Solitary Hymenoptera Aculeata Inhabiting Trap-Nests in Lithuania: Nesting Cavity Choice and Niche Overlap

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Abstract: The study has been carried out during the years 1989-2002 in five localities of Lithuania, using bundles of 25-35 internode fragments of *Phragmites australis* stems as trap-nests. We obtained 3237 nests of 33 identified solitary wasp and bee species. The dominant species were as follows: Symmorphus allobrogus (2030 nests), Ancistrocerus antilope (260), S. murarius (222), Discoelius zonalis (139), S. bifasciatus (115), Trypoxylon figulus (99), S. debilitatus (52), A. trifasciatus (40), T. clavicerum (39 nests), T. minus (36), S. crassicornis (36), and S. gracilis (33). The other 21 wasp and bee species built less than 30 nests each. We appraised the differences in the species preference for the inner diameter of the trap-nest, height above the ground, orientation of the wall, on which the trap-nest was situated, and the nest entrance direction. The studied species formed groups with median nesting cavity diameter of 2.5-4.0 mm (Chelostoma maxillosum, Hylaeus communis, Passaloecus corniger, S. bifasciatus, S. debilitatus, T. clavicerum, T. minus), 4.6-5.2 mm (A. trifasciatus, D. dufourii, S. allobrogus, S. gracilis, T. figulus), and 5.5-6.5 mm (A. antilope, A. nigricornis, D. zonalis, S. crassicornis, S. murarius, Osmia rufa), possibly having synusial dependence on exit holes of particular xylophagous beetles. Most wasp species had wide range of the used nesting cavity diameter and considerable niche overlap. However, some congeneric species seem to avoid competition by different nesting cavity diameter preferences, as D. dufourii and D. zonalis, or S. allobrogus and S. bifasciatus. On the other hand, some other congeneric species that use the same nesting cavity diameter (S. allobrogus and S. gracilis, S. bifasciatus and S. debilitatus, S. crassicornis and S. murarius) coexist in the same habitat due to other niche differences, as different prey.

Key words: Hymenoptera, xylicolous solitary Aculeata, trap-nest, nesting preferences, niche overlap.

Introduction

Solitary predator wasps are potentially useful biological control agents for herbivorous insects such as leafrollers (Jennings, Houseweart, 1984; Collins, Jennings, 1987; Harris, 1994) or larvae of leaf beetles (Bohart et al., 1982; Smiley, Rank, 1986; Sears et al., 2001). On the other solitary trap-nesting Hymenoptera hand, Aculeata are known as bioindicators sensitive to environmental change (Tscharntke et al., 1998). Some species of them have been reported as declining in e.g. southern Finland, probably caused by anthropogenous decrease in nesting sites, their foraging habitats and/or changes of climate (Pekkarinen, Hulden, 1991).

Xylicolous solitary wasps and bees nest in wood borings and other naturally pre-existing tubular cavities (Benno, 1957, 1958; Krombein, 1960, 1964; Parker, Bohart, 1966; Danks, 1970;

Tsuneki, 1973a, 1973b; Matthews, 2000) and construct their larval cells from the inside outwards, partitioning it with the mud or leaf diaphragms and provisioning the cells with stung insects or pollen as food for their larvae. They easily accept artificially prepared trapnests such as burrows drilled into the wood blocks or bundles of cut hollow reed or plastic tubes, greatly facilitating the study of their biology (Fye, 1965; Evans, 1966; Collins, Jennings, 1984; Cowan, 1991; Itino, 1992; McCallan, 1993; Gathmann, Tscharntke, 1999; Münster-Swendsen, Calabuig, 2000).

Availability of suitable nesting cavities is a significant limiting factor of solitary Aculeata (Danks, 1971b). Some studies included a trapnest survey with analysis of different nesting cavity parameters (Koerber, Medler, 1958; Danks 1971a; Thiede, 1981; Gathmann et al., 1994; Weaving, 1994; Steffan-Dewenter, 2002).

It is shown that nesting parameters largely overlap among species, indicating existence of competition (Cooper, 1953; Itino, 1997).

The aims of the present study were as follows:

1) to assess the spectrum of aculeate Hymenoptera species inhabiting trap-nests in the study sites; 2) to determine their preferences in choice of nesting cavity with respect to its inner diameter, height above the ground, the orientation of the wall with trap-nest and direction of the cavity entrance.

We tested three assumptions: 1) the preferred diameter of trap-nests, used by xylicolous wasps and bees, corresponds with the diameter of burrows of particular xylophagous insect species; 2) species with similar ecology (e.g. congenerics) avoid competition by choosing different nesting cavity parameters, and 3) in contrast, coexistence of species with similar nesting preferences is maintained by other differences in their ecology.

