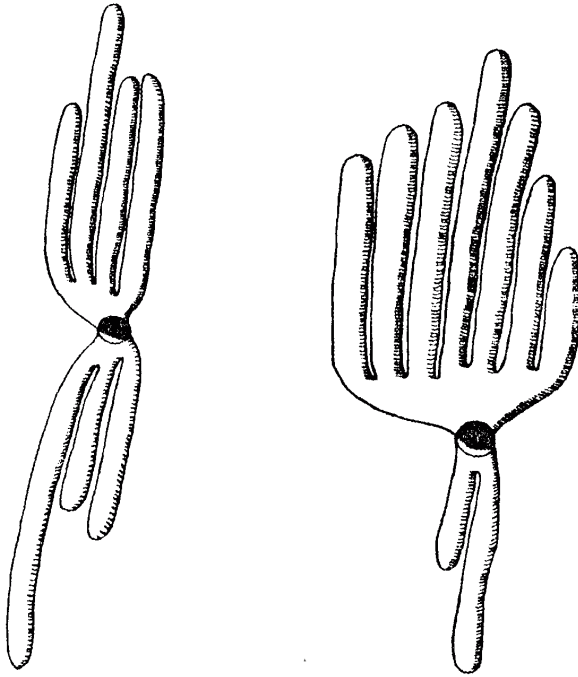
Figure 1: M94/1left; M94/2 right.

DISCUSSIONS

Results show that the difference in the total length of the nests excavated in canes and poles or in branches is so slight that it is probably due pure chance. In fact, if it is admitted that the shape and the size of the cells do not vary between these two kinds of substrate, then this difference must be ascribed almost exclusively to the presence of a vestibule in the nests in poles. In fact, a vestibule cannot be observed in canes, since the nest chamber is almost perfectly linear from the entrance as far as the end.

X. violacea nests excavated in natural substrates (Tab. 3) have the typical branched morphology of the Xylocopini nests (VAN LITH, 1955; CROVETTI, 1963). However, the tunnel numbers are much lower than the ones reported in this study for the M94 nests. Moreover, the VAN LITH (1955) and CROVETTI (1963) nests have two entrances, which might be the result of two subsequent nidifications by two different females. Unfortunately, in GRANDI (1962) there are many doubtful points. It is not known which species dug the 16 tunnels (*valga* or *violacea* ?), whether the nest had one or more entrances and hence whether one or more nidifications had occurred in the same site

Tab. 3 - Comparations among giant nests and some life cycle traits in Xylocopini (? = absence of data; M = multivoltine; U = univoltine; SOL = solitary; SOC = communal nesting).

Xylocopa	Subgenus	Voltinism	Sociality Type	Max N.° Branches	Total MM	N.° Entr.	Literature
X. imitator	Koptortosoma	M	SOL	6	400	1	ANZENBERGER, 1977
X. pubescens	Koptortosoma	M	SOC	8	?	1	VELTHUIS & GERLING, 1983
X. fimbriata	Megaxylocopa	?	?	9	?	1	SAGE, 1968
X. frontalis	Megaxylocopa	M	SOC	8	958	1	SAKAGAMI & LAROCA, 1971
X. frontalis	Megaxylocopa	M	SOC	15	?	4	HURD, 1958
X. frontalis	Megaxylocopa	M	SOC	10	?	1	CAMILLO & GAROFALO, 1989
X. augusti	Neoxylocopa	M	SOL	7	440	1	SAKAGAMI & LAROCA, 1971
X. brasilianorum	Neoxylocopa	?	SOC	3	349	1	SAKAGAMI & LAROCA, 1971
X. grisescens	Neoxylocopa	M	SOC	3	454	1	SAKAGAMI & LAROCA, 1971
X. grisescens	Neoxylocopa	M	SOC	8	366	1	CAMILLO & GAROFALO, 1982
X. hirsutissima	Neoxylocopa	M	SOC	11	680	1	SAKAGAMI & LAROCA, 1971
X. nigrocincta	Neoxylocopa	?	SOC	4	462	1	SAKAGAMI & LAROCA, 1971
X. sonorina	Neoxylocopa	M	SOC	5	622	1	GERLING, 1982
X. suspecta	Neoxylocopa	M	SOC	8	?	1	CAMILLO & GAROFALO, 1989
X. subvirescens	Schoenherria	?	?	11	?	1	SAGE, 1968
X. valga	Xylocopa	M	SOL	5	~ 456	1	MALYSHEV, 1931
X. valga	Xylocopa	M	SOL	10	?	1	MALYSHEV, 1931
X. violacea	Xylocopa	M	SOL	3	400	2	VAN LITH, 1955
X. violacea	Xylocopa	M	SOL	5	?	2	CROVETTI, 1963
X. violacea	Xylocopa	M	SOL	16	?	?	GRANDI, 1962
X. virginica	Xylocopoides	U	SOC	5	274	1	BALDUF, 1962
Lestis aeratus		?	SOC	6	720	1	HOUSTON, 1992
L. aeratus		?	SOC	9	733	1	HOUSTON, 1992
L. bombylans		M	SOC	10	795	1	HOUSTON, 1992

