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Biological observations on the digger-wasp *Passaloecus eremita* Kohl (Hym., Sphecidae, Pemphredoninae)

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ABSTRACT

Passaloecus eremita Kohl inhabits both deserted burrows of xylophageous insects and eaves made of *Phragmites.* The cells are arranged in a linear fashion, and the nests are terminated by an empty vestibular cell. Both the partitions and the final closure of the nests are made of fluid coniferous resin. Only the rather specialized mandibles are used in handling the resin. A barrier of small resin drops surrounds the entrance of the nest, probably serving as an obstruction for parasites. The prey consists of wingless specimens of *Cinara pinea* (Mordv.) which are paralyzed by bites just behind the head.

By rearing the material it was stated that males emerge about two days before the females. The distribution of the sexes in the nests is dependent on both the number and the size of the cells. Generally fertilized eggs (∼ females) are laid in the inner and larger cell(s). The actual sexproportion of *P. eremita* was 0.7 ♀♀/♂♂, but this ratio might very well depend on environmental factors. The number of cells per nest is positively correlated to the length of the internodes of the straws, the mean number being 4.45. As the straws of the roofs were inclining about 60° most prepupae of the narrowest nests were found to be situated partly standing on their heads, pointing towards the entrance of the nest. In the wider straws, allowing the imagines to turn inside, the prepupae were situated in the opposite direction. The degree of parasitism was found to be rather low (6.5 %). A list of parasites is given, the most frequent being *Omalus aeneus* Fabr.

Introduction

The genus *Passaloecus* Shuckard constitutes together with *Pemphredon* Latreille, *Ceratophorus* Shuckard and *Diodontus* Curtis a well defined unit of digger-wasps. Their biology is characterized mainly by their habit of using wingless aphids as prey for their larvae. Because of the small size of the prey and its relative immobility the Pemphredoninae should be regarded as collectors rather than hunting wasps. A relatively large amount of aphids has to be sampled to provision each larval cell. The prey is not always paralyzed with the aid of the sting, but the locomotorical ganglions in the thoracic region of the prey are treated with short series of strong bites by the mandibles of the wasp.

Fig. 1. Final closure of *P. eremita* nest in 4.0 mm boring in an old beech stem. Note the surrounding ring of resin droplets.

Habitat

On March 22. 1972 I made some excursions in North Zealand in the sandy hills, Tibirke Bakker, and the sandy lowlands called Ramløse Sand just south of the large coniferous plantation, Tisvilde Hegn. My primary intention was to collect nests of *Passaloecus* in eaves of roofs made of reed *(Phragmites communis)*. The nests are easily distinguished from the uninhabited straws by the fact that their openings are closed by a white or yellowish plug of resin (Fig. 1). Only once these nests have been described in some detail in a Danish periodical (Jøker 1939). Her material consisted of *P. insignis* van der Linden (erroneously recorded and described as *P. monilicornis* Dahlbom, which is not found in Denmark), *P. singularis* Dahlbom and *P. corniger* Shuckard. *Passaloecus eremita* Kohl was first found in Denmark in 1969 (Lomholdt 1971). The distribution of the *P. eremita* nests in the eaves shows a marked aggregated pattern. About 5–20 were placed just beside each other whereas several meters of eaves might be without inhabitants. This is probably a result of a common tendency of homing. At my place in Virum, north of Copenhagen, where I have made some artificial nests consisting of drilled