Methods

The field research was carried out in 1989-2002 in the localities Varnupys (Anykščiai district, 55°24'N 25°17'E), Bilšiai (Molėtai district, 55°08'N 25°16'E), Kaunas city (54°54'N 23°54'E), Merkinė (Varėna district, 54°10'N 24°10'E), and Papiškiai (Pasvalys district, 55°56'N 24°16'E), Lithuania. The wasp nests were collected using bundles of 25-35 internode fragments of Phragmites australis stems of various natural length (19-299 mm) and diameter (1.9-8.6 mm) as trap-nests. The latter were placed at height 60 - 330 cm on the walls of different orientation of old wooden or (in Papiškiai) daubed buildings with natural colonies of solitary wasps and bees. The trapnests were exposed from the middle of May until the middle of August.

Most of material (ca. 95% of all nests) was obtained in the localities Varnupys, Bilšiai and Papiškiai, where dominating habitat was mixed forest of southern taiga type (*Pinus*, *Picea*, *Betula*, *Alnus*, *Salix*, *Quercus*) with wet sedgy pastures. The trap-nests in Kaunas and Merkinė were exposed in the green zone of settlements. Every 7–14 days stem fragments with

Every 7–14 days stem fragments with completed wasp or bee nests, having visible

external plugs, were substituted with new fragments of similar diameter. As a result, the trap-nests were never completely occupied, and wasp and bee females could have a possibility to build multiple nests during the summer season in the internodes with preferred parameters. The stems with nests were dissected, their inner diameters were measured. After examination, nests with larvae were stored in laboratory thus allowing them to develop up to the adult stage in order to identify the wasp or bee species.

The examination was made using a binocular microscope MBS-10, at a magnification 8× to 56×. Hymenoptera were identified using keys by Tobias and Kurzenko (1978), and Schmid-Egger (1994). Borings of xylophagous beetles – potential providers of the natural nesting cavities in the walls of buildings at study sites – were identified using key by Ehnström and Axelsson (2002). Nest data were processed using the database-managing system Microsoft Access 2000.

Since we used natural reed stem internodes that were not standard, we could not state that some of them were preferred or avoided purely due to the analysed parameters: their diameter, height, or orientation. Therefore, we analysed only the occupied internodes and we compared the species preference for particular parameter in relation to that of the rest species nesting in the trap-nests, but not in relation to the available empty internodes. The reed stems that were not occupied during the whole summer season were excluded from the analysis.

The frequency distribution by 0.5 mm diameter class of the analysed internodes that were occupied by wasps and bees as nesting cavities (Fig. 1) did not essentially differ from that of empty reed internodes in the other studies with application of similar trap-nest type (compare with Gathmann et al., 1994: Fig. 1).

To assess the choice differences and niche overlap, the nests were classified into seven trap-nest diameter classes with range 1 mm (less than 3 mm, 3-4, 4-5, 5-6, 6-7, 7-8, and over 8 mm) and three height classes (0-1, 1-2, and over 2 m).

We expressed the species relative preference for or avoidance of particular class of trap-nest diameter, height and orientation as an estimator PA (preference/avoidance estimator), a natural logarithm of ratio of the number of species nests in particular class to the number of the species nests in the remaining classes, divided by the corresponding ratio of the remaining species:

$$PA = \ln \left(\frac{n_{11} / n_{12}}{n_{21} / n_{22}} \right),$$

were n_{11} – number of nests of a particular species in particular trap-nest class, n_{12} – number of that species nests in the remaining trap-nest classes, n_{21} – number of the remaining species nests in the particular trap-nest class, n_{22} - number of the remaining species nests in the remaining trap-nest classes. For instance, if a wasp species had 20 nests, out of which 10 (50%) were in particular trap-nest class and 10 in the other classes, while the rest wasp species had 200 nests, out of which 10 (5%) in that class and 190 nests in the rest classes, the PA of that species was $\ln((10/10)/(10/190)) = \ln(19) = 2.94$. Thus, estimator was positive if the species preferred the trap-nest class, in comparison with the remaining wasps and bees, and negative if the species used the trap-nest class in lesser extent than the remaining ones.

The significance of estimator PA was assessed

using
$$\Box^2 2\Box 2$$
 test (*df*=1) (Fleiss, 1981):

$$\chi^2 = \frac{(n_{11} + n_{12} + n_{21} + n_{22})(|n_{11}n_{22} - n_{12}n_{21}| - 0.5(n_{11} + n_{12} + n_{21} + n_{22})^2)}{(n_{11} + n_{12})(n_{21} + n_{22})(n_{11} + n_{21})(n_{12} + n_{22})}$$

abbreviations as in the previous formula.

In order to assess the species niche overlap within the diameter and height classes, we used the simplified Morisita-Horn index (Krebs, 1998):

$$C_{H} = \frac{2\sum_{i}^{k} (n_{1i} / n_{1})(n_{2i} / n_{2})}{\sum_{i}^{k} (n_{1i} / n_{1})^{2} + \sum_{i}^{k} (n_{2i} / n_{2})^{2}},$$

where n_{1i} and n_{2i} –number of nests of the two compared species in the ith diameter or height class, n_1 and n_2 – total number of nests of the two compared species, k – number of diameter or height classes, correspondingly.