of the trunk, whether it was a new nest or a nest reused for many years; in addition only a part of the nest is described and photographed (2 trunk sections). For these reasons, the giant nest described by GRANDI (1962), though outstanding for size and tunnel numbers, was not taken into consideration for the present comparison. Therefore, the largest nest of X. violacea, excavated by a single female, would be M94/2 of this paper.

Literature data show the occurrence of as many as four nests of four Xilocopini species, provided with a single entrance, having more than nine branches: X. frontalis 10; X. hirsutissima 11; X. subvirescens 11; Lestis bombylans 10 (Tab. 3). However, one 1 m-nest (8 tunnels) of the first species is the longest among those considered. As far as the two other species are concerned, the length of the X. hirsutissima and L. bombylans nest is 680 and 795 mm, lower than that of M94/2; unfortunately, for X. subvirescens, SAGE (1968) did not report either the nest length nor voltinism or the possible mother-

daughters interactions. Both *X. hirsutissima* and *X. frontalis* (perhaps the largest Apoidea species) essentially show multivoltinism, i.e. the founder female nests two or more times in a year in the same nest, making it longer and more branched every time; also in *L. bombylans*, communal nesting and multivoltinism are reported; these phenomena are widespread in many tropical species (e.g.: Sakagami & Laroca, 1971; Bonelli, 1974, 1976). Moreover, in lengthening the nest after the first generation, the founder female can avail herself of the cooperation of the daughters, which take part actively in the work of cleaning up and lengthening the nest, and therefore, excavation is not carried out by the only founder female. As in all the Xylocopini species, the old nests are regularly reused year after year, and therefore the giant nests reported in literature might also be the result of several years of nesting (e.g.: Gerling *et al.*, 1989). This does not help in elucidating the occurrence of the M94 in *X. violacea* (solitary and univoltine specie), in particular if one considers that: a) the nests do not communicate with each other, but each of them is endowed with an entrance, and the entrance distance is 1250 mm; b) they are not reused nests, since the earliest nesting was observed in the 1994-summer. Some hypotheses (H) in order to explain M/94's existence, can be set forth; they are reported hereafter, together with the relative arguments for and against, resulting from 10-year and literature data.

