BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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Bionomics of five wood-nesting solitary species of bees (Hym., Megachilidae), with emphasis on flower relationships

MARKKU KÄPYLÄ

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A detailed description and comparison was done on the bionomics of five species of wood-nesting bees: *Chelostoma maxillosum* (L.), *C. rapunculi* Lep., *C. campanularum* (K.), *Heriades truncorum* (L.), and *Osmia tuberculata* Nyl.
The diurnal flight activity was best explained by separate temperature and light thresholds. The temperature thresholds of the different species ranged from 16.5 to 19°C. The available nest cavities were divided among the species mainly according to their size, partly according to the sun-shade gradient. The nest structure and the activities of the females at the nest entrances were studied in detail.
The flowers visited for food were studied mainly by pollen and sugar analyses of the pollen loads and guts. The pollen and nectar presentation of the main food plants was also studied. *C. maxillosum* is an oligolege of *Ranunculus*. *C. campanularum* and *C. rapunculi* are both oligoleges of *Campanula*, but do not compete for nest cavities, which are the most limiting resource. *H. truncorum* is widely oligolectic and specialized to the family Compositae. *O. tuberculata* is polylectic. The main nectar sources were the same as the main pollen sources, but many other flower species were occasionally visited for nectar. The pollen in the flowers - and therefore also in the pollen loads - was contaminated with foreign pollen by wind and insects. All the species carry pollen loads dry. The bees mostly collected both pollen and nectar on the same foraging trip, but also only pollen or only nectar. The heaviest loads were about 1/4 - 1/3 of the weight of the bee.

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Contents

1.   Introduction

It is characteristic of the taxonomy of bees (Apoidea) that many of the
genera contain a large number of species. Most of the European species
have a very wide distribution (STOECKHERT 1933) and many related species
can be found in a single favourable habitat (SAKAGAMI & MATSUMURA 1967,
HAESELER 1972, KÄPYLÄ 1974), even using the same principal food source
(POPOV 1958, LINSLEY & MacSWAIN 1959, THORP 1969, LINSLEY *et al.* 1973,
HURD & LINSLEY 1975). Bees should thus be a good subject for studies on
niche separation and species packing. The most effective way of avoiding
competition among bees is food-specialization. The majority of solitary
bees are known or supposed to be oligolectic (LINSLEY 1958, 1961, PESENKO
1975). This means that they have specialized to one plant genus or family
in their pollen collecting. If several bees use the same pollen source,
they may visit the flowers at different times. This kind of resource
partitioning seems to be common among bees in warm, arid climates (LINS-
LEY 1962a, LINSLEY & CAZIER 1970, 1972, LINSLEY *et al.* 1973, HURD & LINS-
LEY 1975), but has not been reported from more northern areas.

Bees visit flowers for various different reasons.
(1) Pollen collecting. Pollen is the principal food of bee larvae. Soli-
tary bees provision their cells with all the food necessary for larval
development, after which the cell is sealed. Apparatus for collecting and
carrying pollen is the most evident morphological adaptation of bees.
Pollen is also a part of the adult diet.
(2) Nectar collecting. Nectar is the main food of adults. Pollen prepared
as larval food is moistened to a varying extent with nectar. Males suck
nectar only for their own nourishment.
(3) Flowers as shelter and resting places. Bees, especially males, are
often found spending the night in flowers. Similarly bees seek shelter in
flowers in daytime during bad weather. Big, more or less bell-shaped
flowers are the most popular shelter or resting places (FRIESE 1923: 61).
(4) Patrolling in searching females. Copulation is frequently performed
in flowers. That is why males are often as specialized in their flower
visits as females. Patrolling flight of male solitary bees by flowers has
been described, e.g. by MICHENER (1953) and ROBERTS (1969).

The purpose of the flower visit often remains obscure to the observer.
In many cases it is impossible to say whether a bee has collected both
nectar and pollen during the same visit. Even in recent papers no dis-

tinction has been made between the different reasons for flower visits (MIYAMOTO 1962, ELFVING 1968, PESENKO 1971, 1975, BELAKOVA 1972, TERÄS 1976). Analysis of the contents of the honey stomachs has shown that a varying proportion of foraging bees collect both nectar and pollen on the same foraging trip (TANIGUCHI 1956, VALLE & BERGT 1965, ORDWAY 1966, FUKU-DA et al. 1969, ERICKSON et al. 1973, MOHAMED 1973a). Bees with a pollen load gathered from one plant species can move to another species to collect nectar (MICHENER 1953, SPENCER-BOOTH 1965, MACIOR 1968, HASLERUD 1974). In such cases an observer easily makes wrong observations about the pollen sources of the bee species concerned. When pollen collecting has just started, a bee may become wrongly grouped as solely a nectar collector.

Pollen analysis offers a valuable means of avoiding the difficulties. It is widely used in studies of honey and honey-bees (e.g. PERCIVAL 1947, SARISALO & VALLE 1969, LOUVEAUX et al. 1970, HODGES 1974, McLELLAN 1976) and bumble-bees (e.g. BRIAN 1951, MACIOR 1968, ANASIEWICZ & WARAKOMSKA 1969, FREE 1970), but rarely in studies of solitary bees (CLEMENTS & LONG 1923, BRITTAIN & NEWTON 1933, THORP 1969, FREE & WILLIAMS 1970, ANASIEWICZ & WARAKOMSKA 1971, TASEI 1972, 1976).

Another aspect of the division of available resources is the use of different nesting sites. In this respect bees can be divided into two major categories. One group dig their nests in sandy well-irrigated soil. In this group competition for nesting sites hardly ever limits the size of a local population. The other major group of bees nest in pre-existing cavities in wood, or dig into the soft pith of some bushes, or use straws. Besides these major groups, there are some special cases, such as mason-bees, which build their nests above ground. For the nesting habits of solitary bees, the reader is referred to MALYSHEV's (1935) comprehensive review.

The species dealt with in this study are (Fig. 1): *Chelostoma maxillosum* Linnaeus 1761, *C. rapunculi* Lepeletier 1841, *C. campanularum* Kirby 1802, *Heriades truncorum* Linnaeus 1758, and *Osmia tuberculata* Nylander 1848. The nomenclature is according to ELFVING (1968), who gives a list of synonyms and the distribution in Finland in the same paper. These species nest in holes in wood, especially in the walls of old log barns. In Finland it is usual to find all the five species nesting in the same barn. There are no detailed studies on the flower relationships of these species, apart from NIEMELÄ's (1934) unpublished material, but a good deal of information is
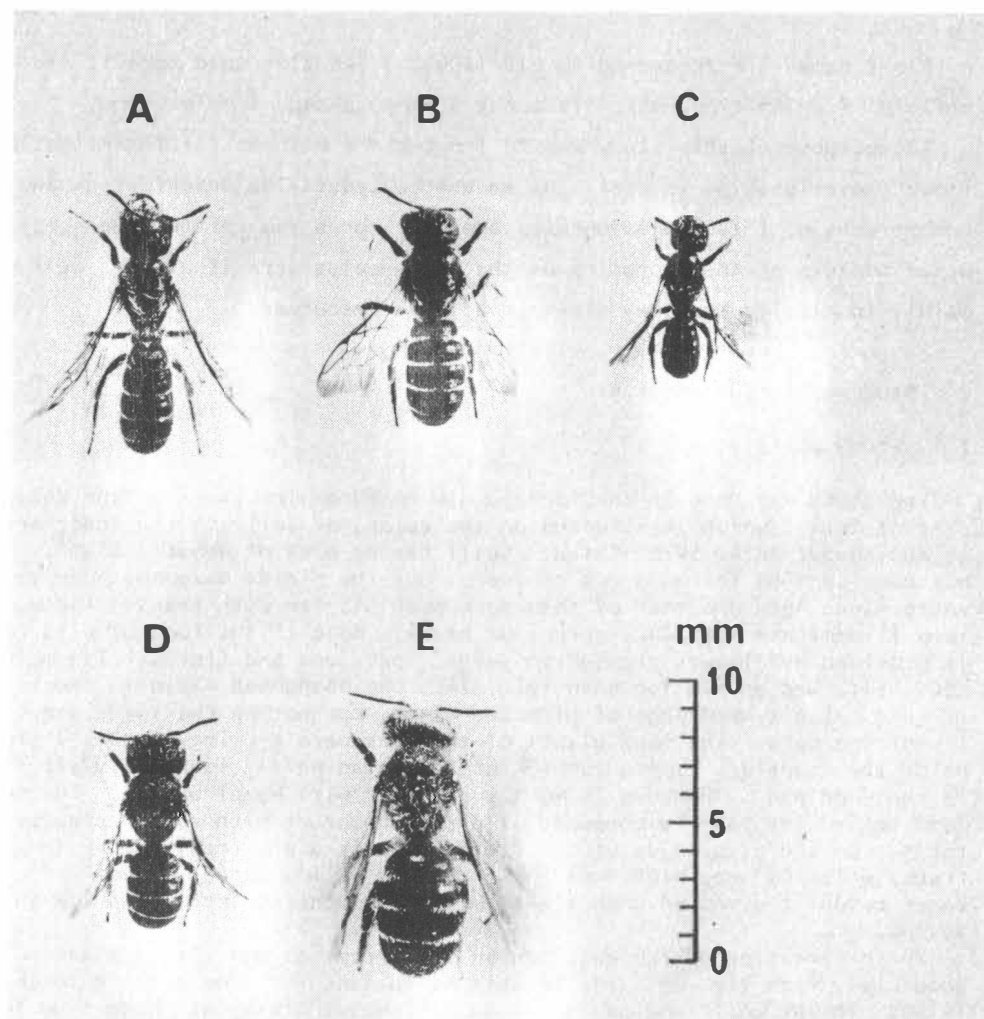
Fig. 1. Females of the bee species studied. The specimens are from Seili, except *O. tuberculata*, which is from Jokioinen. A. *Chelostoma maxillosum*, B. *C. rapunculi*, C. *C. campanularum*, D. *Heriades truncorum*, E. *Osmia tuberculata*. Photo P. Niutanen.

scattered in the literature. The few special studies on these bees concern nesting habits (MARECHAL 1933, VAN LITH 1957, CORREIA 1976a). The flower records in the literature indicate that they all visit many species of flower, but *C. maxillosum* seems to show specialization to buttercups (*Ranunculus*), *C. rapunculi* and *C. campanularum* to bellflowers (*Campanula*), and *H. truncorum* to the family Compositae. Very little is known about the biology of *O. tuberculata*; it does not seem to have specialized to any flowers, but slightly favours the family Leguminosae.

Plant names are according to LID (1963). The time used here is the official Finnish time, which is about 30 min ahead of solar time.

The purpose of this study was to improve the methods for investigating flower relationships in bees. As an example, detailed descriptions and comparisons of these relationships are made for a few related bee species. Other aspects of the bionomics of the bee species were studied as well mainly to clarify how they divide available resources.

2. Study place and material

2.1. Study place

The study was done in the Archipelago Research Institute of the University of Turku, which is situated on the island of Seili in the inner archipelago, about 30 km SW of Turku. Seili has an area of about 1.6 km^2. It has been settled for hundreds of years, but the fields have not been cultivated since 1964 and most of them have been planted with trees. The woodland is dominated by pine, spruce or hazel. Most of the food of wild bees is provided by flowers growing in yards, roadsides and fields. The main study site was an old log barn (Fig. 2). The abandoned field in front of it (Fig. 3) has seedlings of pine and birch, but not in the immediate vicinity of the barn. The food plants of the bees were growing in this field or on the roadside. *Osmia tuberculata* was also partly found to visit flowers in the woodland. The road is mostly bordered with hazel bushes. The woodland behind the barn is composed of pine and spruce with some deciduous trees. On the other side of the field there is a dry rocky hill with pine trees, which is separated from the field by willow scrub. The field extends beyond the map on both sides. In the southwest there is a sea-shore meadow.

The orientation of the barn can be seen from the map (Fig. 3) and more accurately from Fig. 19. The SE wall is in sunshine from sunrise to about 14.50. The NE wall remains in shadow till about 11.10, at which time the first sunbeams also reach the SW wall. Weak sunshine may filter through the foliage to the NW wall after 14.50.

The nearest other barn was about 300 m east of the study barn. Only the east half of that barn was made of logs, and it was partly pulled down. The bee population was similar but smaller.

2.2. Material

Studies were done in Seili during the periods: 2.VI. - 16.VIII. and 22.VIII. - 26.VIII. in 1970 and 4.VI. - 14.VIII., 21. - 22.VIII., 28. - 29.VIII. and 4. - 5.IX. in 1974. During summers 1971 - 1973, bees, mostly collected from other places than the main study barn, were weighed and the contents of their honey stomachs were studied.