The difference in the diameter and height class usage frequency, showing lesser niche overlap between pairs of species, was assessed using γ^2 criterion (Lakin, 1990):

$$\chi^{2} = \frac{(n_{1} + n_{2})^{2}}{n_{1}n_{2}} \left(\sum_{i}^{k} \frac{n_{1i}^{2}}{n_{1i} + n_{2i}} - \frac{n_{1}^{2}}{n_{1} + n_{2}} \right),$$

abbreviations as in the previous formula. The significance of differences (p<0.05, df=6 for trap-nest diameter and df=2 for height) was probability estimated using distribution calculator (Chi² distribution) of the computer program StatSoft STATISTICA, release 6.0.

the preferences of nest site Assessing orientation, we separately analysed the direction of the surface (wall of the building), on which the trap-nest was placed, and direction of the nest entrance. Dependently on the way of attachment, the latter was directed either to the same side as the wall surface, or it made an angle of 90 degrees with the latter. The preferences were assessed separately for the north-south (N/S; percentage of S-directed nests) and the east-west (E/W; percentage of Edirected nests) directions. For instance, in the N/S analysis, all nests were classified into two classes: one having north (N, including NE and NW), the other south (S, including SE and SW) orientation. The nests oriented strictly to the west or east were considered as having "no estimable N/S orientation" and excluded from the N/S analysis. The same method was used for the E/W analysis, for both the nesting surface and the nest entrance directions.

Height and orientation of some nests obtained in earlier years of the study was not estimated, therefore they were excluded from corresponding analyses.

The calculation was done using the computer program Microsoft Excel 2000.

Results and Discussion

We obtained 3237 nests of 33 identified xylicolous solitary wasp and bee species, out of them 15 Eumeninae, 11 Crabronidae, and 7 Apidae. The list of species was nearly three times shorter than in the studies, where trapnests of similar type were applied to explore possibilities of solitary Hymenoptera usage for bioindication of agricultural and grassland habitats (Gathmann et al., 1994; Tscharntke et al., 1998; Gathmann and Tscharntke, 1999; Steffan-Dewenter, 2002). Particularly striking was nearly five times shorter list of bees. On the other hand, the number of eumenine species in our study (15) was nearly as high as in the

mentioned studies (up to 17). We may suggest that forest and wet meadow habitats of the biome of southern taiga type have noticeably different from the agricultural and grassland habitats spectrum of xylicolous wasp and bee species.

The dominant species were as follows: Symmorphus allobrogus (2030 nests),

Ancistrocerus antilope (260), S. murarius (222), Discoelius zonalis (139), S. bifasciatus (115), Trypoxylon figulus (99), S. debilitatus (52), A. trifasciatus (40), T. clavicerum (39), T. minus (36), S. crassicornis (36), and S. gracilis (33). The other 21 wasp and bee species built less than 30 nests each.

Table 1. Diameter of trap-nests used by xylicolous solitary wasp and bee species (mm).

| Species | n | Mean±SE | Range |
|----------------------------|------|-----------------|---------|
| Eumeninae | 2977 | | |
| Ancistrocerus antilope | 260 | 6.46 ± 0.04 | 5.0-8.5 |
| Ancistrocerus gazella | 1 | 6.1 | |
| Ancistrocerus nigricornis | 23 | 5.57 ± 0.20 | 4.0-7.1 |
| Ancistrocerus parietinus | 3 | 5.30 ± 0.98 | 4.5-6.9 |
| Ancistrocerus parietum | 1 | 5.0 | |
| Ancistrocerus trifasciatus | 40 | 4.96 ± 0.13 | 3.0-6.8 |
| Discoelius dufourii | 19 | 4.72 ± 0.13 | 3.8-6.0 |
| Discoelius zonalis | 139 | 5.55 ± 0.08 | 3.4-8.0 |
| Euodynerus notatus | 3 | 6.07 ± 1.02 | 5.0-7.7 |
| Symmorphus allobrogus | 2030 | 5.15 ± 0.02 | 2.8-8.1 |
| Symmorphus bifasciatus | 115 | 4.09 ± 0.06 | 3.0-6.3 |
| Symmorphus crassicornis | 36 | 5.81 ± 0.13 | 4.6-8.0 |
| Symmorphus debilitatus | 52 | 3.63 ± 0.07 | 2.7-4.9 |
| Symmorphus gracilis | 33 | 4.99 ± 0.12 | 3.4-6.3 |
| Symmorphus murarius | 222 | 5.94 ± 0.05 | 4.2-7.8 |
| Crabronidae | 204 | | |
| Passaloecus corniger | 13 | 2.72 ± 0.22 | 1.9-5.0 |
| Passaloecus eremita | 1 | 3.2 | |
| Passaloecus gracilis | 1 | 2.1 | |
| Passaloecus monilicornis | 3 | 3.10 ± 0.12 | 3.0-3.3 |
| Pemphredon lugens | 1 | 4.8 | |
| Psenulus fuscipennis | 9 | 4.87 ± 0.21 | 4.0-6.0 |
| Psenulus pallipes | 1 | 4.2 | |
| Rhopalum clavipes | 1 | 4.8 | |
| Trypoxylon clavicerum | 39 | 3.13 ± 0.12 | 2.0-5.1 |
| Trypoxylon figulus | 99 | 4.97 ± 0.07 | 3.0-6.8 |
| Trypoxylon minus | 36 | 3.84 ± 0.09 | 2.8-5.0 |
| Apidae | 56 | <u></u> | |
| Chelostoma fuliginosum | 6 | 3.00 ± 0.00 | 3.0 |
| Chelostoma maxillosum | 19 | 4.04 ± 0.29 | 3.0-8.6 |
| Hylaeus annulatus | 1 | 3.0 | |
| Hylaeus communis | 11 | 3.75 ± 0.18 | 3.0-4.6 |
| Hylaeus minutus | 1 | 4.3 | |
| Hoplitis adunca | 1 | 6.3 | |
| Osmia rufa | 17 | 6.21 ± 0.18 | 5.0-7.3 |