I (H) – M94 might have been built by more than a female, not daughters –
In the large number of papers on the nests and the life cycle of these species, this phenomenon has never been reported. Moreover, in *Xylocopa* species, intraspecific parasitism is greatly developed; in this area it resulted to be the main cause of *X. violacea* pre-imaginal mortality (pathogens and congenital malformations excluded), and appears to be correlated with nest density in this area; *X. violacea* females defend their nests even violently against conspecific individuals which come too near the entrance (Vicidomini & Picariello, 1994). Some investigators report cases of more nests in the same substrate, also at a short distance from each other, and nests having tunnels in common as the result of the fortuitous tunnel mergence during excavation: *X. confusa* (Jacobson, 1927); *X. varipuncta, X. frontalis* (Hurd, 1958); *X. augusti, X. hirsutissima,* (Hurd & Moure, 1960); *X. californica, X. tabaniformis* (Crudden, 1966); *X. fimbriata* (Janzen, 1966); *X. virginica, X. sauteri, X. aestuans, X. carinata, X. combusta* (Bonelli, 1976); *X. imitator, X. nigrita, X. flavorufa* (Anzenberger, 1977); *X. tranquebarorum* (Maeta *et al.*, 1985) *X. valga, X. violacea* (Dindo *et al.*, 1992; personal observations). However, cases of common nesting starting from a single entrance have not been reported in the Xylocopini species. Moreover, Janzen (1966) observed a very aggressive

behavior in females of *X. fimbriata* nesting at a very close distance from each other in the same substrate, which resulted in the departure of one of the contenders and decreased possibility of intra-specific-klepto-parasitism of their own nests.

II (H) – M94 might have been excavated by a bivoltine founder female, which after the brood emergence (July?), would have nested again, lengthened the nest herself – My and licterature data seem to confirm the *X. violacea* univoltinism. Only FRIESE (1923) (see DUHAYON & RASMONT, 1993 hypothesis) reported occasional bivoltinism in the mediterranean area. In this case, the nest might have been excavated by a mutant founder female, but the energetic cost would be very high, the nest being excavated by the only founder female. In view of the M94/2 length, the number of the cells might be three times the average fecundity of *X. violacea* in this area (7.45 x 3 = 22.35, VICIDOMINI, 1996, in press); however, this would involve a huge reproductive effort that cannot be sustained by a carpenter bee which produces the largest eggs among all insects (IWATA & SAKAGAMI, 1966), considering energy investment in eggs and excavation of the whole nest (LOUW & NICOLSON, 1983). Conversely, if the hypothetical number of deposited eggs is intermediate between 7.45 and 22.35, then it cannot be understood why tunnels are excavated and not used. The same considerations can be brought forward if fecundity remains unchanged (7.45).

III (H) – M94 might be the result of the founder female-daughters cooperation in nest excavation. This hypothesis also includes bivoltinism suggested in the II (H) – All the observations reported in literature are against this hypothesis. However, both literature data and my 80 nest-observations do not provide any data on an aspect of *X. violacea* life cycle: the behavior and the life length of the founder female after the nest completion. Only one of the nests studied in these years was followed up in July 1994, after its completion. The founder female remained in the nest until the brood emergence (about 20 days). For more than 20 times, she was seen flying out, feeding on *Althea rosea* flowers and flying back to the nest; when she entered the nest, she approached a juvenile (of unidentified sex), and the two came into contact with oral portions, in a way similar to the trophallaxis observed in *Xylocopa* genus (e.g.: MICHENER, 1972; GERLING *et al.*, 1981, 1983; VELTHUIS & GERLING, 1983; VAN DER BOM & VELTHUIS, 1988). Moreover, 75% of the nests completed, taken away and studied in the laboratory, still contained the founder female after 1 to 5 days from their completion. In some cases, the founder female had remained inside the nest for 12 or even 21 days. This would imply that canes and poles nests are reused by the founder female in cooperation with their daughters after the soons emergence.