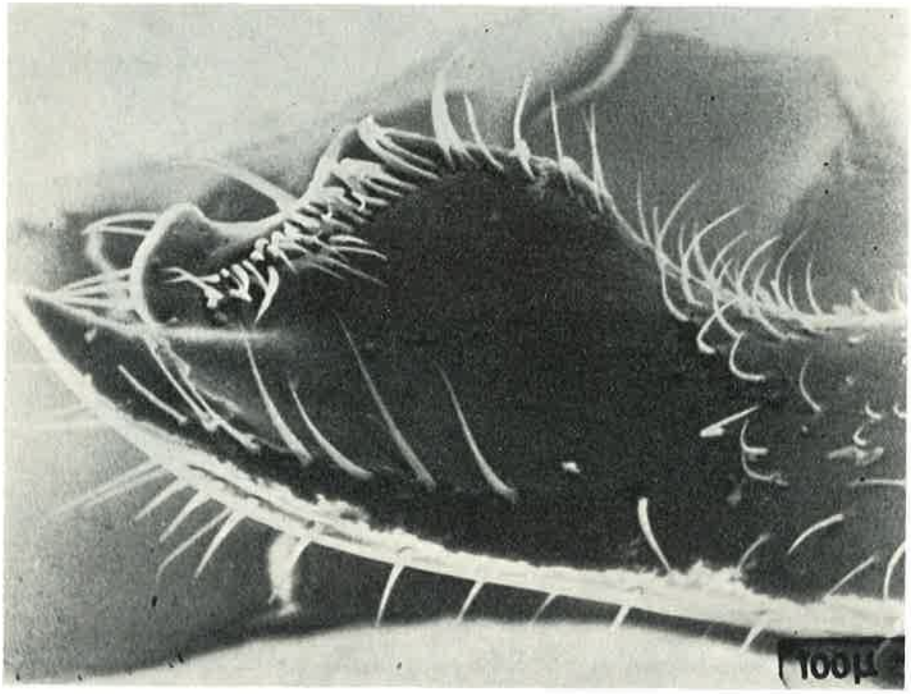

Fig. 2. Left mandible of *P. eremita* ♀ seen from the inner side. Scanning micrograph by B. Rasmussen, Zool. Mus. Copenhagen.

holes of varying length, diameter and density in an old stem of beech *(Fagus silvatica)*, this also was a very significant feature. The plugs of last summer are markedly darker and more dull than the newly made ones, and the presence of two-coloured resin plugs serves as evidence for this phenomenon. *P. eremita* also inhabits isolated posts in which e. g. *Anobium* or other xylophagous insects have made holes of suitable length and diameter.

The greater part of the nests were located in the lower half of the eaves, apparently because fluctuations in temperature and moisture are less marked here than in the upper and more exposed half. In collecting the material, on which this paper partly is based, I was well aware not to sample more than a fourth or a fifth of the total number of nests in each eave in order to avoid damage to the population of this rare species. It was, however, stated that a single eave may give shelter to up to 179 nests. The total number of collected nests was 103 taken from nine roofs.

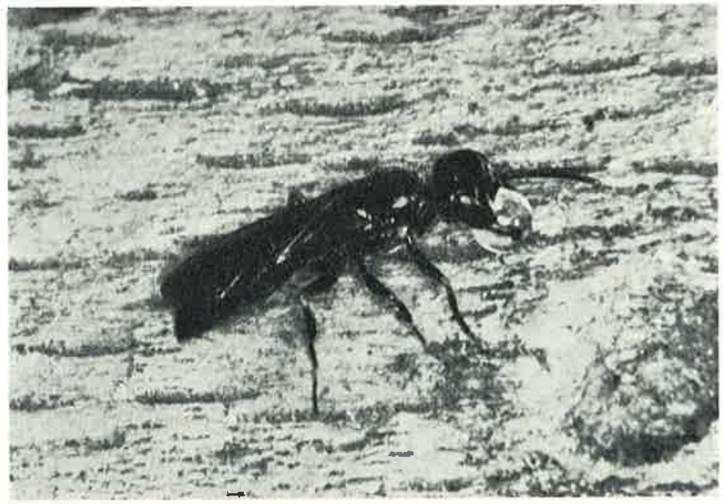

Fig. 3. Female just outside the nest, carrying a drop of resin. Length of female appr. 8 mm.

Construction of nest

It has long been known that at least some of the species of *Passaloecus* have developed a rather unique behaviour in using coniferous resin for the construction of their nests. In this context the rather specialized mandibles with their covering of wax are of great importance. The inner side of each female mandible forms a spoon-like depression at the apex which is surrounded by a row of long and rigid bristles (Fig. 2). This arrangement constitutes a basket-like construction, suitable for the collection and transport of fluid resin. Small drops are collected on pine, *Pinus silvestris* and *P. nigra*, probably by biting off the needles. It was noted that the drop was not in touch with the mandible itself, but was only supported by the bristles. The resin is used to close the larval cell and also makes up the final closure of the nest.