Legends: The frequency distribution of all nests by 0.5 mm diameter class is presented in Fig. 1. The average and range of the trap-nest diameter of all species are in Table 1. Median and quartiles

that more evidently show the cavity diameter of 50% and 100% of nests of the most common species are in Fig. 2.

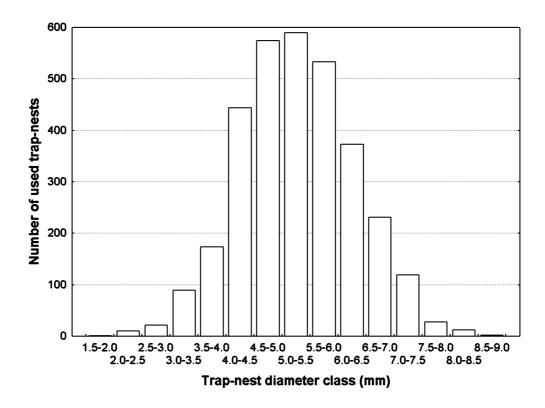


Figure 1. Frequency distribution of trap-nests, used for nesting by xylicolous solitary wasps and bees in 0.5 mm diameter classes (*N*=3237).

Some species seemed to be very flexible in their nesting cavity choice, using wide range of diameters, as *Chelostoma maxillosum* (3.0-8.6 mm) and *S. allobrogus* (2.8-8.1 mm). However, in overall, most of them demonstrated selectivity. Out of the most common species that made more than 10 nests, six used only three diameter classes; other five species used

only four diameter classes. Five most selective species (*D. dufourii*, *Passaloecus corniger*, *S. gracilis*, *T. clavicerum*, and *T. minus*) made more than 88% of their nests in two adjacent diameter classes; *P. corniger*, *D. dufourii* and *S. debilitatus* showed an apparent fidelity (more than 67% of nests) to a single diameter class (Table 2).

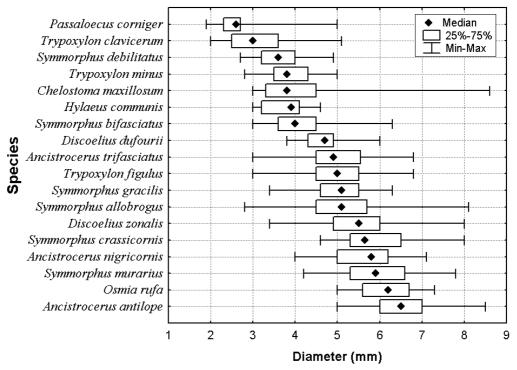


Figure 2. Diameter (median and quartiles) of trap-nests, used for nesting by xylicolous solitary wasp and bee species that have made more than 10 nests with estimated diameter.

Table 2. Choice of nesting cavity by diameter: percentage of species nests in each trap-nest diameter class. Brackets: estimator PA (see Methods), only presented if usage frequency of the class is significantly different (p<0.05, χ^2 2×2 test, df=1) from that of the remaining species. For highly significantly different frequencies (p<0.001) PA in bold. Only species with more than 10 studied nests in the table.