Most of the material presented here is from Seili and the summers mentioned. The field observations on flower visiting (Table 13) include records made in other parts of SW Finland since 1963. The material concerning the flower visiting and phenology of *C. rapunculi* and *O. tuberculata* also includes data from other places in SW Finland.

Fig. 2. The study barn viewed from the south. Beside the barn is a tall lime tree. Photo M. Käpylä 12.VIII. 1972.
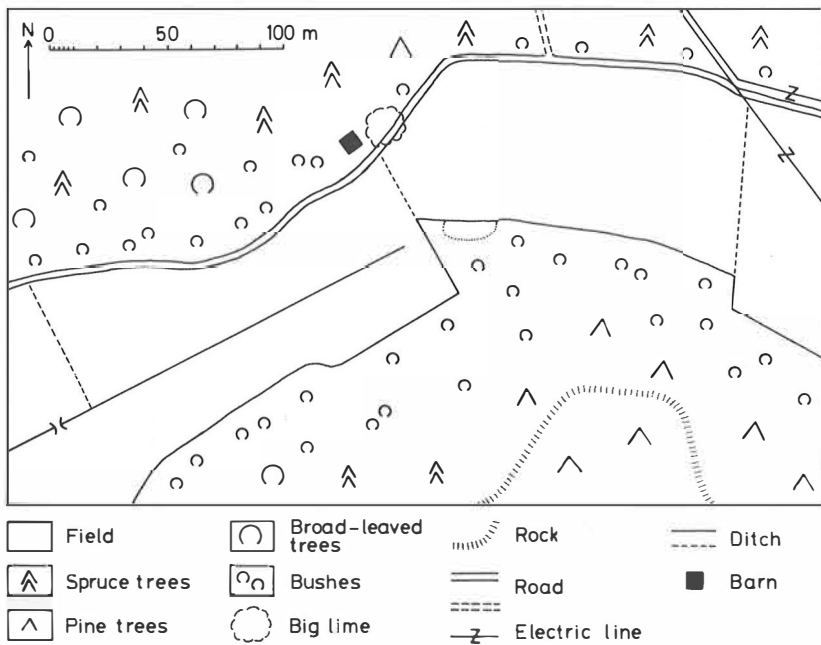

Fig. 3. Map of the surroundings of the study barn.

All the bees that were not destroyed during the study are kept in my private collection.

Other details about the material are given in different sections.

2.3. Weather conditions

Temperature and relative humidity were measured with a thermohydrograph, which was placed in a shelter near the ground in front of the SE wall of the study barn. Fig. 4 is based on these measurements. Temperature and humidity by the other walls was measured with a mercury thermometer and a hair hygrometer, which were protected from direct sunlight with a piece of white cardboard.

Wind velocity was measured with a thermoanemometer. Light was measured with a camera exposure meter, held at breast level and directed straight away from the wall. The hours of sunshine were recorded with a solaro-graph. The amounts of sunshine in Fig. 4 are percentages of the period from 8.00 to 16.00 hours.

In 1970 June was exceptionally warm, dry and sunny (Table 1). June 1970 was rather cold and rainy. Summer 1974 was near normal but a little colder.

Table 1. Monthly weather records at Turku airport (nearest weather station to Seili) in summers 1970 and 1974 compared with long-term averages (ANON. 1970, 1974). Mean hours of sunshine obtained directly from Ilmatieteen laitos (Meteorological Institute).

	1970				1974				Mean 1931-1960 (Sunshine hours 1963-1973)			
	V	VI	VII	VIII	V	VI	VII	VIII	V	VI	VII	VIII
Mean temperature °C	9.7	17.0	16.1	15.4	8.0	14.4	15.2	14.9	8.7	13.9	17.1	15.7
Precipitation mm	15	7	140	45	21	46	131	33	29	43	72	86
Mean cloudiness %	54	33	73	55	52	51	71	61	64	62	66	66
Sunshine hours	284	420	225	300	300	308	201	251	267	316	287	229

3. Seasonal and diurnal flight activity and population ecology

3.1. Methods

The amount of bees caught within 15 min with an insect net was used to measure flight activity and the relative size of the population. Activity depends on the weather being highest when it is warm and sunny. In esti-mating the relative sizes of the populations the effects of the weather on catch size was minimized by using only the biggest catch of each day and omitting the results of the days when the temperature failed to pass certain thresholds (see sect. 3.2.4.).

Every new individual caught was marked by cutting the edge of one fore-wing (LINSLEY & MacSWAIN 1959). Individuals of *C. campanularum* were not marked, because of the very small size of the species. Some individuals were marked with spots of paint on the thorax, five different colours, being used in combinations of two. The spots of paint usually flaked off after some time, as was also found by MICHENER *et al.* (1955), but in some individuals the paint stayed on sufficiently long to give information on
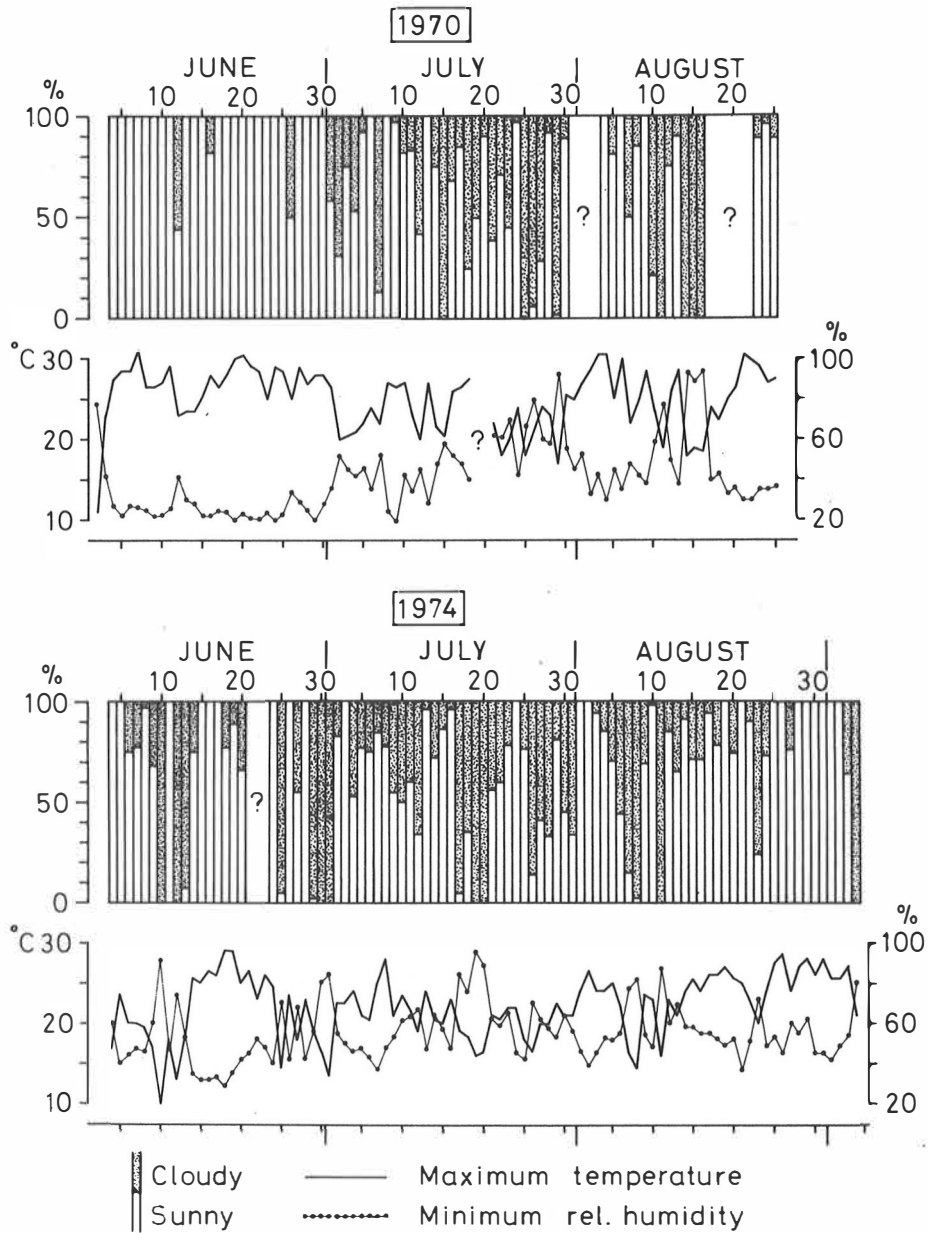
Fig. 4. Weather conditions in Seili during summers 1970 and 1974.

the life span.

Before marking, the bees were slightly narcotized with ether. After treatment they were placed in the shade in an open cardboard box, where their recovery could be followed. After recovery the bees climbed up the side of the box and flew away. Some bees died of the narcotization, but

no injury could be seen in the bees that recovered from it.

In 1970 the time of flowering was studied by counting open flowers in nine quadrats (50 x 50 cm) and recording the start and end of flowering of each species. In 1974 the flowering intensity was estimated subjectively with the scale 0 - 5. To make the results comparable, records for 1970 were afterwards changed to the same scale. Where this was not possible, only the flowering time is shown.

3.2. Results and discussion

3.2.1. Phenology of bees and flowers

In all the bee species the flight period is fairly long (Fig. 5, Table 2). The first males and females seem to emerge at about the same time, but the males reach their peak before the females and their flight period is shorter. Bees are generally considered proterandric (FRIESE 1923: 59, ROBERT-SON 1929, SAKAGAMI & MATSUMURA 1967), and observations on the emerging time of megachiline bees have confirmed that the males emerge earlier than the females (HOBBS 1973, HAWKINS 1975). But the present results do not show clear proterandry.

Table 2. Earliest and latest observations of the bees in SW Finland. A. According to M. Käpylä's collection. B. According to NIEMELÄ (1934).

C. maxillosum	A ♀♀	26.V.	-	5.VIII.
	♂♂	14.VI.	-	30.VI.
	B ♀♀	14.VI.	-	27.VII.
	♂♂	13.VI.	-	30.VI.
C. rapunculi	B ♀♀	22.VI.	-	16.VIII.
	♂♂	13.VI.	-	16.VIII.
C. campanularum	A ♀♀	24.VI.	-	17.VIII.
	♂♂	14.VI.	-	28.VII.
	B ♀♀	21.VI.	-	27.VII.
	♂♂	2.VII.	-	27.VII.
H. truncorum	A ♀♀	16.VI.	-	13.VIII.
	♂♂	16.VI.	-	10.VIII.
	B ♀♀	22.VI.	-	28.VIII.
	♂♂	21.VI.	-	14.VIII.
O. tuberculata	B ♀♀	14.VI.	-	14.VII.
	♂♂	18.VI.	-	28.VI.
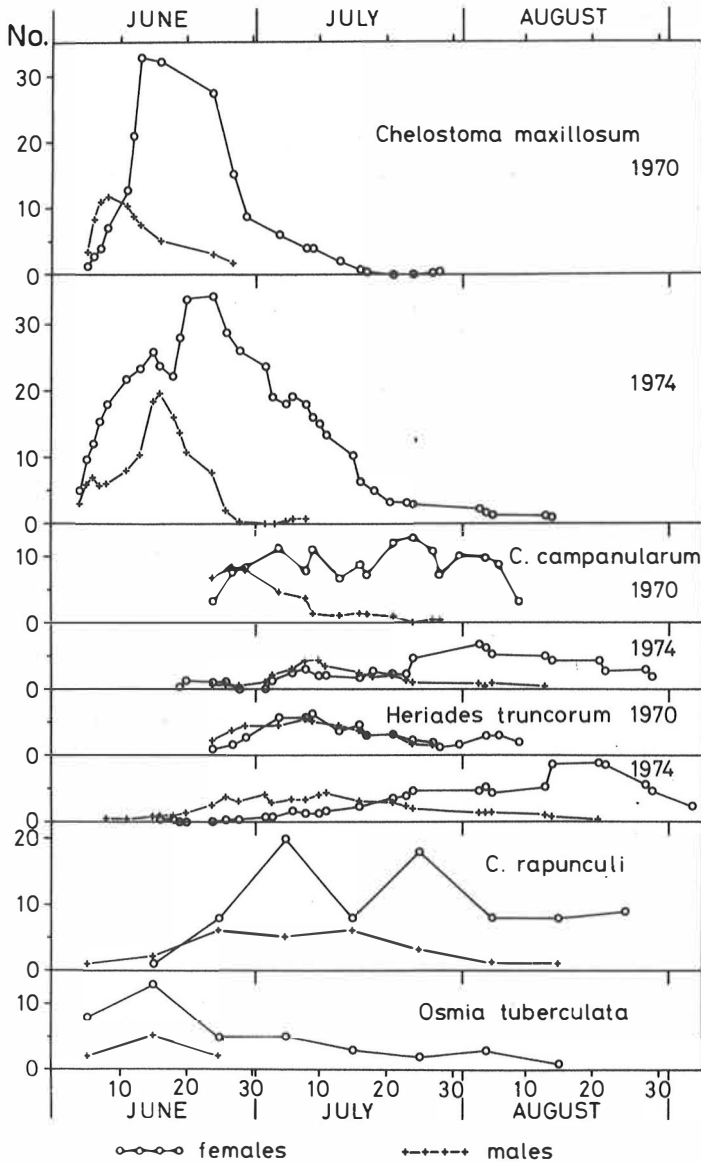
Fig. 5. Seasonal flight curves of the bees based on relative population estimates. The numbers of *C. maxillosum*, *C. campanularum* and *H. truncorum* are running means (records of the previous and following day included) of the biggest catch per 15 min in each day in Seili. The populations of *C. rapunculi* and *O. tuberculata* were too small for this kind of calculation, and their curves are based on the numbers of individuals in my collection caught in each 10-day period in SW Finland. Records from Seili are included in these numbers.