As mentioned above *P. eremita* inhabits the hollow stems of e. g. *Phragmites* and burrows in dead, soft wood. All the observed nests in dead wood were of the linear type although it has been stated (Janvier 1961) that the species is capable of constructing branched tunnels like *P. monilicornis* (Tsuneki 1955). Having searched out suitable conditions for the future nests, the female cleans the burrows by throwing out small pieces of wood and the like. Then, having made a short orientation flight, she flies out to find a source of resin and aphids.

Only the construction of the final closure of the nests has been directly observed in this species, but the partitions between the cells are presumably constructed in exactly the same fashion. Having brought home a drop of shining resin (Fig. 3) the female begins to roll the drop in a circular track on

Fig. 4. Female at the construction of the closure of the nest, rolling a drop of resin on the inner margin of the entrance.

the inner margin of the opening. Only the mandibles are used for this manoeuvre (Fig. 5). About ten drops are necessary to make the final closure.

Gradually as the opening narrows the female levels the surface of the resin plug. The closure is almost always on a level with the surrounding wood or stem. The colour of the plug is light whitish and transparent to begin with. Later it turns dull and yellowish. Its thickness is about 1–2 mm. Although the nest is not finally closed until it is fully provisioned, some resin is deposited around the opening already at the beginning of the provisioning. Several drops are deposited in a distance of two to three millimeters from the opening on the outer side. This is done while the female is moving clockwise, only with the anterior of her body projecting from the entrance (Fig. 5).

This barrier of sticky resin probably serves both to draw other females' attention to the fact that the nest is occupied, and as a rather effective obstruction for e. g. ants, ichneumonids, chrysidids and tachinids (see below). The nest most often fills out the whole boring, stem or burrow, anyhow there is no empty space at the bottom of the nest. An empty vestibular cell of varying length was always found ending the row of cells (Krombein 1967).

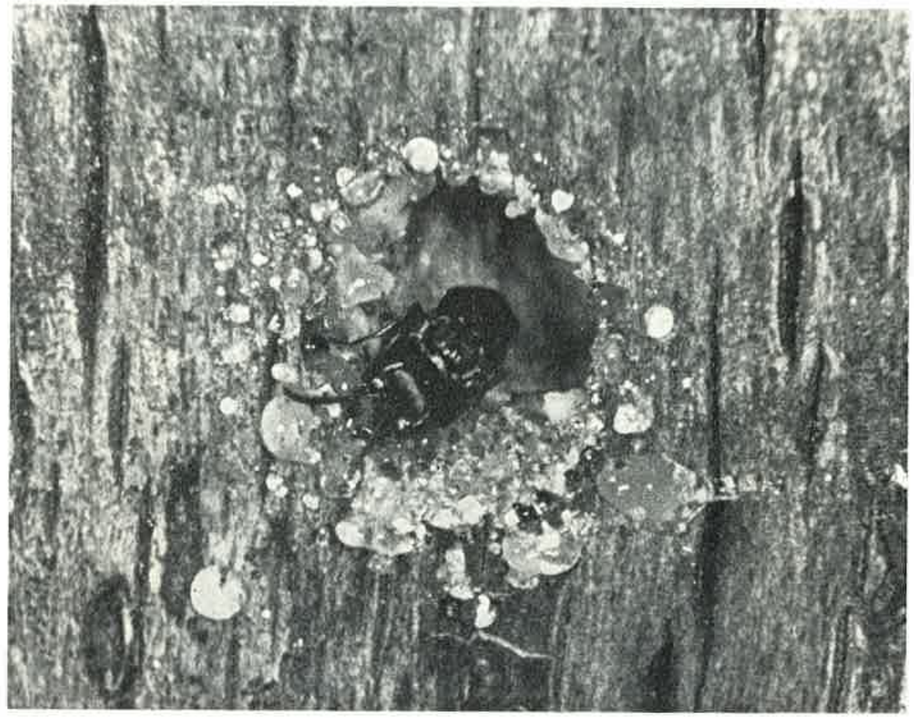

Fig. 5. Construction of the surrounding resin obstruction. The presence of the white droplets shows that the nest was used also last year.

As mentioned above, nests were often re-used next year. Future investigations may show to which extent this species re-use the nest from which they are bred themselves. It is obvious that only a single female from a given nest may have this opportunity. On the other hand dead imagines of both *P. eremita, insignis* and *singularis* were frequently found in the bottom of the inhabited *Phragmites*-nests. (See also Danks 1971, p. 334). Competition of other genera than *Passaloecus* was not observed.