| | | Diameter o | class | | | | | |
|----------------------------|------|---------------------|---------------------|----------------------|---------------------|----------------------|-----------|-------|
| Species | n | <3 mm | 3-4 mm | 4-5 mm | 5-6 mm | 6-7 mm | 7-8 mm | >8 mm |
| Ancistrocerus antilope | 260 | - | _ | 1.5 (-3.6) | 28.1 (-0.3) | 51.5 (1.9) | 17.7 | 1.2 |
| • | | | | | , | • | (2.2) | (2.4) |
| Ancistrocerus nigricornis | 23 | _ | 13.0 | 17.4 | 39.1 (n/s) | 26.1 | 4.3 | - |
| Ancistrocerus trifasciatus | 40 | 5.0 | 10.0 | 47.5 (0.6) | 22.5 | 15.0 | - | - |
| Chelostoma maxillosum | 19 | 15.8 (2.1) | 47.4 (2.1) | 31.6 | _ | _ | - | 5.3 |
| | | , | , | | | | | (3.6) |
| Discoelius dufourii | 19 | _ | 10.5 | 68.4 (1.5) | 21.1 | _ | - | - |
| Discoelius zonalis | 139 | - | 2.2 (-1.7) | 25.9 | 51.1 (0.7) | 12.2 | 8.6 (1.0) | _ |
| Hylaeus communis | 11 | 18.2 (2.3) | 54.5 (2.4) | 27.3 | - | _ | - ` ´ | _ |
| Osmia rufa | 17 | - | - | 5.9 (-2.1) | 35.3 | 41.2 (1.2) | 17.6 | - |
| v | | | | . , | | , , | (1.8) | |
| Passaloecus corniger | 13 | 84.6 (5.6) | 7.7 | 7.7 | _ | _ | - | - |
| Symmorphus allobrogus | 2030 | 0.4 (-2.5) | 7.8 (-0.7) | 39.5 (0.9) | 36.8 (0.3) | 13.7 (-0.6) | 1.7 (- | 0.1 |
| | | , , | ` , | ` ′ | ` , | , , | 1.4) | |
| Symmorphus bifasciatus | 115 | 3.5 | 48.7 (2.3) | 38.3 | 8.7 (-1.7) | 0.9 (-3.2) | - | _ |
| Symmorphus crassicornis | 36 | _ | - | 19.4 | 44.4 | 33.3 (0.9) | 2.8 | - |
| Symmorphus debilitatus | 52 | 13.5 (2.0) | 67.3 (3.0) | 19.2 (-0.7) | _ | - | - | - |
| Symmorphus gracilis | 33 | - | 6.1 | 42.4 | 48.5 | 3.0 (-1.9) | - | - |
| Symmorphus murarius | 222 | - | _ | 12.6 (-1.3) | 44.1 (0.5) | 34.7 (1.1) | 8.6 (1.0) | _ |
| Trypoxylon clavicerum | 39 | 51.3 (4.1) | 38.5 (1.7) | 7.7 (-1.8) | 2.6 (-3.0) | - | - ` ´ | - |
| Trypoxylon figulus | 99 | 1.0 | 14.1 | 38.4 | 38.4 | 8.1 (-0.9) | - | - |
| Trypoxylon minus | 36 | 11.1 (1.7) | 55.6 (2.4) | 33.3 | - | - | - | - |
| All species | 3203 | 2.0 | 10.3 | 32.6 | 34.3 | 17.1 | 3.7 | 0.2 |

The preference for particular diameter class was assessed by the estimator PA and χ^2 2×2 test (see Material and Methods). The results revealed that even the users of wide range of diameters, as A. antilope, D. zonalis, S. allobrogus and S. bifasciatus, demonstrated preference for some diameter classes (PA positive) and avoided the other ones (P negative) (Table 2, numbers in brackets). For instance, A. antilope preferred trap-nests with diameter larger than 6 mm, in comparison with the other species, and avoided those of 4-5 mm, despite it was able to use them. S. allobrogus demonstrated obvious preference for the nesting cavities of 4-6 mm and apparently avoided those smaller than 4 mm and larger than 6 mm. S. bifasciatus showed strong preference to trapnests of 3-4 mm diameter. On the other hand, some species (A. nigricornis, S. gracilis, T. figulus) had no strongly expressed preference for any of the used trap-nest diameter classes, in comparison with the remaining species using them as well.

Study of the usage distribution between the diameter classes of 0.5 mm revealed that the highest number of species occupied the trapnests with 3.0-3.5, 4.0-5.5 and 6.0-6.5 mm diameter (Fig. 3). We could segregate the

eighteen most abundant species into three groups of the cavity diameter preference (Fig. 2), corresponding with burrows of the most common xylophagous inhabitants of the wooden buildings. The first group, having median diameter of the used trap-nests of 2.5-4.0 mm, included P. corniger, T. clavicerum, debilitatus, T. minus, Ch. maxillosum, Hylaeus communis, and S. bifasciatus. Possibly, these species naturally nest in narrow burrows of anobiid beetles. The second group, having median nesting cavity diameter of 4.6-5.2 mm, included D. dufourii, A. trifasciatus, T. figulus, S. gracilis, and S. allobrogus. Possibly, they use burrows of cerambycid beetle Hylotrupes bajulus, having similar diameter. The third group, having median nesting cavity diameter of included 5.5-6.5 mm. D. zonalis. crassicornis, A. nigricornis, S. murarius, Osmia rufa, and A. antilope. This group may be connected with the burrows of cerambycid Callidium violaceum, having width of 6-7 mm (Ehnström, Axelsson, 2002). The listed beetles commonly develop in dry wood of timbered buildings; they are common in the sites of our field research.