The flight curves of these species are of two types. *C. maxillosum* and *O. tuberculata* are early summer bees with a clear peak. The shape of the curve shows a relatively short emerging time (cf. Fig. 9). The emergence of *C. maxillosum* was especially rapid in 1970 because a cold May was followed by a very warm and sunny June (cf. Table 1). The other species (*C. rapunculi*, *C. campanularum* and *H. truncorum*) have flight periods in mid
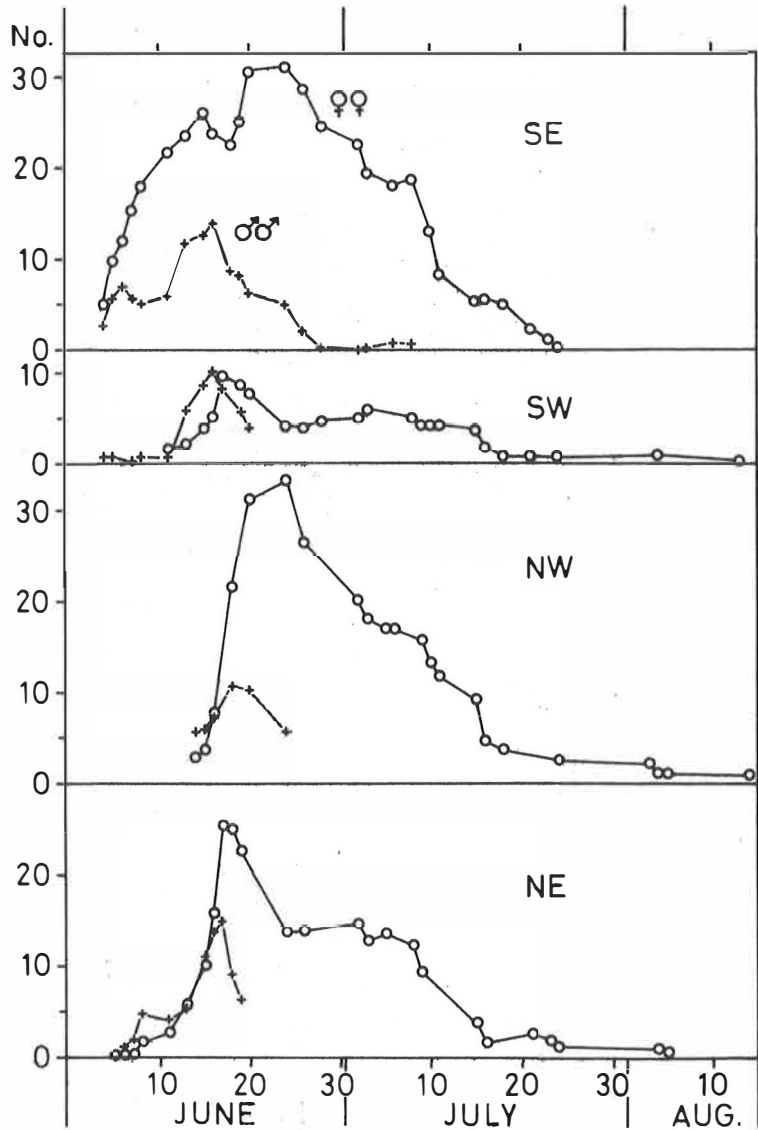
Fig. 6. Seasonal flight curves of *C. maxillosum* from different walls of the barn in 1974. For further explanation see Fig. 5.

and late summer with no definite peak. The shape of the curve reflects a relatively long emerging time. New individuals of *H. truncorum* were caught as late as August (Fig. 10).

The flight curves of *C. maxillosum* differed somewhat between the different walls of the barn (Fig. 6). The peaks in the flight curves occurred at about the same time, but flight started about 10 days later from the NW wall than from the other walls and ended sooner from the SE wall than from the others. The flowering times of the potential food plants of the bees in the vicinity of the barn are shown in Figs. 7 - 8. The early summer species (e.g. *Anthriscus silvestris, geranium silvaticum, Hieracium pilosella* and *Vaccinium vitis-idaea*) started flowering later and stopped earlier in 1970 than in 1974, because in the former year May was colder and June was warm and dry. At the end of June 1970, the vegetation was partly wilted, but it recovered after the rain in July (e.g. *Campanula patula*). The mid and late summer species flowered at about the same time in the two year, or a little later in 1974.

The flight periods of the bees agree well with the flowering times of the most important food plants. There is a clear fit between *C. maxillosum* and *Ranunculus*, and between *C. rapunculi* and *C. campanularum* and *Campanula*. The flight of *H. truncorum* started earlier than the flowering of the most important food plants, *Matricaria inodora* and *Leontodon autumnalis*, but other Compositae flowers were always available. This species must change its main food source in the course of the flight period. *O. tuberculata* is very opportunistic in its choice of food plants and is not dependent on any particular flower species in its flight period.

3.2.2. Sizes of populations and sex ratios

The sizes of the populations were taken as the sums of individuals marked in the barn (Figs. 9 - 10). As could be expected from the seasonal flight curves, the emerging time was shorter in *C. maxillosum* than in *H. Truncorum* and was shorter in 1970 than 1974. The populations were about the same size in both years in both species. The sex ratio in *H. truncorum* was near 1. In *C. maxillosum* the ratio $\male\male:\female\female$ was about 1:3 in 1970 and about 1:4 in 1974.

The absolute population size of *H. truncorum* is known (Fig. 10). Suppose that on the average the same proportions of the populations of *C. campanularum* and *H. truncorum* were caught with an insect net during a 15-min
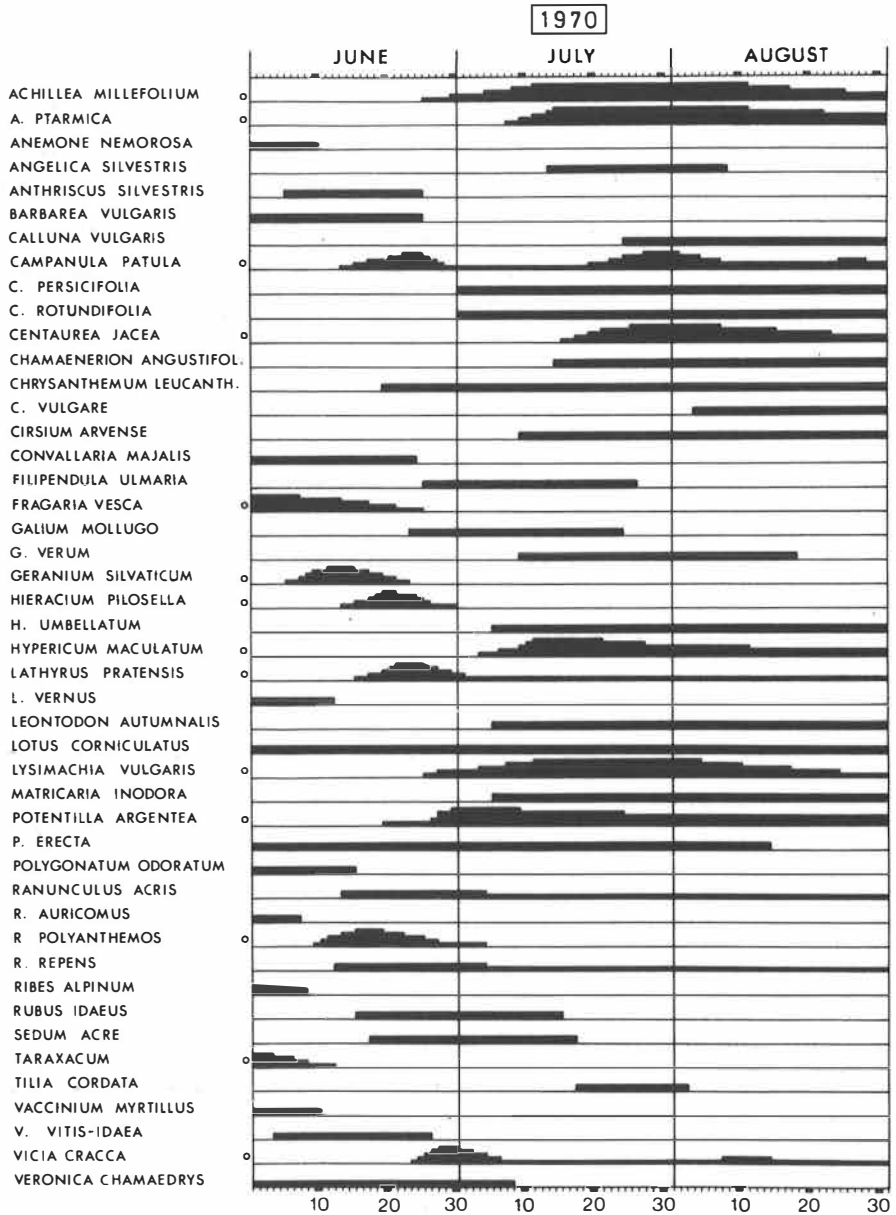
Figs. 7-8. Flowering of the common bee plants in Seili in summers 1970 and 1974. In the graph for 1970 the scale 0-5 is used for the species marked with a small circle. Only the flowering time is shown for the other species, not the intensity. In 1974 the scale is used for all the species.

1974

	JUNE	JULY	AUGUST

ACHILLEA MILLEFOLIUM
A. PTARMICA
ANEMONE NEMOROSA
ANGELICA SILVESTRIS
ANTHRISCUS SILVESTRIS
BARBAREA VULGARIS
CALLUNA VULGARIS
CAMPANULA PATULA
C. PERSICIFOLIA
C. ROTUNDIFOLIA
CENTAUREA JACEA
CHAMAENERION ANGUSTIF.
CHRYSANTHEMUM LEUCANTH.
C. VULGARE
CIRSIUM ARVENSE
CONVALLARIA MAJALIS
FILIPENDULA ULMARIA
FRAGARIA VESCA
GALIUM MOLLUGO
G. VERUM
GERANIUM SILVATICUM
GEUM RIVALE
HIERACIUM PILOSELLA
H. UMBELLATUM
HYPERICUM MACULATUM
LATHYRUS PRATENSIS
L. VERNUS
LEONTODON AUTUMNALIS
LOTUS CORNICULATUS
LYSIMACHIA VULGARIS
MATRICARIA INODORA
POTENTILLA ARGENTEA
P. ERECTA
POLYGONATUM ODORATUM
RANUNCULUS ACRIS
R. AURICOMUS
R. POLYANTHEMOS
R. REPENS
RIBES ALPINUM
RUBUS IDAEUS
SEDUM ACRE
STELLARIA GRAMINEA
TARAXACUM
TILIA CORDATA
VACCINIUM MYRTILLUS
V. VITIS-IDAEA
VICIA CRACCA
VERONICA CHAMAEDRYS

10 20 30   10 20 30   10 20 30

Fig. 8.