IV (H) – In nests excavated in natural substrates (middle-large trunks), females lay a larger number of eggs than in nests excavated in artificial substrates (poles and canes) – This hypothesis implies that, in natural substrates the female fecundity would be increased, since the larger size of the nest would allow the construction of a larger number of pedotrophic cells. Conversely, artificial substrates would limit the number of eggs that a female can lay. The percentage of the substrate occupied by 9 out of 11 unbranched nests in poles was of only 9-21% of the whole substrate length; in the other 2 nests, instead, the percentage was very high (37-48%), but they might be subjected to further lengthening. In canes, in order to lengthen the nest chamber (more than 1000 mm) females should only break down 3-4 nodes, connecting 4-5 internodes with a negligible energetic cost; in contrast, in this area, 80% of the nests in canes was established in the 1st internode, 18.5% in the 1st and 2nd internodes and only 1.5% also in the 3rd; however, no difference in fecundity was observed in the nests in canes of different length. One might suppose that oxygen may be better distributed in the deep cells of a branched nest than in those of an unbranched one of the same length, and that there is a limit to the length of the tunnels/internodes harboring the cells, or, rather, to the number of cells per tunnel/internode. However, this problem might be removed, by starting excavation of a new nest after the first has been completed, so that oxygen distribution is optimal and the reproductive success of the female (egg number) is not reduced of necessity. The theoretical considerations on cell number already made for the II-(H) are valid for this hypothesis; in addition, the maximum number of generations per year in *Xylocopa* species is 4 (BONELLI, 1976), and therefore, on the basis of the data on the average fecundity of the multivoltine species reported by VICIDOMINI (1996, in press), it can be drawn that a female might produce even 23 cells per year. This would be practically the theoretical value for *X. violacea*, if the M94/2 tunnels had been full of cells, which seems unlikely also in the case of two following generations without the cooperation of the daughters (see II-(H)).

V (H) – Multibranched nests are a device against predators or parasites – *X. violacea* nest predators in this area are: *Podarcis sicula*, *Crematogaster scutellaris* and *X. violacea* itself. The last two species would not have any difficulty in identifying the tunnels containing larval food, eggs and larvae, since they follow the intense scent emitted by the nests. Neither is *P. sicula* likely to be led astray by a highly branched nest, since perhaps it also makes use of the smell sense to recognize tunnels at a short distance; moreover, none of the predators and parasites identified for the other Xylocopini species might be

deceived by the presence of greatly branched nests (see: GERLING *et al.*, 1989; HOUSTON, 1992).

These data shows that I- and V-(H) are to be rejected. The II-(H) would be plausible, if an intermediate fecundity value (7.45-22.35) is supposed; however, the question of the useless, energetically expensive, tunnel construction, would remain unsolved. The same considerations can be made for the IV-(H); moreover, to draw any conclusion, oxygen permeation at the bottom of the Xylocopini nests (wood or canes) should be studied. Though all literature data are against the III-(H), my observations, as well as FRIESE's (1923) and DUHAYON & RASMONT (1993) results, seem to support it. Moreover, it does not show any inconsistency as the II- and IV-(H), but it is based on a trait never considered of the *X. violacea* life history. A plausible explanation may be that several factors may have contributed to them, multivoltinism, mother-daughters cooperation, optimization of oxygen permeation in the nest. The simultaneous occurrence of these three factors may explain the occurrence of the M94 nests, the absence of unbranched nests showing a total length higher than 450 mm (except a 598 mm nest in cane, 12 cells), and the averagely shorter length of the tunnels of the M94 nests in respect to unbranched nest tunnels.

CONCLUSIONS

The following conclusions can be drawn: a) the number of giant nests, which are not reused nests, is too low to draw general conclusions on the phenomenon with certainty; b) a deeper insight into III- and IV-(H) (or the H-resulting) is necessary in order to get more data on the average fecundity in giant nests and the minimum oxygen required by the larvae at the bottom of the tunnels; c) investigations should be carried out on the phenotypic and phylogenetic limits of the maximum fecundity in uni- and multivoltine, communal and solitary nesting Xylocopini species, in order to establish whether the theoretical fecundity expressed in the II- and IV-(H) are realizable; d) the natural history of the nest after its completion should be extensively studied, evaluating the founder female life length after nest completion, identifying and quantifying the possible interactions between mother and juveniles, etc. More importantly, this comparative study shows that, in several even widespread and well-studied species, literature data are generalized and/or takes for granted, though a long-term study may not have been carried out on the species itself. The occurrence of giant nests in social and/or multivoltine species can be easily explained, also in view of their probable reuse. In contrast,