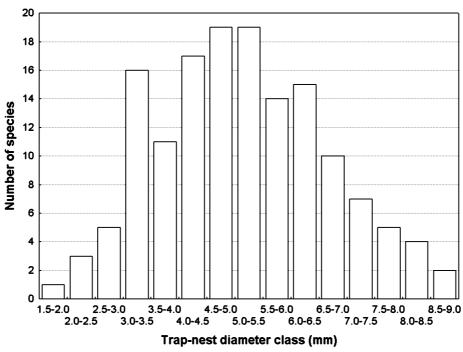


Figure 3. Number of xylicolous solitary wasp and bee species that have used each 0.5 mm diameter class of the trap-nests.

The above facts support our assumption, that each xylicolous solitary Aculeata species may have a synusial link to the exit holes of particular xylophagous insect species and use the trap-nests of diameter corresponding with its burrows. However, wide range of used diameters lets us raise an opposite assumption as well: most xylicolous aculeate species use for nesting the burrows of multiple xylophagous insects, having suitable range of diameters. Further studies are required to answer the question, what is the extent of dependence of

xylicolous aculeate species on particular xylophagous insect species.

The selectivity of the studied species to the trapnest height classes was less expressed than that to the diameter classes. Out of 12 species having more than 10 nests with measured height, six did not show significant preference to any height class. However, some species demonstrated significant differences from the rest, as *S. crassicornis*, *S. gracilis* and *S. murarius* preferably occupying higher than 2 m trap-nests (Table 3). In contrast, *S. allobrogus* preferred low positioned nesting cavities.

Table 3. Choice of nesting cavity by height of the trap-nest: percentage of species nests in each trap-nest height class. Brackets: estimator PA (see Material and Methods), only presented if the usage frequency of the class is significantly different (p<0.05, χ^2 2×2 test, df=1) from that of the remaining species. For highly significantly different frequencies (p<0.001) PA in bold. Only species with more than 10 studied nests having estimated trap-nest height in the table.

| | | Height class | | | | | | | | |
|------------------------|------|---------------------|---------------------|----------------------|--|--|--|--|--|--|
| Species | n | 0-1 m | 1-2 m | >2 m | | | | | | |
| Ancistrocerus antilope | 248 | 23.0 | 60.5 | 16.5 | | | | | | |
| Ancistrocerus | 20 | 25.0 | 55.0 | 20.0 | | | | | | |
| trifasciatus | | | | | | | | | | |
| Discoelius dufourii | 19 | 15.8 | 73.7 | 10.5 | | | | | | |
| Discoelius zonalis | 120 | 19.2 | 64.2 | 16.7 | | | | | | |
| Osmia rufa | 12 | 16.7 | 50.0 | 33.3 | | | | | | |
| Symmorphus | 1899 | 23.4 (0.4) | 64.6 | 12.0 (-0.7) | | | | | | |
| allobrogus | | | | | | | | | | |
| Symmorphus | 79 | 22.8 | 51.9 (-0.5) | 25.3 (0.7) | | | | | | |
| bifasciatus | | | | | | | | | | |
| Symmorphus | 35 | 8.6 | 31.4 (-1.4) | 60.0 (2.2) | | | | | | |
| crassicornis | | | | | | | | | | |
| Symmorphus gracilis | 33 | 27.3 | 36.4 (-1.1) | 36.4 (1.2) | | | | | | |
| Symmorphus murarius | 175 | 6.3 (-1.4) | 66.3 | 27.4 (0.8) | | | | | | |
| Trypoxylon | 12 | - | 83.3 | 16.7 | | | | | | |
| clavicerum | | | | | | | | | | |
| Trypoxylon figulus | 57 | 3.5 (-2.0) | 96.5 (2.8) | - | | | | | | |
| All species | 2709 | 21.3 | 63.8 | 14.8 | | | | | | |

The majority of species were inclined to occupy the trap-nests with southern and eastern exposition of the wall surface as well as the direction of the nest entrance (Table 4). Out of 11 species having more than 10 nests with estimated orientation class, four did not demonstrate any significant preferences, in comparison with the remaining species. Some other, as *S. bifasciatus*, *S. crassicornis* and *S. gracilis* seemed to avoid the dominating S and E

orientation (PA<0). Possibly, they were tolerant to the north and west orientation, thus avoiding competition with the dominant S. allobrogus. The latter species demonstrated significant preference for nesting cavities with southern wall surface and southern or eastern nest entrance direction (Table 4).

Comparison of the trap-nest diameter and height class choice frequencies, using the simplified Morisita-Horn niche overlap index (C_H) and χ^2

test, revealed broad overlap and little choice differences for most species pairs (Table 5). However, some of the latter showed comparatively low overlap and significant differences in their nesting cavity choice. Low value of the Morisita-Horn index and difference in the distribution of diameter or height class choice we interpret as a behavioural adaptation of species to avoid competition, leading to differentiation of niche.