Prey

Passaloecus eremita preys on wingless aphids found on various trees and bushes, but mainly on pines. Normally only one species is collected, but it seems unlikely that *P. eremita* and the other aphid-collecting Pemphredoninae have specialized in certain species rather than simply collecting the available species, assuming that the species fulfills demands such as sufficient size of the individuals and density of the population. The wasp walks around among the sucking aphids, searching out the largest specimens. Sometimes it happens to pick up a prey that apparently is too small. The specimen is then rejected

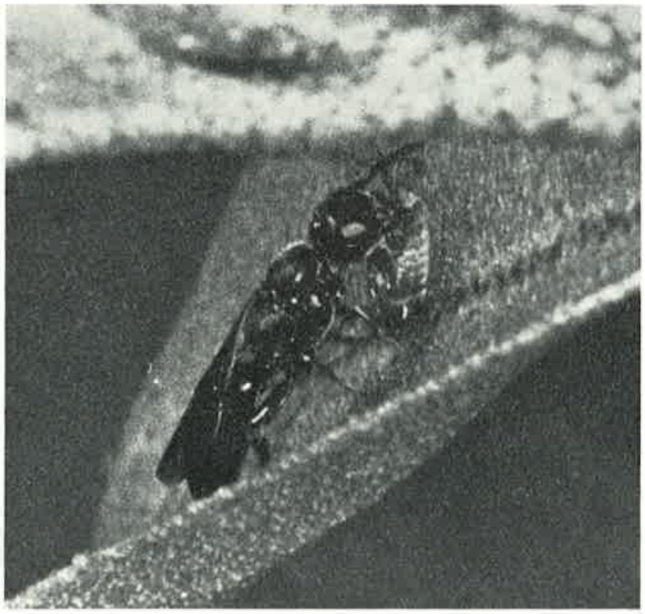

Fig. 6. Female with prey which is held behind the head only by the mandibles.

in favour of another one which is paralyzed by a series of firm bites just behind the head. The victim is then turned over and flown home to the nest, held by the mandibles of the wasp. I have often observed that having landed on either a sunny leaf or in the proximity of the nest, especially the largest aphids were given some additional bites. The wasp was never seen using her sting to paralyze the prey. The species of aphid used by the Virum-population was *Cinara pinea* (Mordv.) (Lachnidae) (Fig. 6) found on pines 10–12 m from the nest. In a few instances it was observed that the female stole the collected aphids from one another. The thieves simply visited other nests, and if nobody happened to be at home, they rapidly crawled inside to fetch a paralyzed specimen. A single female was observed to steal six aphids within two minutes from a single nest about 20 cm from its own. This behaviour has never been reported as regards sphecid wasps. It sometimes happens that a female cannot find her way home and enters one of her neighbours' nests. Usually she realizes her fault rather quickly and hurries out. But if somebody is in, a small fight usually takes place. The combatants wrestle, pulling in either direction until they get tired and the intruder escapes the arena.