sampling period. The the absolute population size of *C. campanularum* can be estimated with the formula $\hat{Y} = \frac{\bar{y}}{\bar{x}} X$, where $\hat{Y}$ = population of *C. campanularum*, $\bar{x}$ = mean sample size of *H. truncorum*, $\bar{y}$ = mean sample size of
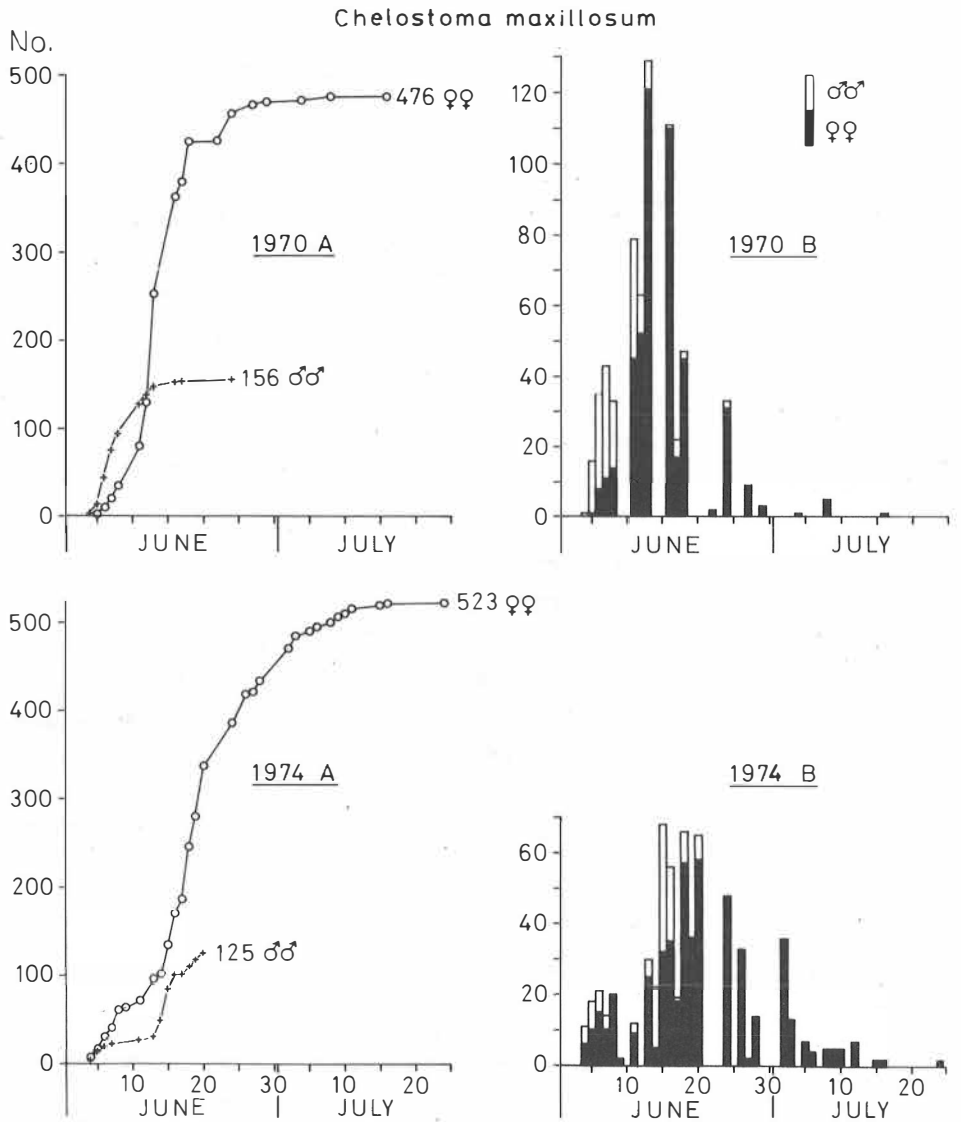
Figs. 9-10. Cumulative sums of new individuals marked in the barn (A) and the amounts of new individuals marked each day (B).

C. campanularum, X = population of *H. truncorum*. The confidence limits were calculated according to COCHRAN (1963, p. 164), but the finite population correction (1-f) was omitted (see COCHRAN 1963, pp. 30 - 31). The standard deviation of $\hat{Y}$ was thus estimated with the formula:

$$s(\hat{Y}) = \frac{X}{\sqrt{n}x} \sqrt{s_y^2 - 2\hat{R}r_{xy}s_x s_y + \hat{R}^2 s_x^2} \quad , \text{ where } \hat{R} = \frac{\bar{y}}{\bar{x}} , \; n = \text{number of obser-}$$

Fig. 10.

In 1970 the catch of *C. rapunculi* was 13 ♀♀ and 0 ♂♂. As only one nest
was observed, most of the females were wandering. In 1974 the catch was
the same, but six nests were seen, three of which were in newly placed trap
nests.

In 1970 the catch of *C. tuberculata* was 9 ♀♀ and 1 ♂, in 1974 2 ♀♀,
several of the females were not resident and stayed in the barn only a
short time. In 1970 there were at least five nests. None of the bees

built more than one nest; one female started another but did not finish it. In 1974 there were three nests, all made by the same female.

3.2.3. Life span, death rate and emigration

The decrease of adult bee populations depends on the death rate and emigration, their increase on emergence and immigration. Immigration must have been low, or restricted to a short time just after emergence (Figs. 9-10). The new individuals caught later in the flight period were mostly quite newly emerged and not worn, though some were worn and apparently immigrants.

In this study the effects of the death rate and emigration cannot be separated. In Fig. 11 the size of the *C. maxillosum* populations are shown in a logarithmic scale. The decrease is almost linear, which means that the rate of decrease of the population was fairly constant during the flight period, or at least after the peak. The rate of decrease (death rate + emigration) can be expressed with the coefficient of the regression of the log population on time (days).

The decrease of the population is different in *C. campanularum* and *H. truncorum*. The size of the populations of these species increased towards the end of the flight period, since emergence was prolonged. (The situation in C. campanularum is assumed to be analogous to that in *H. truncorum*). The deaths in these species must be concentrated to the end of the flight season, and the activity of the populations is probably stopped by cold autumn weather rather than by ageing of the bees. There is no reason why the death rate should be much higher in *C. maxillosum* than in *C. campanularum* and *H. truncorum*, and the decrease in its population can thus be partly attributed to emigration caused by increasing competition for nest cavities.

Emigration was actually observed a few times: on 3.VII. 1974 *O. tuberculata* no. 1 was found on the other barn (see sect. 2.1.), apparently searching for a suitable nesting site; in both 1970 and 1974, two marked females of *C. maxillosum* were found in this same barn; in 1974 one marked *H. truncorum* female was found about one kilometer away, beyond a wood, carrying pollen into a nest in a wooden building.

The causes of death are unknown, but one very peculiar case may be mentioned. During July 1974 several females of *C. maxillosum* were found dead, with their heads inside the nest hole, in the posture assumed in making end plugs (see Fig. 23). Their heads were tightly cemented into the nest hole
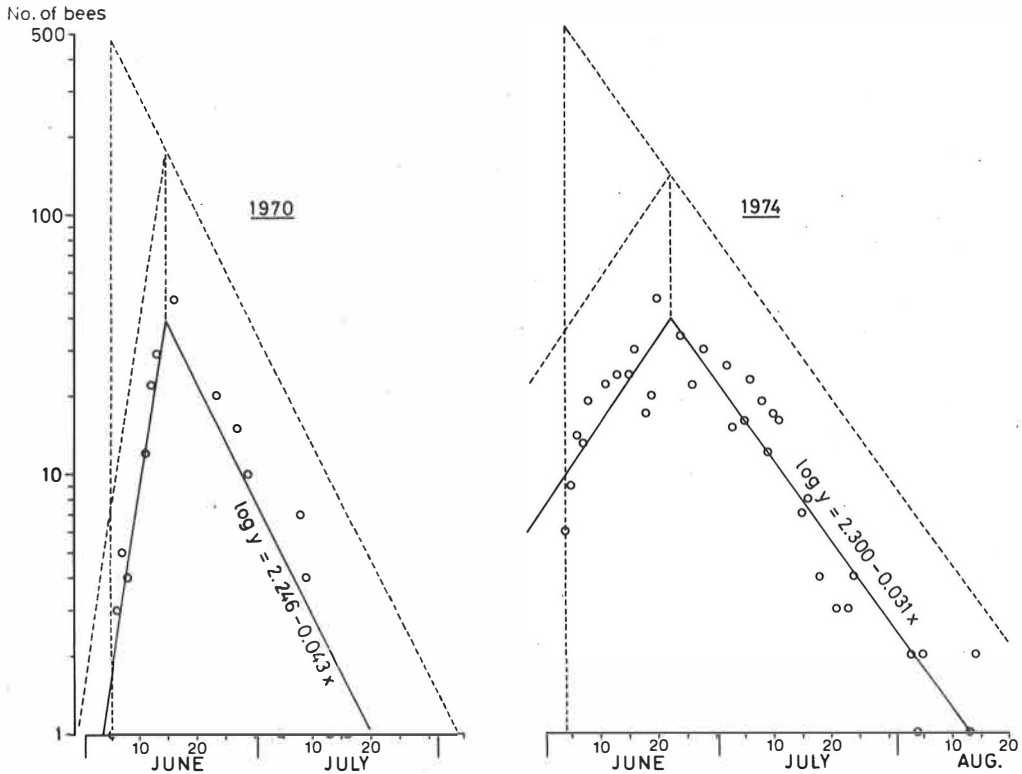
Fig. 11. Curve of population of *C. maxillosum* females in logarithmic scale. The largest number of bees caught within 15 min in each day was used as a relative population estimate. Time (abscissa) is days from 1 June. The dotted parallel lines represent the graphical estimation of the absolute population size in different times of the flight season. Further explanation in text.

and could not be removed without breaking the insect.

Fig. 11 can be used to determine the approximate absolute population size on each day. RICHARDS & WALOFF (1954) knew the absolute size of an insect population throughout the flight period and used the speed of decrease of the population to determine graphically the total amount of individuals that emerged. In the present case the amounts of emerged individuals are known, but the population size on each day has been estimated relatively. The absolute size of the population on each day can be determined graphically as follows. A vertical (y) axis is drawn through the first day of observation. From the point on the y axis showing the total amount emerged a line is drawn parallel to the population decrease line. A vertical line is drawn

from the peak to the parallel line, and from the point where these lines meet a line is drawn parallel to the population increase line.

The colour markings were used to determine the life span (Table 3). As could be expected from the flight and emergence curves, the maximum age of the females in all the species studied seems to be about one month.

Table 3. Data on the longest-lived marked individuals. In females only individuals over 20 days old are shown. The numbers mean the numbers of individuals.

		17	18	19	20	21	22	23	24	25	26	27	28	29	30	days
C. maxillosum	♀♀					-	-	-	1	1	-	-	4	-	-	
- " -	♂♂	4	-	3	1	-	1	-	-	-	-	-	-	-	-	
H. truncorum	♀♀					-	1	2	-	-	1	3	-	2	-	
- " -	♂♂	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
O. tuberculata	♀					-	-	-	-	-	-	-	-	-	1	

The effects of death and emigration were assumed to be the same before and after the peak of the seasonal flight curve, and a survivorship curve was drawn for *C. maxillosum* females (Fig. 12).
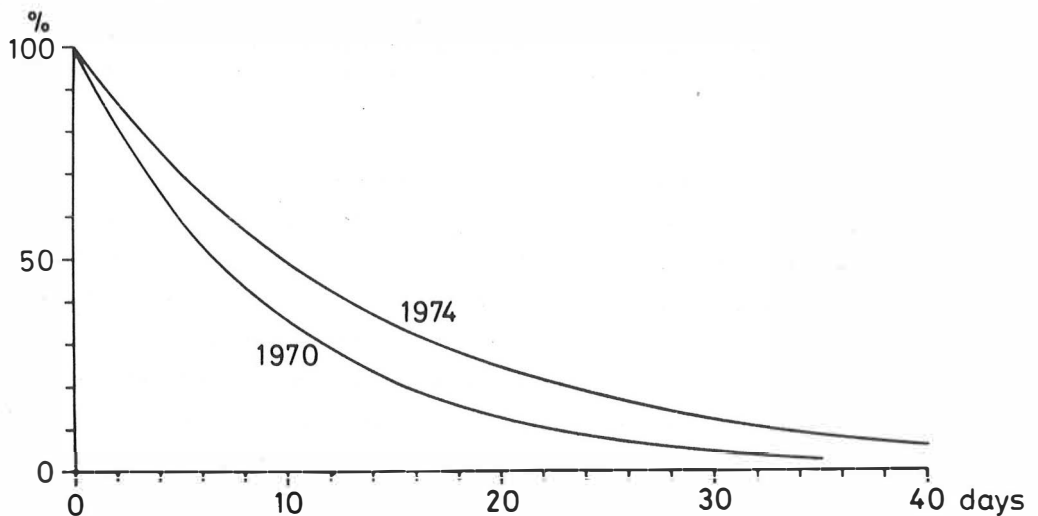

Fig. 12. Survivorship curves of *C. maxillosum* females.