the occurrence of *X. violacea* M/94 nests (univoltine-solitary?) remains completely unexplained; further investigations are necessary, since the most plausible hypotheses (III and IV) would involve a complete re-examination of *X. violacea* life cycle. In fact, only a long-term study will allow us to detect variants of life history strategies and tactics of a species, as has happened for two extensively studied species: *X.* (*Koptortosoma*) *pubescens* and *X.* (*Ctenoxylocopa*) *sulcatipes* (e.g.: GERLING *et al.*, 1981, 1983, 1989; VELTHUIS & GERLING, 1983; VAN DER BLOM & VELTHUIS, 1988; STARK, 1992; HOGENDOORN & VELTHUIS, 1995).

RIASSUNTO

BIOLOGIA DI *XYLOCOPA* (*XYLOCOPA*) *VIOLACEA*, (L., 1758): NIDI GIGANTI! (HYMENOPTERA: APIDAE)

Oggetto di questo studio è quello di trovare una spiegazione alla presenza di nidi eccezionalmente ramificati e lunghi nelle specie della tribù Xylocopini in seguito al ritrovamento di due nidi giganti in *X. violacea* nel 1994, scavati in un tronco di *Prunus persica*: M94/1 e 2. Il primo è dotato di 7 tunnel, di cui 4 ascendenti con una lunghezza media di 111 mm e 3 discendenti aventi una lunghezza media di 108 mm; la lunghezza totale del nido era di 795 mm. M94/2 è dotato di 9 tunnel, 7 ascendenti con una lunghezza media di 98 mm, e 2 discendenti con una lunghezza media di 66 mm; la lunghezza totale del nido era di 856 mm. Nidi di dimensioni simili o di poco maggiori sono stati riportati per *X. frontalisi*, *X. hirsutissima* e *Lestis bombylans* (comunali e multivoltine) e *X. subvirescens*. Per le specie sia sociali che multivoltine l'esistenza di nidi giganti è normale in quanto la fondatrice viene coadiuvata dalle figlie della I generazione nella costruzione delle celle della II generazione, per lo scavo del nido (ampliamento) ed anche nella deposizione delle uova. Inoltre il nido può essere usato per vari anni e quindi soggetto ad ulteriore ampliamento. I due nidi giganti M94 di *X. violacea* non trovano una semplice spiegazione per i seguenti motivi: 1) *X. violacea* è ritenuta da tutti gli autori univoltina e solitaria, senza interazione madre-figlie; 2) M94 non sono il frutto di ampliamenti dovuti al riuso; 3) M94 non sono il risultato casuale o non della fusione di due o più nidi. Vengono, per questi motivi, effettuate 5 ipotesi e vengono portati dati pro e contro di esse derivanti da 10 anni di studi su *X. violacea* e dalla letteratura disponibile sugli Xylocopini. La principale conclusione è che è necessaria una rivisitazione dell'intero ciclo vitale di *X. violacea*, di un'indagine sulla vita della fondatrice dopo l'ultimazione del nido (aspetto totalmente trascurato in bibliografia) e di un esteso studio sulla fecondità delle specie di Xylocopini in chiave evolutiva.

Parole Chiave: *Xylocopa violacea*, morfometria nidi, nidi ramificati giganti, nidi giganti di Xylocopini, Sud-Italia.

REFERENCES

ANZENBERGER G., 1977 - Ethological study of african carpenter bees of the genus *Xylocopa* (Hymenoptera, Antophoridae) - *Z. Tierpsychol.,* 44: 337-374.

BONELLI B., 1974 - Osservazioni eco-etologiche sugli Imenotteri Aculeati dell'Etiopia (VI) - *Boll. Ist. Entomol. Grandi Bologna,* 32: 105-132.