Comparing the diameter classes, the average Morisita-Horn index was slightly higher in the congeneric pairs of species (mean \pm SE 0.58 \pm 0.06, n=22) than in the pairs from different genera (0.50 \pm 0.03, n=131), meaning that the species have wider niche overlaps with congenerics than with the rest. Consequently, the average competition for particular nesting cavity diameter classes is higher within genera than between them. This fact disagrees with our second assumption (see chapter "Introduction").

Table 4. Choice of nesting cavity by trap-nest exposition surface and nest entrance north-south (N/S) and east-west (E/W) orientation: percentage of species nests in S and E orientation classes. Brackets: estimator PA (see Material and Methods), only presented if usage frequency of the exposition class is significantly different (p<0.05, χ^2 2×2 test, df=1) from that of the remaining species. For highly significantly different frequencies (p<0.001) PA in bold. Only species with more than 10 studied nests having at least one estimable orientation class in the table.

| | Expo | sition surfa | ice | | Nest entrance | | | | | |
|------------------------|-------|----------------------|-------|----------------------|---------------|----------------------|------|----------------------|--|--|
| Wasp | N/S S | | E/W E | | N/S | S | E/W | E | | |
| | n | | n | | n | | n | | | |
| Ancistrocerus antilope | 183 | 87.4 | 170 | 56.5 | 174 | 76.4 | 179 | 56.4 (-0.5) | | |
| Ancistrocerus | 15 | 80.0 | 12 | 58.3 | 13 | 76.9 | 14 | 64.3 | | |
| trifasciatus | | | | | | | | | | |
| Discoelius dufourii | 16 | 93.8 | 8 | 62.5 | 8 | 75.0 | 16 | 87.5 | | |
| Discoelius zonalis | 104 | 87.5 | 81 | 60.6 | 91 | 72.3 | 94 | 70.2 | | |
| Osmia rufa | 9 | 88.9 | 12 | 75.0 | 12 | 58.3 | 9 | 88.9 | | |
| Symmorphus allobrogus | 1527 | 94.8 (1.4) | 1284 | 64.1 | 1369 | 82.2 (0.6) | 1442 | 71.2 (0.6) | | |
| Symmorphus bifasciatus | 61 | 75.4 (-1.2) | 64 | 57.8 | 56 | 58.9 (-1.0) | 69 | 63.8 | | |
| Symmorphus | 29 | 27.6 (-3.4) | 27 | 18.5 (-2.1) | 27 | 22.2 (-2.6) | 29 | 17.2 (-2.3) | | |
| crassicornis | | | | | | | | | | |
| Symmorphus gracilis | 26 | 73.1 (-1.3) | 24 | 29.2 (-1.4) | 26 | 50.0 (-1.3) | 24 | 12.5 (-2.7) | | |
| Symmorphus murarius | 149 | 85.9 (-0.6) | 166 | 71.1 (0.4) | 148 | 75.7 | 167 | 64.7 | | |
| Trypoxylon figulus | 57 | 78.9 (-1.0) | 49 | 73.5 | 53 | 86.8 | 53 | 43.4 (-1.0) | | |
| All species | 2176 | 91.0 | 1897 | 63.3 | 1977 | 78.9 | 2096 | 67.2 | | |

Table 5. Species niche overlap (simplified Morisita-Horn index C_H) in trap-nest diameter class (lower left part of table) and height class (upper right part of table). Values for the species pairs with significant differences in distribution between trap-nest diameter and height classes (p<0.05, χ^2 test, df=6 for diameter, df=2 for height) in bold. Only species with, correspondingly, more than 10 studied nests, or more than 10 nests having estimated trap-nest height in the table.