It is actually the same curve as in Fig. 11, but in a different scale. The rate of decrease of the population was lower in 1974 than in 1970. In 1970 it took about 23 days for 90 % of the population to die (or emigrate), in 1974 32 days. The effect of the time spent actively on the rate of decrease was then studied. If the dates when 50 % of the population had emerged (Fig. 9) are used as starting-points, in 1970 a 90 % decrease was reached after 23 favourable days (maximum temperature 20°C or more) in 1974 after 22 favourable days. If the hours favourable for activity (above threshold temperature, Fig. 15, between 8.00 and 16.00 are calculated, in 1970 a 90 % decrease was reached after 172 hours, in 1974 after 160 hours. The ageing of a bee population seems to depend more on the time spent actively than on the actual age. HOBBS (1956), who observed longer flight periods in cold summers in a species of Megachile, came to a similar conclusion.

3.2.4. Diurnal flight activity

In all these species the activity is concentrated around midday, and there are no clear differences between the species, except that *C. maxillosum* starts its flight slightly earlier and flies slightly longer in the afternoon than the others (Fig. 13). The occurrence of males at the barn is more irregular than the occurrence of females. The occurrence of *C. campanularum* and *H. truncorum* by the SW wall is clearly concentrated in the period 14.00 - 16.00. This is the time when that wall is in the strongest sunshine. The occurrence of these species by the NW and NE walls was negligible.

Stepwise linear regression analysis was performed to clarify the significance of different weather factors for flight activity. The calculations were done in two ways: (1) by using the original numbers, (2) by calculating a curve that fits the population trend and then using percentage deviations from this trend. Only the results from the SE wall were used in the calculations. With *C. maxillosum* females and the total bees, the percentage deviations gave better results. With the other species, which showed no clear peak in the flight season, the original numbers gave better results. In most cases the results of regression analysis were not significant and the regression model does not seem to explain the flight activity (Tables 4 – 5).

The best correlation was generally obtained with light and then with
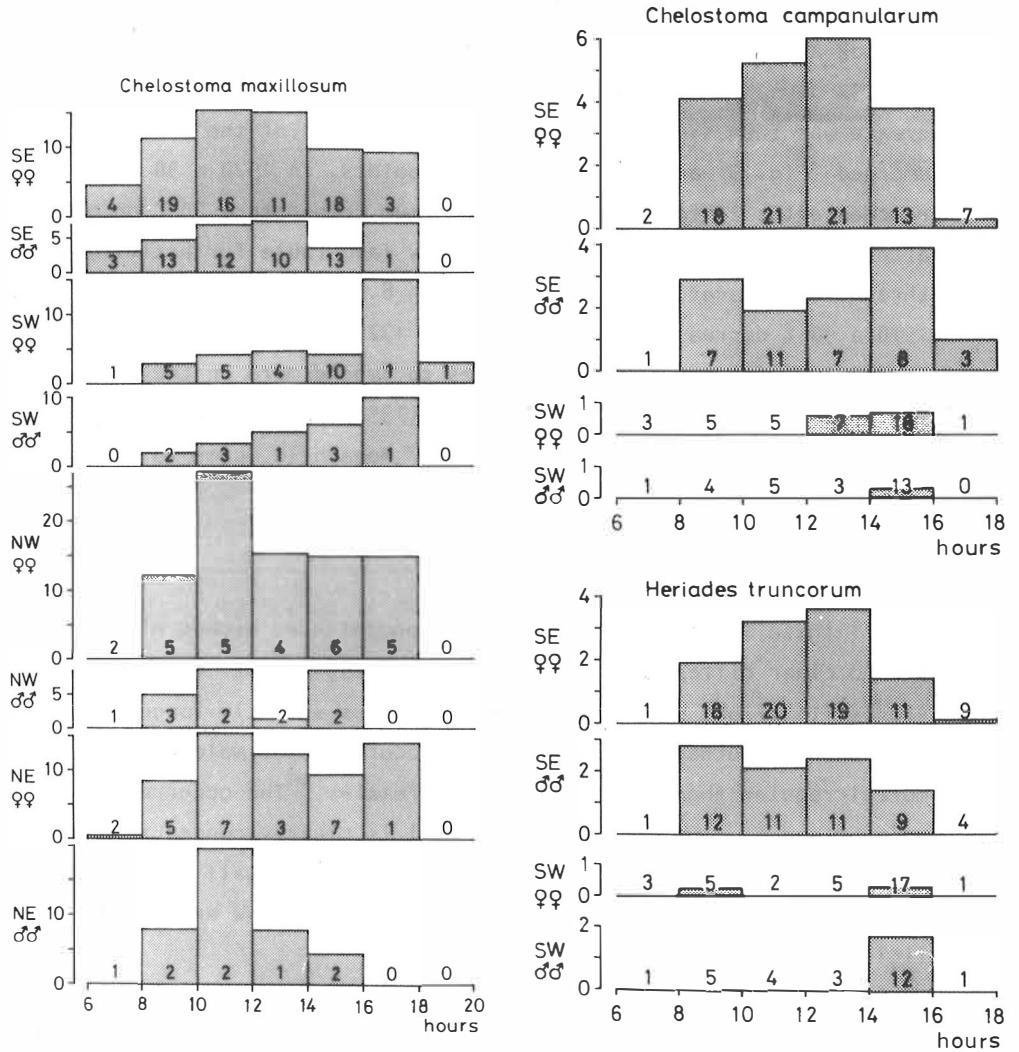
Fig. 13. Diurnal flight activity of bees by different walls of the barn. The height of the columns is the mean number of bees caught within 15 min during the flight seasons of each species and sex. The numbers of observations are given at the base of each solumn.

temperature and relative humidity. Wind had no significant correlation in any case. The picture was obscured by strong correlations between the weather factors.

Comparison of the activity of the females suggests that the smaller the species, the more its flight depends on weather conditions (cf. KÄPYLÄ 1974).

Table 4.   The results of stepwise linear regression analysis of the effect of weather factors on flight activity in bees. Only the significant results are shown. C.D. = coefficient of determination (100 x multiple r^2).

	All bees % dev.	C. max. ♀♀ % dev.	C. camp. ♀♀ orig.	H. trunc. ♀♀ orig.	H. trunc. ♂♂ orig.
C.D. Light	19.4	9.1	4.1	15.0	3.8
C.D. Temperature	4.7	5.5	22.8	0.5	14.8
C.D. Rel. humidity	0.7	1.4	2.4	4.4	0.0
C.D. Wind	0.9	2.0	0.7	1.9	0.0
C.D. Multiple regression	25.7	18.0	30.0	21.8	18.6
Significance of the multiple regression	p <0.001	p <0.025	p <0.001	p <0.01	p <0.05

Table 5.   Matrix of correlation coefficients between the weather factors and the activity of bees. The significance level is shown by the following symbols: ^{O} (P < 0.1), * (P < 0.05), ** (P < 0.01), *** (P < 0.001).

	n	Wind	Temp.	R. hum.	Light
Temperature	121	-0.17^O			
Rel. humidity	121	0.13	-0.70^{***}		
Light	121	0.10	0.32^{***}	-0.28^{**}	
Bees together, % dev.	121	-0.10	0.35^{***}	-0.32^{***}	0.44^{***}
C. maxillosum ♀♀, % dev.	71	-0.07	0.17	-0.00	0.30^{**}
- " - ♂♂, orig.	45	-0.14	0.36^*	-0.18	0.11
C. campanularum ♀♀, orig.	71	0.04	0.49^{***}	-0.46^{***}	0.40^{***}
- " - ♂♂, orig.	36	-0.18	0.36^*	-0.32^*	0.08
H. truncorum ♀♀, orig.	69	-0.11	0.28^*	-0.33^{**}	0.39^{***}
- " - ♂♂, orig.	47	0.01	0.39^{**}	-0.27^O	0.35^*

The flight activity of males does not correlate well with the weather conditions.

The effects of weather conditions can best be explained with threshold values (Figs. 14 - 15) obtained by a method decribed by TAYLOR (1963). The observations are scored as + (catch) or - (no catch), and the percentage of + values is then calculated for each weather value. The threshold value corresponds to the point of 50 % + observations. The temperature thresholds are quite clear (Fig. 14). The temperature threshold of C. maxillosum is 16.5^O, and the same result was obtained from the SE wall as from the other,
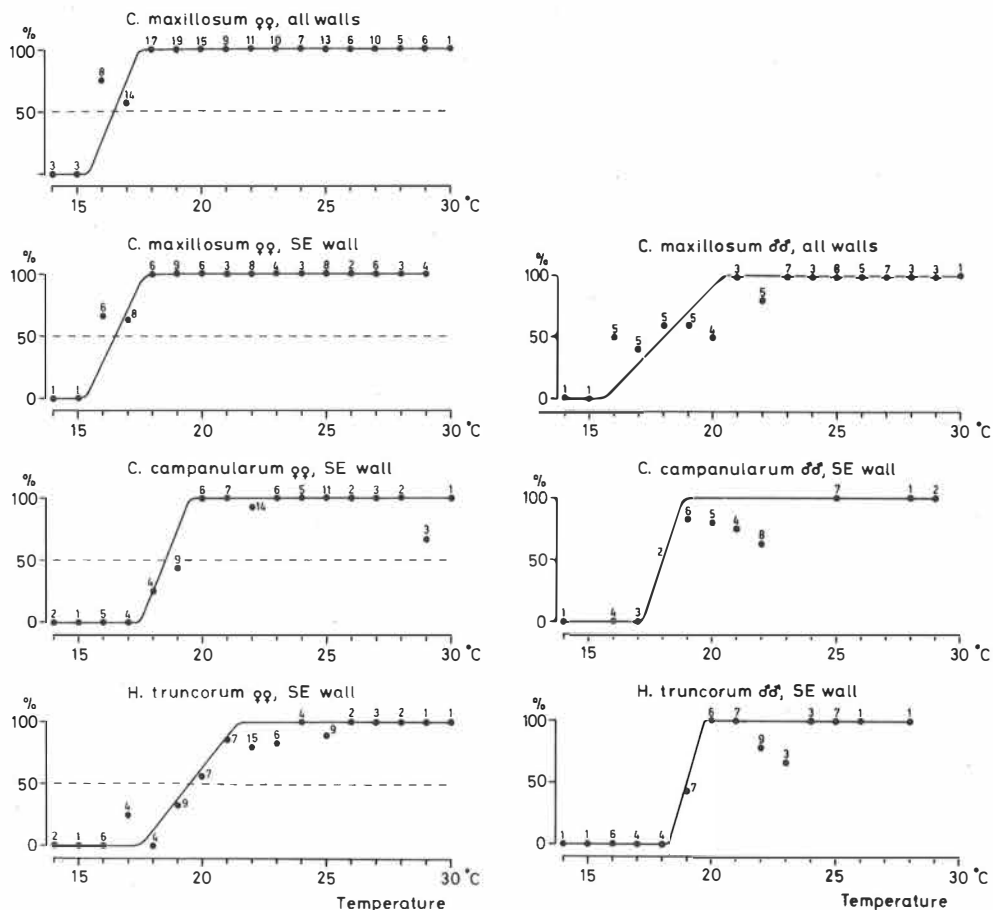
Fig. 14. Temperature thresholds of the bee species studied. The observations made within the flight seasons of each species and sex are included, their numbers being shown above each dot. Further explanation in text.

generally colder walls. This suggests that the temperature at the nest entrance is decisive. The NW wall warms up much slower in the morning than the sunny walls. Accordingly the bees start their flight later from the NW wall (Figs. 13 and 16) even if the weather in the field is favourable for foraging earlier. The result is not as clear for males of this species; their temperature threshold is probably also 16.5°, but 100 % values are reached only at temperatures above 20°. This is because at lower temperatures the males seek out sunny places, such as the leaves of bushes, to bask in the sun. Females also sometimes spend some minutes basking

in the sun beside the nest entrance before flying away in the morning.

The temperature threshold is about the same in the two sexes in two of the other species, 18 - 18.5° for *C. campanularum* and 19° for *H. truncorum*. The temperature threshold of *O. tuberculata* seems to be about 16° (Fig. 28).