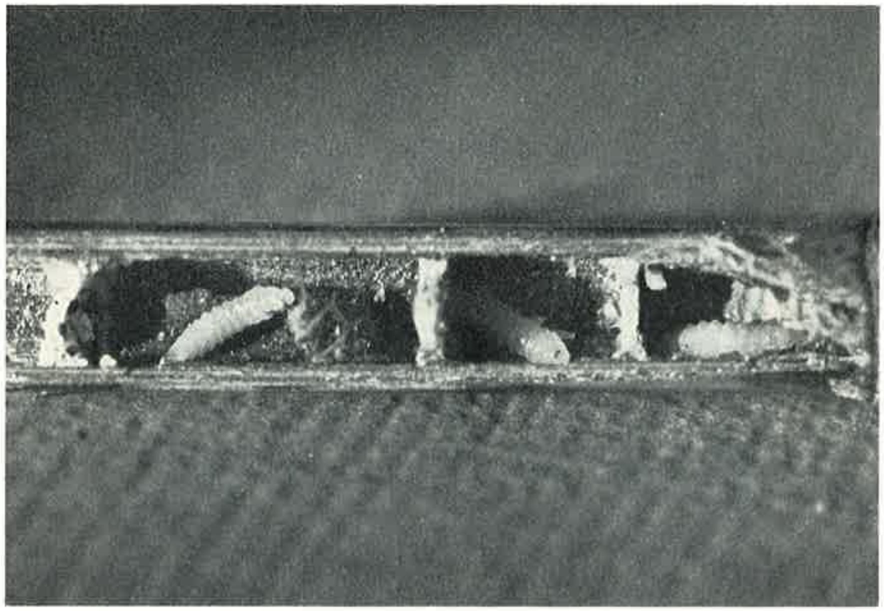

Fig. 7. Three adult larvae of *P. eremita* in *Phragmites*-nest. The opening of the nest is towards left. Inner diameter of straw 5 mm.

Material

As the material from the eaves was collected in March, all the specimens were adult larvae (prepupae), the hibernating stage (Fig. 7). For description of the larva see Janvier 1961. Each larva was dissected out of its cell and placed in a small glass-tube. In these the larvae metamorphosed, and the date on which the imagines were able to fly was defined as the breeding date.

All larvae were kept in a dark and moist place at room-temperature. In Table 1 the mean dates of breeding and the number of males and females are shown in relation to the nine localities.

Results

Kept under the conditions mentioned above the males emerged on an average of two days before the females. This nicely agrees with the habits of several Hymenoptera aculeata. (Evans 1966, Danks 1971). The reason why only 57 of a total sample of 124 cells contained prepupae might be one or more of the following. 1. Some did neither contain larvae nor aphids in spite of the fact that the nests were closed in the usual fashion. 2. Some contained stored aphids, but apparently either the females of last summer did not lay any eggs in the cells, or the eggs may not have hatched. 3. Some nests contained vari-

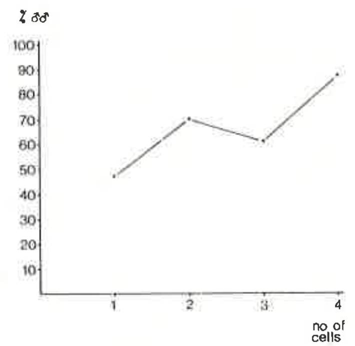

Fig. 8. Curve showing the relative number of males in the first (outmost) cell in nests containing one to four cells.

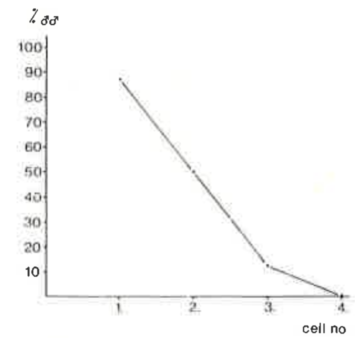

Fig. 9. Distribution of males in nests containing four cells. The innermost cells (no. 4) were in this case always a breeding chamber for a female.

ous parasites (see below). 4. A few (2) were made by *P. insignis,* who closes the nests in a way that cannot be told apart from *P. eremita's.* 5. Some larvae and pupae had died because of infection by some unidentified Fungi. The first imagines of the natural populations in North Zealand were seen on June 3.

From the total number of imagines it is evident that females outnumber the males (73♀♀, 51♂♂) (Table 1), but the distribution of male and female cells in relation to nest-size is highly dependent on the length of the nests (i. e. number of cells) and size of the cells. The diagrams given below show this dependence (Figs 8, 9). In the diagrams a few nests containing more than four cells have been omitted.

Table 1. Breeding dates of males and females from eaves from nine localities. The males emerge on the average of two days before the females. The dates are only to be regarded as relative because the animals were kept under indoor-conditions.

locality	breeding dates		nos. of specimens		nos. of nests
	♂♂	♀♀	♂♂	♀♀	
I	8.V	10.V	8	14	17
II	8.V	10.V	15	27	15
III	7.V	10.V	7	5	5
IV	9.V	12.V	4	12	7
V	9.V	11.V	1	2	1
VI	9.V	12.V	2	1	2
VII	7.V	10.V	6	5	3
IIX	7.V	8.V	4	4	4
IX	7.V	10.V	4	3	3
		total:	51	73	57

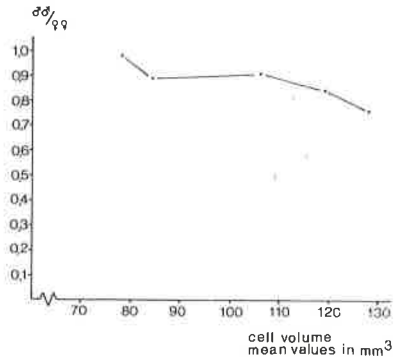

Fig. 10. An increase in cell-volume is followed by a decrease in the relative number of males.