BONELLI B., 1976 - Osservazioni eco-etologiche sugli Imenotteri Aculeati dell'Etiopia (VII) - *Boll. Ist. Entomol. Grandi Bologna,* 33: 1-31.

CROVETTI A., 1963 - Contributi alla conoscenza dell'entomofauna di *Ferula communis* L. IV - *Studi Sassaresi Sez*. III, 11: 651-908.

CRUDDEN R.W., 1966 - Observations on the behavior of *Xylocopa c. californica* and *X. tabaniformis orpifex* (Hymenoptera: Apoidea) - *Pan-Pacific Entomol.,* 42(2): 111-119.

DINDO M.L., CAMPADELLI G., GAMBETTA A., 1992 - Note su *Xylocopa violacea* L. e *Xylocopa valga* Gerst. (Hym. Anthophoridae) nidificanti nei tronchi della foresta fossile di Dunnarobba (Umbria) - *Boll. Ist. Entomol. Grandi Bologna,* 46: 153-160.

DUHAYON G., RASMONT P., 1993 - Phenologie des grands apoïdes (Hymenoptera, Apoidea: *Bombus, Xylocopa, Habropoda*) dans le Massif des Maures (France, Var) - In: Lhonore J., Maurin H., Guilbot R., Keith P., Eds - Inventaire et cartographie des invertebres comme contribution a la gestion des milieux naturels francais - Actes Sem. Mans 6-7/Nov./1992; (Mus. Nat. Hist. Nat. Paris) Collec. Patr. Natur. Ser. Patr. Ecol., 13: 165-168.

FRIESE H., 1923 - Die europaischen Bienen (Apidae) - W. Cruyter, Berlin & Leipzig. 456 pp.

GERLING D., HURD P.D., HEFETZ A., 1981 - In-nest behavior of the carpenter bee, *Xylocopa pubescens* Spinola (Hymenoptera: Anthophoridae) - *J. Kansas Entomol. Soc.,* 54(2): 209-218.

GERLING D., HURD P.D., HEFETZ A., 1983 - Comparative behavioral biology of two middle east species of carpenter bees (*Xylocopa* Latreille) - *Smith. Contr. Zool.,* 369: 1-28.

GERLING D., VELTHUIS H.H.W., HEFETZ A., 1989 - Bionomics of the large carpenter bees of the genus *Xylocopa* - *Ann. Rev. Entomol.,* 34: 163-190.

GRANDI G., 1962 - Contributi alla conoscenza degli Imenotteri Aculeati (XXXI) - *Boll. Ist. Entomol. Grandi Bologna,* 26: 69-88.

HOGENDOORN K., VELTHUIS H.H.W., 1995 - The role of young guards in *Xylocopa pubescens* - *Ins. Soc.*, 42(4): 427-448.

HOUSTON T., 1992 - Biological observations of the Australian green carpenter bees, genus *Lestis* (Hymenoptera: Anthophoridae: Xylocopini) - *Rec. W. Australian Mus.,* 15(4): 785-798.

HURD P.D., 1958 - Observations on the nesting habits of some new world carpenter bees with remarks on their importance in the problem of species formation (Hymenoptera: Apoidea) - *Ann. Entomol. Soc. Amer.*, 51: 365-375.

Hurd P.D., Moure J.S., 1960 - A new world Subgenus of bamboo-nesting carpenter bees belonging to the Genus *Xylocopa* Latreille - *Ann. Entomol. Soc. Amer.*, 53: 809-821.

HURD P.D., MOURE J.S., 1963 - A classification of the large carpenter bees (Xylocopini) (Hym.: Apoidea) - *Univ. Calif. Publ. Entomol.,* 29: 1-365.

IWATA K., SAKAGAMI S.F., 1966 - Gigantism and dwarfism in bee eggs in relation to the mode of life, with notes on the number of ovarioles - *Jap. J. Ecol.,* 16(1): 4-16.