The light thresholds are not as clear (Fig. 15). This is partly because the observations were mainly made in full sunshine. The material for the males was too meagre for diagrams, but their light thresholds seem to be about the same as those of the females. The light threshold of *C.*
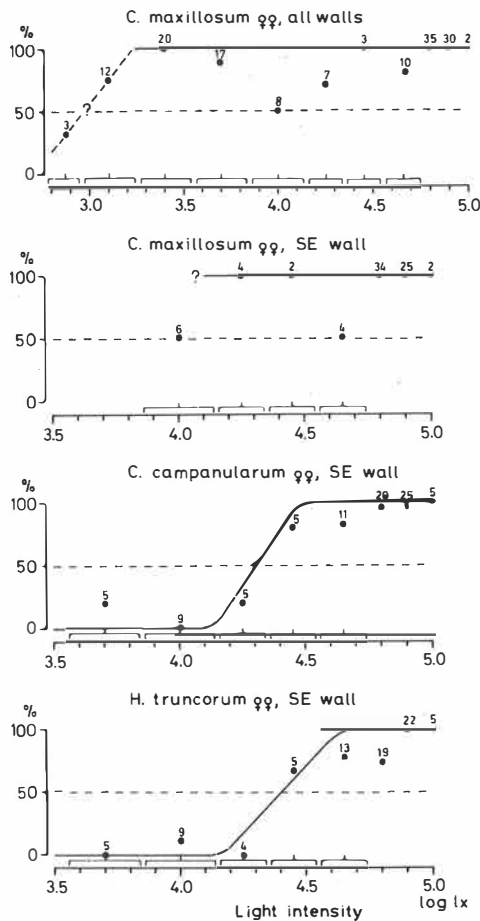
Fig. 15. Light thresholds of the bee species studied. Further explanations in text and in Fig. 14.
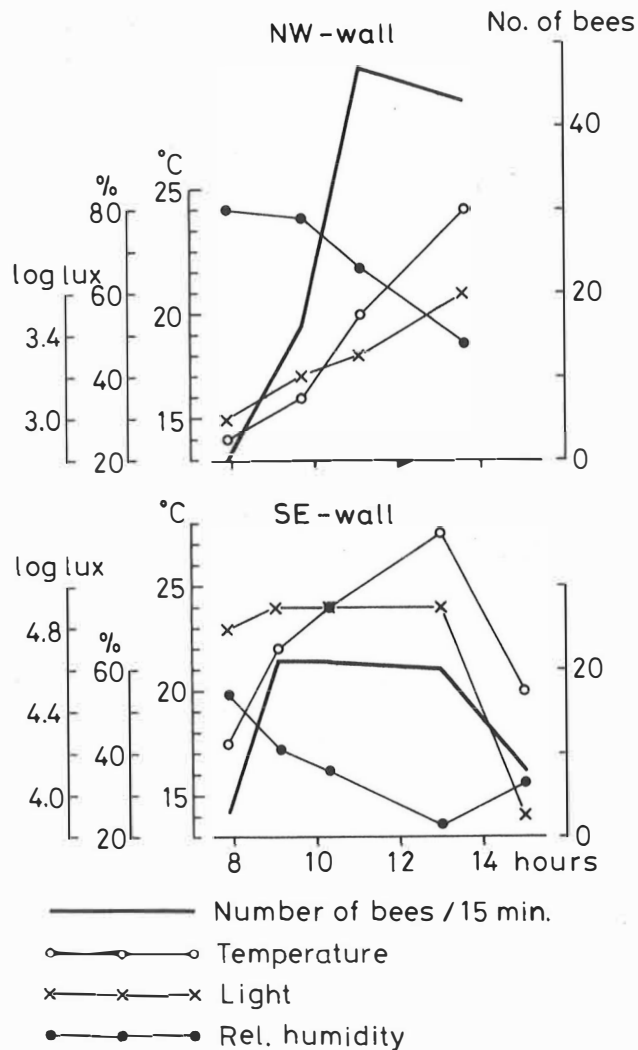
Fig. 16. Flight activity of *C. maxillosum* females and weather conditions by the sunniest (SE) and shadiest (NW) walls of the barn, 16.VI. 1970.

maxillosum is low and was not reached in this study. The light thresholds of *C. campanularum* and *H. truncorum* seem to be about 25000 lux.

The flight activity cannot be explained by a temperature threshold alone, because the activty increases as the temperature rises (Fig. 17). This may be explained in two ways

(1) The temperature threshold differs between individuals. Some individuals

were often seen to remain in their nests while the others were flying. This was observed in both the morning and evening, and also at midday, in temperatures below 20°.

(2) The more favourable the weather, the more active the insects are and the bigger the size of the catch. The optimum temperature for *C. maxillosum*
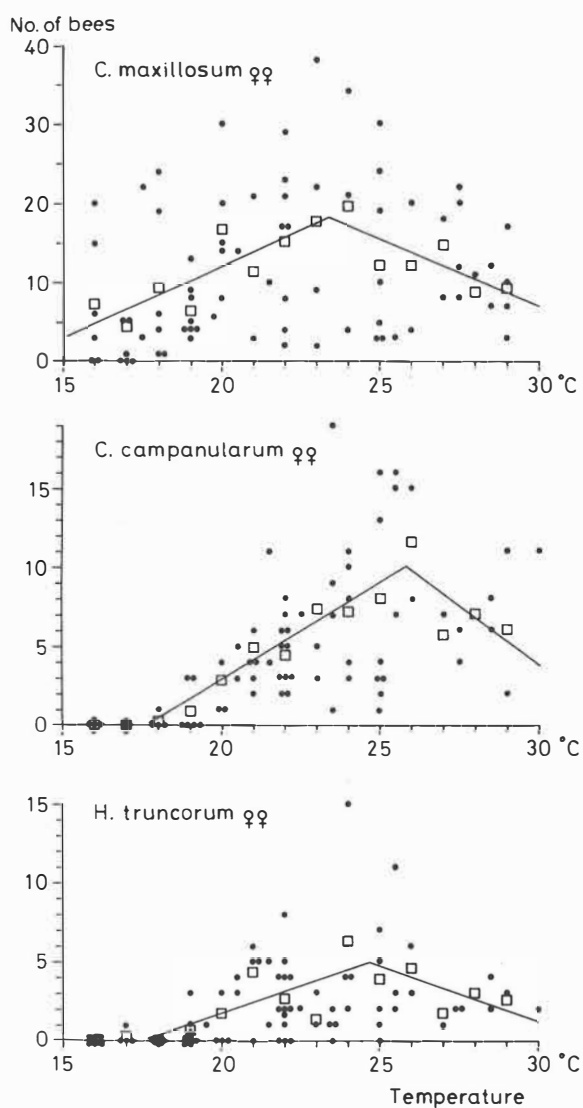
Fig. 17. The effect of temperature on flight activity. The whole scatter is shown by the black dots. The squares are the means corresponding to each degree of temperature (next half degree included). The regression lines are given for the left and right sides of the peaks.

females seems to be about 24°, for *C. campanularum* females about 26° and for *H. truncorum* females about 25°. Above this temperature catches become smaller. The upper thresholds were not found for temperature or light. If the lines in Fig. 17 are continued to the right, it seems that the upper temperature thresholds may lie somewhere between 30 and 32°.

Sunshine may affect the activity of insects directly or by raising their
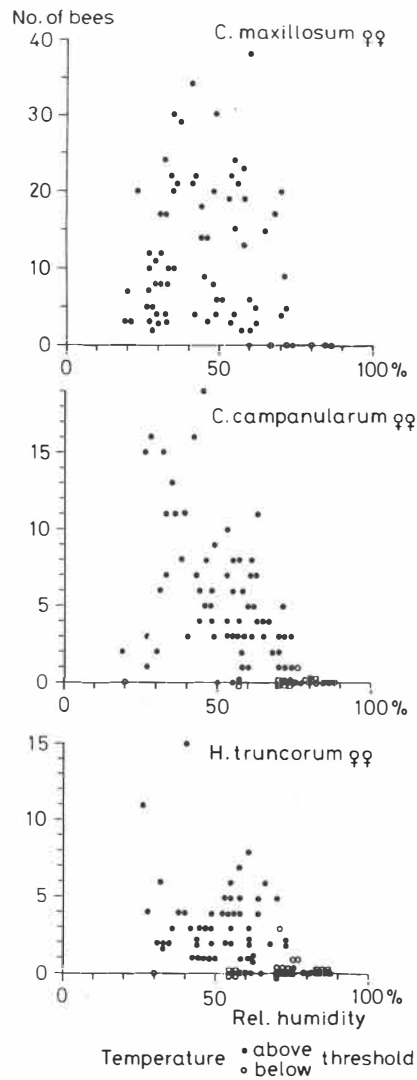
Fig. 18. Relative humidity and flight activity.

body temperature above the ambient temperature. The indirect effect has been demonstrated by, e.g., PARRY (1951), DIGBY (1955), MÜNSTER-SWENDSEN (1968) and SOLBRECK (1976). SZABO & SMITH (1972) found a dual light and temperature threshold for flight commencement in *Megachile rotundata*. Aculeate bees and wasps have been observed to start their flight at lower temperatures during sunshine than in cloudy weather (KÄPYLÄ 1974). In the present material this combined effect of temperature and sunlight is not evident. The multiple correlations of light and temperature with the catches of bees were not substantially higher than the separate correlations (cf. Tables 4-5). Thus the activity of the bees can best be explained with separate light and temperature thresholds. Either one of these may be limiting. In the morning, the rising temperature usually determines the start of flight activity. In the evening, the light most often becomes limiting first (cf. ABRAHAM 1975).

The high negative correlations between the activity of bees and relative humidity are probably due to the intimate correlation between relative humidity and temperature. When studied graphically (Fig. 18), relative humidity does not seem to have any meaning within the values met with in this study.

Wind does not normally seem to have any effect on flight activity, but may decrease it in two ways: (1) by making flying difficult when it is strong, (2) by increasing convection and promoting the escape of warmth from the insects body (DIGBY 1955). In the latter case it may raise the temperature threshold. Winds hard enough to make flying difficult are usually found only in conditions when some other factor is already limiting, I saw bees foraging in wind which apparently made landing on flowers very difficult.

4. Nesting behaviour

4.1. Occurrence of bees by different walls

Direct counting of *C. maxillosum* nests was made possible by the conspicuous end plugs (Fig. 24). In this species the occurrence of nests corresponds well with the occurrence of bees (Fig. 19), and this has been supposed to be the case with the other species, as well.

C. maxillosum lived in all the walls, but the majority of the individuals were found in shady northerly walls. In contrast, *C. campanularum* and *H. truncorum* were clearly concentrated by the sunny walls, especially the SE wall. In 1970 some individuals of *C. campanularum* were occasionally found
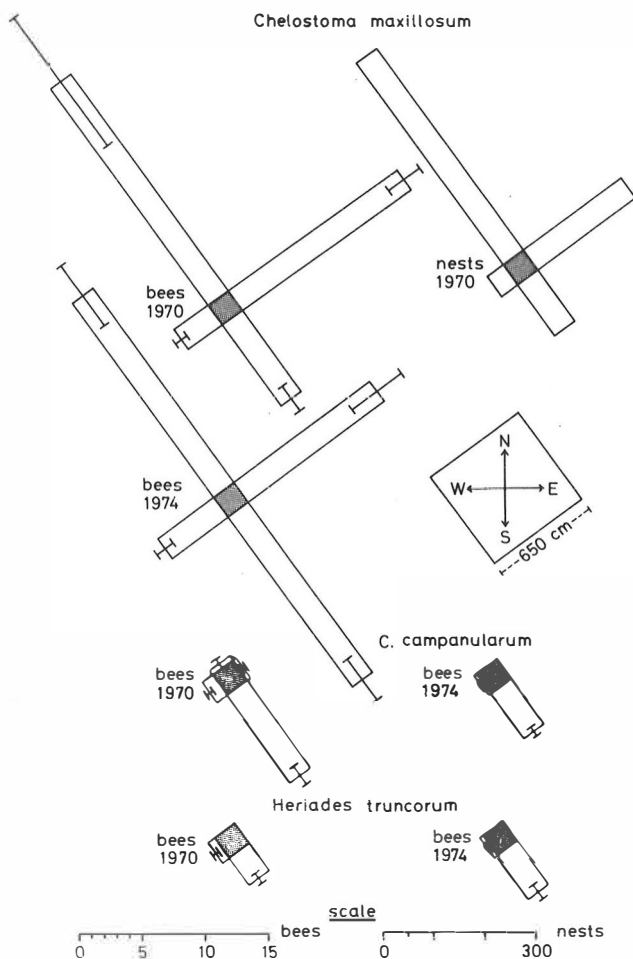
Fig. 19. The occurrence of female bees and *C. maxillosum* nests at different walls. The scale for bees is the mean number caught within 15 min during the flight periods of each species and year. The standard errors of the mean are shown at the tops of the solumns. The columns for nests represent the absolute amounts.

by northerly walls, but none was observed to nest there.