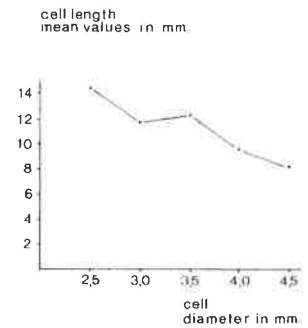

Fig. 11. As the cell-diameter increases the mean length of the cells decreases.

In 69 % of the cases the first (outmost) cell is a breeding chamber of a male, but the more cells the nest contains, the greater the chance of finding a male in the first cell. Fig. 8 shows this relationship as regards nests with one to four cells. Thus, the males more often can escape their cells unhindered before the females are bred in spite of having had a shorter developing period. (The inner cells are the first to be provisioned). One can wonder what makes the female produce female (fertilized, diploid) eggs for the inner, and larger cells. Several theories have been proposed (Krombein 1967, Bischoff 1927, Jayakar 1963) but sufficient evidence seems still to be missing. This mechanism has great biological advantage, and to elucidate this statement the sex-ratio has been plotted against the volume of the cells in Fig. 10.

The increase of the cell volume is proportional to a decrease in the relative number of males. The average amount of food stored for each female is thus greater than for the males even if the mother wasp has tried to compensate for the varying straw diameters by regulating the length of the cells (Fig. 11).

This is, however, a general feature of Sphecidae and several other solitary Hymenoptera aculeata (Krombein 1967). Normally the adult larva produces a thin silk-web attached to the resin plug in front of it, but in the narrowest straws (less than 3 mm in diameter), where each cell is up to three or four times as long as the larvae, the web is placed in such a way that the larva is enclosed in a room that is only a few millimeters longer than itself.

The sex-ratio of *P. eremita* in my material is 0.7 ♀♀/♂♂, but several other Sphecidae produce more males than females (Kohl 1915, Evans 1966, Krombein 1967, Danks 1971). This ratio should not be regarded as a characteristic feature of *P. eremita* rather than just an example based upon the present material. Climatic variations may influence the sex-ratio to a significant degree.

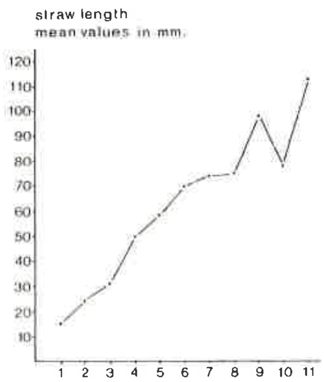

Fig. 12. The correlation between increasing straw-length and number of cells in *Phragmites*-nests. The irregular shape of the last part of the curve is due to a small number of samples.

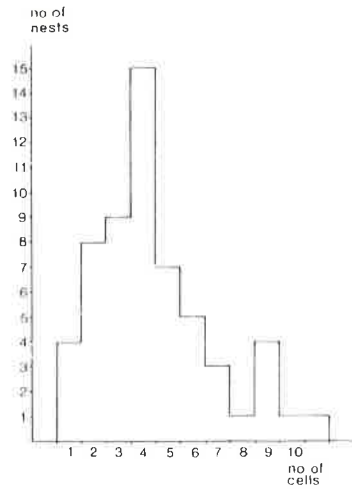

Fig. 13. Histogram showing the preferred nest-size in eaves.

The fact that females are generally somewhat larger as a result of their higher »standard of living« during their preimaginal stages, must be regarded as advantageous. A female is born to do hard work in collecting the provision for the next generation (about twenty aphids per cell). She produces eggs that also involves rather energy-demanding processes, and she collects resin to make the partitions in the nest and the final closure.