| | A. antilope | A. nigricornis | A. trifasciatus | Ch. maxillosum | D. dufourii | D. zonalis | H. communis | O. rufa | P. corniger | S. allobrogus | S. bifasciatus | S. crassicornis | S. debilitatus | S. gracilis | S. murarius | T. clavicerum | T. figulus |
|-----------------|-------------|----------------|-----------------|----------------|-------------|------------|-------------|---------|-------------|---------------|----------------|-----------------|----------------|-------------|-------------|---------------|------------|
| A. antilope | | | 0.99 | | 0.97 | 1.00 | | 0.95 | | 1.00 | 0.98 | 0.68 | | 0.87 | 0.96 | 0.91 | 0.86 |
| A. nigricornis | 0.79 | | _ | | | | | | | | | | | | | | |
| A. trifasciatus | 0.43 | 0.77 | | _ | 0.95 | 0.99 | | 0.97 | | 0.98 | 0.99 | 0.72 | | 0.92 | 0.94 | 0.87 | 0.81 |
| Ch. maxillosum | 0.02 | | | | _ | | | | | | | | | | | | |
| D. dufourii | 0.15 | | | | | 0.99 | | 0.89 | | | 0.92 | | | | 0.96 | | |
| D. zonalis | 0.62 | 0.91 | 0.78 | 0.26 | 0.66 | | | 0.94 | | 1.00 | 0.97 | 0.68 | | 0.85 | 0.97 | 0.94 | 0.89 |
| H. communis | 0.01 | 0.35 | 0.54 | 0.99 | 0.53 | 0.22 | | | | | | | | | | | |
| O. rufa | 0.97 | 0.88 | 0.53 | 0.05 | 0.27 | 0.77 | 0.04 | | | 0.92 | 0.99 | 0.87 | | 0.96 | 0.96 | 0.85 | 0.74 |
| P. corniger | 0.00 | 0.05 | 0.17 | 0.36 | 0.10 | 0.04 | 0.38 | 0.01 | | | | | | | | | |
| S. allobrogus | 0.53 | 0.88 | 0.95 | 0.49 | 0.85 | 0.93 | 0.42 | 0.66 | 0.08 | | 0.96 | 0.62 | | 0.83 | 0.95 | 0.92 | 0.89 |
| S. bifasciatus | 0.09 | 0.50 | 0.72 | 0.96 | 0.72 | 0.42 | 0.94 | 0.16 | 0.17 | 0.63 | | 0.79 | | 0.95 | 0.95 | 0.86 | 0.77 |
| S. crassicornis | 0.84 | 0.96 | 0.74 | 0.18 | 0.52 | 0.92 | 0.14 | 0.92 | 0.03 | 0.86 | 0.31 | | | 0.88 | 0.77 | 0.61 | 0.44 |
| S. debilitatus | 0.01 | 0.31 | 0.40 | 0.93 | 0.39 | 0.15 | 0.97 | 0.03 | 0.29 | 0.31 | 0.90 | 0.09 | | | | | |
| S. gracilis | 0.40 | 0.81 | 0.88 | 0.42 | 0.85 | 0.94 | 0.36 | 0.56 | 0.07 | 0.96 | 0.58 | 0.80 | 0.26 | | 0.83 | 0.69 | 0.57 |
| S. murarius | 0.90 | 0.95 | 0.65 | 0.12 | 0.42 | 0.89 | 0.09 | 0.96 | 0.02 | 0.80 | 0.25 | 0.99 | 0.06 | 0.73 | | 0.96 | 0.88 |
| T. clavicerum | 0.02 | 0.21 | 0.29 | 0.75 | 0.21 | 0.11 | 0.79 | 0.04 | 0.82 | 0.20 | 0.58 | 0.07 | 0.74 | 0.16 | 0.06 | | 0.97 |
| T. figulus | 0.45 | 0.87 | 0.93 | 0.56 | 0.85 | 0.92 | 0.51 | 0.59 | 0.09 | 0.99 | 0.70 | 0.81 | 0.41 | 0.97 | 0.75 | 0.27 | |
| T. minus | 0.01 | 0.37 | 0.59 | 0.98 | 0.60 | 0.25 | 0.99 | 0.05 | 0.28 | 0.47 | 0.98 | 0.17 | 0.96 | 0.41 | 0.11 | 0.70 | 0.55 |

However, some congeneric species pairs had different ($C_H < 0.5$) nesting cavity diameter choice (Table 5, lower left part): A. antilope -A. trifasciatus, S. allobrogus- S. debilitatus, S. bifasciatus – S. crassicornis, S. bifasciatus – S. murarius, S. crassicornis – S. debilitatus, S. debilitatus - S. gracilis, S. debilitatus - S. murarius, T. clavicerum- T. figulus. Lesser but significant differences ($C_H < 0.67$) were found between congeneric species D. dufourii - D. zonalis, S. allobrogus - S. bifasciatus, S. bifasciatus - S. gracilis, T. clavicerum - T. minus, T. figulus - T. minus. The single example of congeneric species pair with significantly different ($C_H < 0.67$) height class choice was S. allobrogus - S. crassicornis (Table 5, upper right part). It means that some congeneric species use different nesting cavity parameters, thus avoiding competition.

Interestingly, *D. dufourii* and *D. zonalis*, having similar body size and the same type of prey, preferred nesting cavities of significantly different diameter (Fig. 2; Table 5). Another

example is *S. allobrogus* and *S. bifasciatus* that partly use the same prey (Budrienė, 2003) but utilize nesting cavities of different diameter. These examples support our second assumption. On the other hand, the congeneric species that have close nesting cavity preferences may coexist due to other niche differences. The examples in our data set are the species pairs *S. allobrogus – S. gracilis, S. bifasciatus – S. debilitatus* and *S. crassicornis – S. murarius*. Each of them uses the same or close nesting cavity diameter (Fig. 2) but different prey (Budrienė, 2003). Thus, our third assumption may be credible as well.

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