The numbers of *C. rapunculi* and *O. tuberculata* were too small for diagrams. *C. rapunculi* was found only by the SE and SW walls, slightly more by the former. In 1970 the only nest was found in the SW wall. In 1974 two nests were found in the SW wall and four in the SE wall. *O. tuberculata* was found only by the SE wall, in which all the nests were situated (Fig. 20).

NW-wall   489 nests

SE-wall   123 nests

NE-wall   239 nests

SW-wall   38 nests ⊢————— 1 m
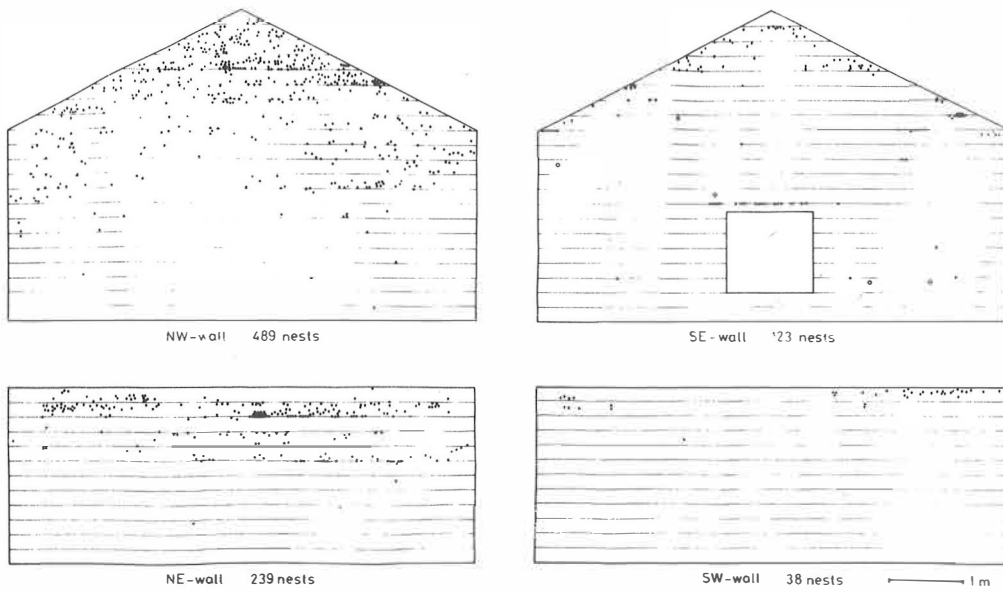
Fig. 20. The location of the nests of *C. maxillosum* (black dots) and *O. tuberculata* (small circles) in 1970.

NW

SE

NE

SW
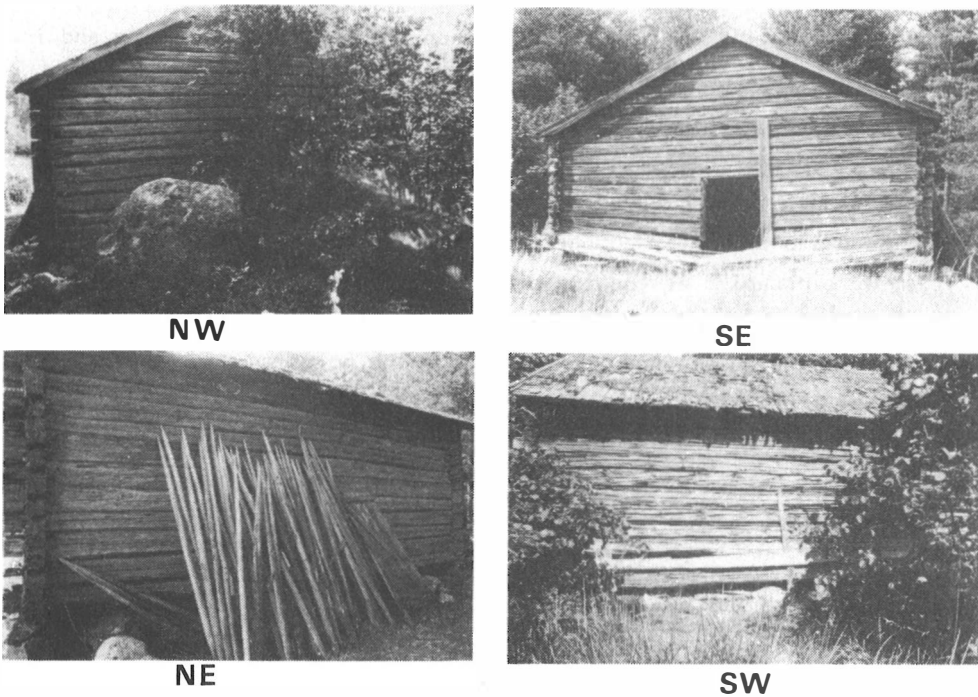
Fig. 21. The walls of the study barn.   Photo M. Käpylä, 12.VIII. 1972.

The location of the C. maxillosum nests indicates a preference of shade (Fig. 20). The nests were widely scattered in the NW wall, but were concentrated in its upper part. The lower part was shaded by a rock and hazel bushes (Fig. 21), and was also partly decayed. It was probably too moist or too shady for nesting. There seemed to be no clear difference in the availability of suitable nest holes between different walls and between the upper and lower parts of the walls, but this was not actually studied.

The NE wall was in sunshine in the morning. When the sun was shining directly on this wall, it was shaded by the big lime tree in Fig. 2. In this wall the nests were clearly concentrated in the shadow of the eaves. In the northern part of this wall, which remained longest in the shadow of the lime tree, there were some nests lower down in the wall, as well. No nests were found under a pile of stakes, propped against the southern end of the wall.

In the SE wall the nests were situated in the shadow of the eaves and in shadow in slits between some logs, especially in the slit just above the door opening (Fig. 21). The small increase of the population in 1974 was mostly due to bees coming to the SE wall. This was probably because the barn was decaying and the slits between the logs were widening and increasing. The nests were not counted in 1974.

In the SW wall the nests were restricted to the shadow of the eaves. There were fewer nests in this wall than in the others, perhaps because it was the most badly decayed.

There was evidently competition for nest holes, because almost all of them were occupied at the end of the season. Besides these bee species, there were scores of other aculeate Hymenoptera (belonging to Sphecidae, Eumenidae and Pompilidae) competing for the holes as well as the nest parasites of these wasps and bees. The occurrence of these other species is dealt with in a separate paper.

4.2. Nest structure

The study of nest structure was not originally included in this investigation and is impossible when the nests are located in thick logs. The best method would have been to use trap nests, but this would have disturbed the population during the study. Observations were made at the nest entrance on the foraging behaviour and the construction of the end plugs and cell partitions. In this section the nest construction is described mostly according to the

C. rapunculi

K E | Dl1 | Aσ | E | Sm♀ | Aσ | E | 5

K E | A♀ | Aσ | Aσ | Dl1 | Dl2 | Dl1 | Dl1 | Dc | E | E | 5

| Sm♀ | Sm♀ | E | Ax | E | 4

C. campanularum

Dl1 Aσ   E   2

H. truncorum

A♀ | Aσ | Aσ | E | 3   Dc | Sb♀ | Aσ | E | 3.5

Sb♀ | Dl2 | Dl1 | E | E | 3.5

Dc   Aσ   Dl2   Dl2   E | 2.5

0 ———— 30 mm
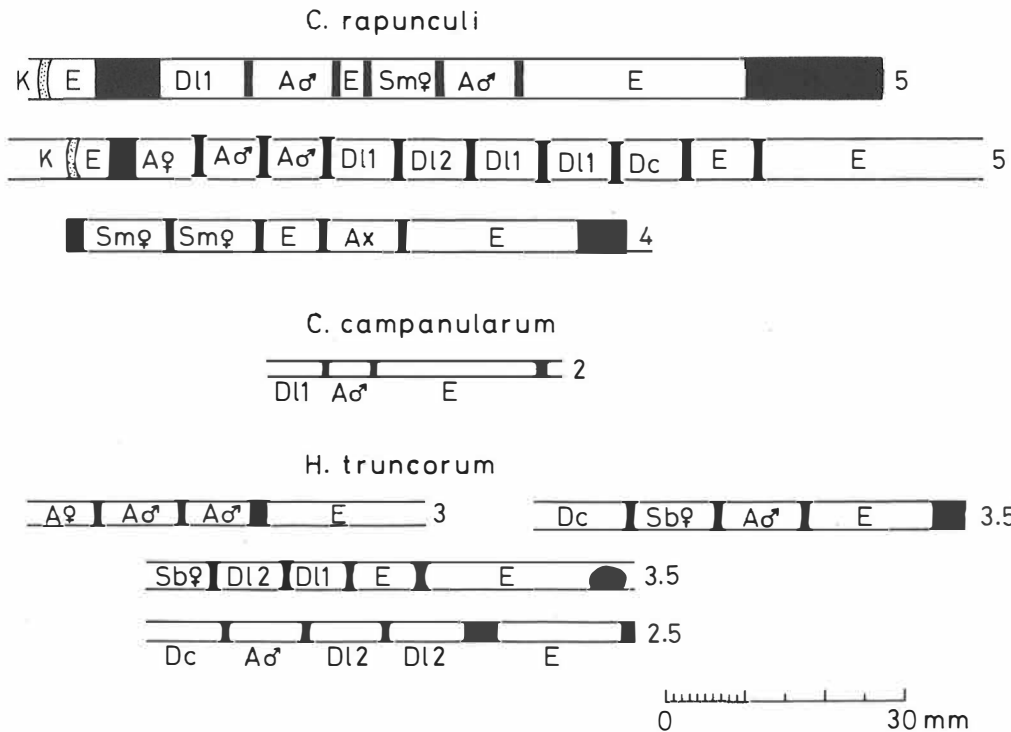
Fig. 22. Structure of the nests in straws placed in holes drilled in wood.
For the material of the end plugs and partitions, see Table 6 and text. In
these nests of *H. truncorum* the material was pure resin, except the small
terminal plug of the last nest, which was a mixture of earth and resin. The
diameter (mm) of the nest is given beside the outer end. A = adult bee emerged,
Sm = *Stelis minima* emerged, Sb = *Stelis breviuscula* emerged, Ax = *Anthrax* sp.
(Diptera) emerged, Dl1 = died during early larval or egg stage (uneaten pollen),
Dl2 = died during later larval stage (after defaecation), Dc = died inside
cocoon, E = empty space, K = knot in straw.

available literature. In 1974 some trap nests made of straw of varying di-
ameter were placed in holes bored in logs of the barn. The straws were not
accepted by the bees unless put right inside the wood. The results of this
small material are presented in Fig. 22.

The bee species studied mostly nest in wood, in pre-existing holes. In-
formation on the nest structure has mainly been obtained in those rather
exceptional cased when the bees have been found nesting in straws. Lately
trap-nests have also been used.

This short general account is based on the literature referred to in
Table 6. My own observations mostly agree with the earlier descriptions. I
have not found any records on the nest structure of *O. tuberculata*, so I have
used observations made with other species of Osmia with apparently similar
nesting habits.

The nest holes are preferably just big enough for the bee to enter, and
the cells are arranged linearly. The sides of the cells are unlined; only

Table 6. Some details about the nest structure. (1) My own observations, cf. Fig. 22 and text, (2) MARECHAL 1933, (3) VAN LITH 1957, (4) GRANDI 1961, (5) CORREIA 1976a, (*) average, (**) unusual values omitted.

Species	Diameter of nest cavity (mm)	Length of cells (mm)	Number of provisioned cells per nest	Length of terminal plug (mm)	Material of terminal plug and transverse partitions
C. maxillosum	3-4 (1) 3-4 (2) 3-5.5 (3)	8-15 (2) 9.5-16 (3)	2-10 (2) 2-6 (3)	2-4 (2) 6 (* 3)	Loam and small stones (2,3). Earth moistened with nectar and probably also with saliva (1).
C. rapunculi	4-5 (1)	8-11 (1)	3-7 (1)	5, 17, missing (1)	Same as in C. maxillosum (1).
C. campanularum	2 (1) 2-2.5 (4)	6 (1) 7 (4 **)	2 (1) 2-4 (3)	1 (1)	Loamy earth (1,4)
H. truncorum	2.5-3.5 (1) 3-4 (4) 2.5-5 (5)	8-12 (1) 8-11 (4 **) 8-9 (5)	3-4 (1) 2-3 (4) 2-4 (5)	2-4 (1) 2-5 (4) 2.7-3.3 (5)	Resin (1,4,5), a mixture of earth and resin (1,4), a mixture of decayed wood and resin (1), a mixture of pieces of plants and resin (5)
O. tuberculata	6 (1)				Sand grains, pieces of decayed wood and pieces of masticated leaves (1).

transverse partitions are made between the cells. The outer end of the nest hole is closed with a terminal plug, whose thickness and composition vary. The transverse partitions and end plugs are of the same material. Comparatively dry pollen moistened with a small amount of nectar is placed on the bottom of the cell (moist, dough-like in *C. campanularum*, according to MALYSHEV 1935: 248) and the egg is laid upon it.