At present it is not known how many cells a single female may produce during her lifetime (about two months), but if she is able to provision 20, she must collect about 400 aphids. It takes about five minutes to find and bring home a single specimen (a figure taken from my unpublished observations on *Pemphredon shuchardi* A. Morawitz). When searching out the suitable nesting conditions the wasp has to choose either a reed in the eave, a ready-made beetle-burrow, or one of my drilled holes that have a suitable inner diameter and a suitable length. The diameters of the reeds were varying between 2 and 5 mm, and the length was determined by the distance from where the reed was cut to the first node. In Fig. 12 the average straw-length is plotted against the number of cells containing adult larvae in each nest. The first part of the curve shows a practical linear correlation, but when the straw-lengths exceed about 80 mm there seems to be a slight drop in the curve. It is rather difficult to state whether this drop is significant because of the small number of nests containing more than eight cells. In Fig. 13 the total sample is presented in a way to show the frequency of the females' choice of different straw-lengths.

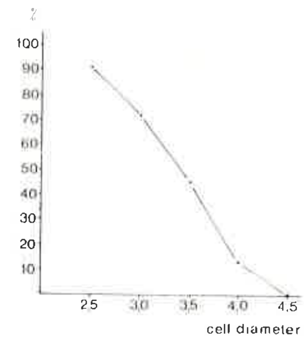

Fig. 14. Orientation of adult larvae in relation to increasing cell-diameter (mm). 91 % of the larvae in the narrowest straws are pointing their heads towards the entrance of the nest (see text.).

Nests containing 2–5 cells (25–60 mm) are the most frequent ones found in this sample (68 %). The sample fits a Poisson-distribution. The mean number of cells per nest is 4.45 and an applied chi^2-test makes this highly significant, $0.01 < p. < 0.25$.

The orientation of the adult larvae in the straws presents some very interesting aspects. In Fig. 14 the relative amount of larvae whose heads are pointing towards the opening of the nest is plotted against the inner diameter of the cells. One should keep in mind the fact that the nests of the eaves are inclining about 60°. Therefore the larvae orientated towards the opening are situated in a rather awkward position, partly standing on their heads. The curve shows an equal distribution of larvae pointing their heads in either direction when the cell diameter is about 3.4 mm. When the diameter exceeds this value the greater part of the animals are situated in a »normal«, partly upright position. The cells smaller than 3.4 mm are so narrow that it would be disastrous to the newly bred imagines because of their missing ability to turn inside the straws. The results is a number of dead specimens at the bottom of the nest. To escape the nest, the specimens have to gnaw a hole in the hardened resin partitions, but if a newly bred individual from the last cell begins to gnaw the wrong way through his brothers' and sisters' cells, he may very well destroy the whole nest. The degree of damage is depending on which larva is wrongly orientated. The compensating mechanisms that hinder such catastrophes might very well be that the position of the larvae is determined at the moment the eggs are laid. If the inner diameter is great enough (allowing the mother wasp to turn inside), she creeps in foreward, if not she must back into the nest. As the eggs in the ovaries are always so arranged that the head of the embryo is pointing in the same direction as the female's, the problem seems to be solved by this explanation.

But not all larvae in the narrowest nests seem to maintain their original position (9 %). Even if they are rather immobile they must have turned in the wrong direction, perhaps by chance, perhaps reacting to the forces of gravity.

Parasites

It must be mentioned primarily that the degree of parasitism is rather low, only 8 out of 124 completed cells (6.5 %) were affected. In Danks' analysis of *Passaloecus singularis* Dahlb. (1971, p. 339–41) the figure is 8.8 %. Other genera show a much higher degree of parasitism that might be due to their missing ability to protect the entrance of the nest. The most frequent parasite was the chrysidid wasp *Omalus (Omalus) aeneus Fabr.* For the description of the cocoon, see Krombein 1967. *Chrysis (Trichrysis) cyanea* L. was only bred in a single male specimen in spite of this species beeing frequently observed swarming close to both the eaves and the nests in dead wood. Two species of Ichneumonidae were bred from the nests. One was identified as *Perithous mediator* Fabr. (Pimplinae), the other as *Perithous* ? sp. The above-mentioned species only occupy a single cell, whereas the dermestid beetle, *Megatoma undata* L. destroys 2–4 cells. Two specimens were found.

The parasitic Hymenoptera, bred in this case, were all found as adult larvae in March. They pupated early in May and the imagines emerged from May 14. to 20., two to three weeks later than their hosts. The larvae of *Megatoma* did not metamorphose.

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