JACOBSON VON E., 1927 - Fauna sumatrensis. Xylocopinae - *Suppl. Entomol.,* 16: 93-103.

JANZEN D.H., 1966 - Notes on the behavior of the carpenter bee *Xylocopa fimbriata* in Mexico. (Hymenoptera: Apoidea) - *J. Kansas Entomol. Soc.,* 39(4): 633-641.

LOUW N.G., NICOLSON S.W., 1983 - Thermal energetics and nutritional consideration in the foraging and reproduction of the carpenter bee *Xylocopa capitata* - *J. Entomol. Soc. South Afr.,* 46(2): 227-240.

MAETA Y., SAKAGAMI S.F., SHIOKAWA M., 1985 - Observation on nest aggregation of the taiwanese bamboo carpenter bee *Xylocopa* (*Biluna*) *tranquebarorum tranqueba-*

rorum. (Hymenoptera: Anthophoridae) - *J. Kansas Entomol. Soc.,* 58(1): 36-41.

MALYSHEV S.J., 1931 - Lebensgeschichte der holzbienen, *Xylocopa* Latr. (Apoidea) - *Z. Morphol. Oekol. Tiere,* 23: 754-809.

MICHENER C.D., 1972 - Direct food transferring behavior in bees. *J. Kansas Entomol. Soc.,* 45(3): 373-376.

MINCKLEY R.L., 1994 - Comparative morphology of the mesosomal gland in male large carpenter bees (Apidae: Xylocopini) - *Biol. J. Linn. Soc.,* 53: 291-308.

ROUBIK D.W., 1989 - Ecology and natural history of tropical bees - Cambrige University Press. 514 pp.

SAGE R.D., 1968 - Observations on feeding, nesting, and territorial behavior of carpenter bees Genus *Xylocopa* in Costa Rica - *Ann. Entomol. Soc. Amer.,* 61(4): 884-889.

SAKAGAMI S.F., LAROCA S., 1971 - Observations on the bionomics of some neotropical Xylocopinae bees, with comparative and biofaunistic notes. (Hymenoptera, Anthophoridae) - *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.,* 18(1): 57-127.

STARK R.E., 1992 - Cooperative nesting in the multivoltine large carpenter bee *Xylocopa sulcatipes* Maa: do helpers gain or lose to solitary females? - *Ethology,* 91: 301-310.

VAN DER BLOM J., VELTHUIS H.H.W., 1988 - Social behavior of carpenter bee *Xylocopa pubescens* (Spinola) - *Ethology,* 79: 281-294.

VAN LITH J.P., 1955 - Ean nest van *Xylocopa violacea* (L.) - *Entomol. Berich.,* 15: 452-454.

VELTHUIS H.H.W., GERLING D., 1983 - At the brink of sociality: interactions between adults of the carpenter bee *Xylocopa pubescens* Spinola - *Behav. Ecol. Sociobiol.,* 12: 209-214.

VICIDOMINI S., PICARIELLO O., 1994 - Observations on the nest defence behaviour in the female carpenter bee, *Xylocopa violacea* L., 1758 (Hym.: Apidae) - *Boll. Zool. Suppl.,* 61: 80.

VICIDOMINI S., 1995 (in press) - Biology of *Xylocopa* (*Xylocopa*) *violacea* (L., 1758): nest morphology (Hymenoptera: Apidae) - *Atti Soc. Ital. Sci. Nat. Milano,* 136(20):

VICIDOMINI S., 1995 - Biologia di *Xylocopa* (*Xylocopa*) *violacea* (L., 1758): specie di fiori visitate dalla femmina (Hymenoptera: Apidae) - *Entomologica Bari,* 29: 211-226.

VICIDOMINI S., 1996 (in press) - Biology of *Xylocop* (*Xylocopa*) *violacea* (L., 1758): in nest ethology - Ital. J. Zool. (= Bool. Zool.), 63.