These bees are univoltine. Species of *Osmia* are known to hatch in late summer, pass the diapause as adults and emerge next spring or early summer (MAETA & KITAMURA 1968, TASEI 1973, HAWKINS 1975). Species of *Chelostoma* are said to hibernate as larvae (MALYSHEV 1935: 295) or in both the larval and pupal stage (MARECHAL 1933, VAN LITH 1957). *Heriades truncorum* hibernates in the last larval stage (prepupa) (CORREIA 1976a). I collected the trap nests (Fig. 22) on 16.V. and opened them on 26.V. By that time one *C. rapunculi* ♂ and one *H. truncorum* ♂ had hatched. All the other individuals were at the pupal stage.

C. maxillosum makes its end plug from earth. According to a microscopical study, the end plug consisted of soil particles of all size classes from clay to sand. The bee was seen collecting earth from the road and the side of a ditch, and carrying it between its mandibles to the nest. The earth is then moistened and carefully placed in the nest hole (Fig. 23). The time spent in making a terminal plug is given in the next section (4.3.). The liquid used to moisten the earth must be nectar: the stomachs of some individuals caught while carrying earth to the nest contained large amounts of nectar. When just finished, the terminal plug is dark and moist. I
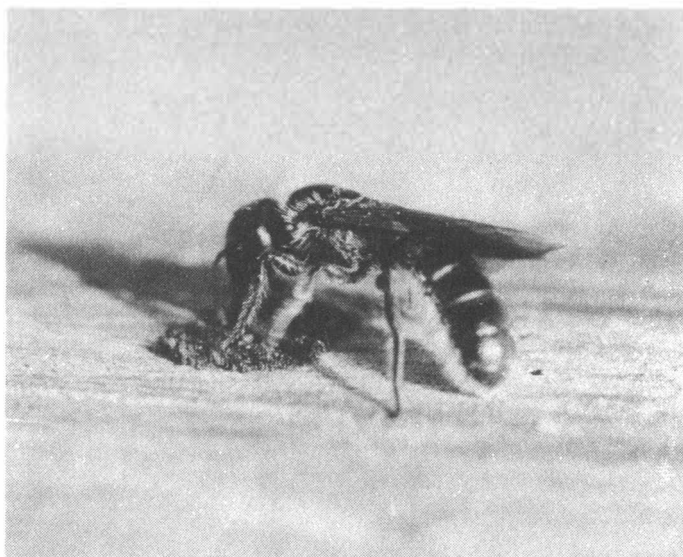
Fig. 23. *C. maxillosum* female making a terminal plug. The bee turns slowly around the nest hole, head facing inwards, arranging the earth with her mandibles and moistening it with regurgitated nectar. Photo M. Käpylä.

removed the projecting outer parts of two plugs for chemical analysis, and they contained 2.1 and 3.7 mg of sugar. The older plugs are lighter and break more easily; they contain very little sugar because the rain has washed it away. An observation of VAN LITH (1957) also indicates that nectar is used as a moistening liquid: *Lasius* ants repeatedly licked a moist unfinished plug when the bee was away. It seems that the female first goes to flowers to collect nectar, then takes some earth, comes to the nest and starts preparing the plug. Saliva is probably also used to bind the soil particles. This could explain the elasticity of the transverse partitions observed by VAN LITH (1957). The appearance of the finished terminal plug is very characteristic (Fig. 24). It projects out of the wall and extends over the margins of the nest entrance. By late summer this outer part has dropped off from some of the nests, and a characteristic loamy ring is seen around the hole. MARECHAL (1933) has reported this type of end plug in some nests but not in nests situated in straws.

Thatched roofs are commonly reported as nesting sites of *C. maxillosum* in Central Europe (FRIESE 1923: 229, VAN LITH 1957). FRIESE (1923: 229) also reports nests in the clay walls of barns. In Finland I have sometimes
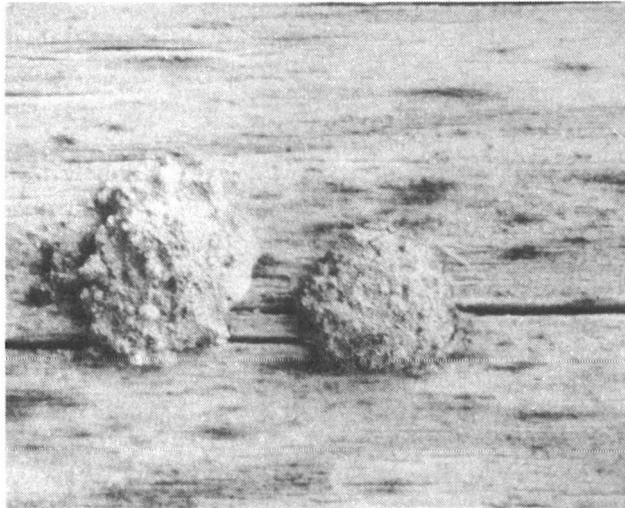
Fig. 24. Finished terminal plugs of the nests of *C. maxillosum*. Photo M. Käpylä.

found this species by vertical sand banks, where it may also nest.

C. rapunculi makes transverse partitions and end plugs from material similar to that of *C. maxillosum*. According to E. Valkeila (personal communication), its end plugs also project, but in all the nests found in Seili the end plug never reached beyond wall level. The females were seen several times collecting earth from the road in their mandibles. One female caught while collecting earth regurgitated a large drop of nectar on my hand, and analysis of part of an end plug scratched into a test tube showed that it contained sugar. Thus nectar is evidently used to moisten the earth in end plugs in this species as well. In the barn, the species nested in fairly wide cavities (4-5 mm), although 3 - 4 mm would have been enough. Other species seemed to favour as small cavities as possible.

C. campanularum nests in smaller cavities than the other species. They are often so narrow that part of the pollen load is removed when the bee backs in, and a ring of pollen thus forms around the hole. This also happens in the smallest nests of *C. maxillosum*.

The end plug made of loam is at first level with the wall, but usually shrinks a little on drying. In the trap nest (Fig. 22) the end plug was short and ended inside the nest. It had perhaps not been completed for some reason. No sugar test was done on the end plug of this species.

H. truncorum makes the end plugs from pure resin or resin mixed with grains

of sand or plant material. In some of the nests there were pieces of wood mixed with the resin in the outer part of the end plug. Females were several times seen gnawing wood from walls with their mandibles. The purpose of this behaviour is probably to camouflage the nest entrance (cf. MATTHEWS 1965).

O. tuberculata makes the end plugs and transverse partitions from small stones, masticated leaves and pieces of rotten wood, all taken from the proximity of the nest. The flights undertaken while making the end plug follow each other with very short intervals. The particles in the end plug are not cemented together and pieces can easily fall off. The purpose of the elastic pieces of masticated leaves is probably to press the particles together in the plug. There are no direct observations on the inner structure of the nest in this species.

4.3. Activities of females observed at the nest entrance

In 1974 some bees were watched continuously at the nest entrance; their behaviour is presented in Figs. 25-30 and Table 7. The following comments refer to the encircled numbers in the figures.

Fig. 25. (1) A strange conspecific female visited the nest several times while the resident female was away, (2) Seven trips of 1.5 - 2.5 min duration to collect material were each folowed by working periods of 1 - 3 min. The two preceding long trips were probably to collect neactar for making the transverse partition, (3) Behaviour before going to sleep: a 14-min trip to collect nectar (?); 30 min with the head at the entrance, after which the bee turned in the entrance and assumed a typical sleeping position (cf. Fig. 31), (4) The terminal plug was finished and the bee flew away, (5) The bee went into the nest several times and probably found it too short; then went into another cavity half a meter away to spend the night, (6) Weak rain from 14.25 to 15.00, (7) The bee was in a typical sleeping position until 10.10., when it turned at the nest entrance and stayed with its head near the entrance, (8) The bee spent some time beside the nest hole but went back in, (9) For some reason the bee had abandoned its former nest and studied other cavities, bringing out litter from one.

Fig. 26. (1) The bee accepted a trap nest at about 10.25. Between cleaning it made short search flights, (2) After the bee had left a *Stelis* entered. (3) The bee flew away and did not continue making this nest, (4) The bee was caught and accidentally slightly narcotized, (5) The bee went into the nest at 16.06, flew away at 16.15 and did not come back before 16.40, when observation ended. Next morning at 7.00, it was in its hole in a typical sleeping position, abdomen outwards.

Fig. 27. (1) *Stelis breviuscula* entered while the resident bee was still in, (2) The bee pushed pollen out of the nest. (3) The bee made a circuit flight before going in. Afterwards it went in several times within a short
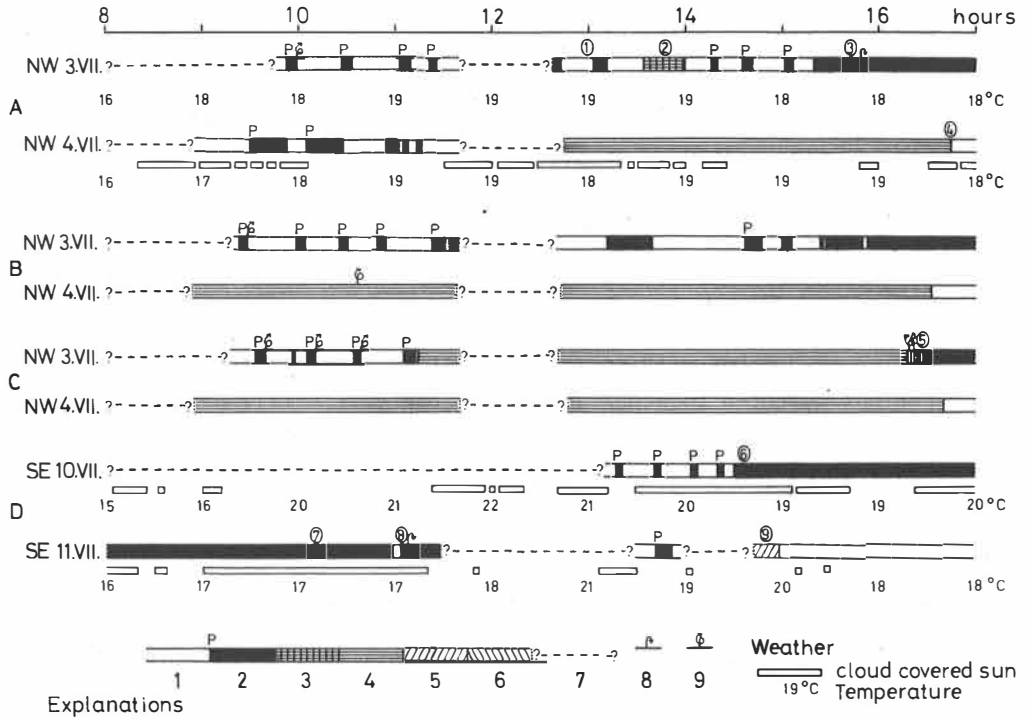
Fig. 25. Behaviour of four (A, B, C, D) *C. maxillosum* females observed at the nest entrance in 1974. Explanations: (1) out, (2) in, P = with a pollen load, (3) making a transverse partition, (4) making a terminal plug, (5) searching for a suitable nest cavity, (6) cleaning and studying a new nest cavity, (7) no observations, (8) turned at the nest entrance, (9) orientation flight.
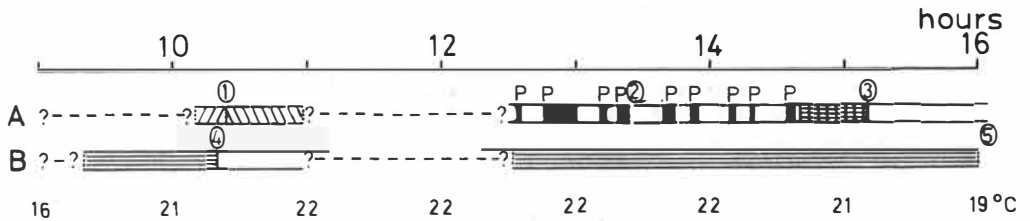
Fig. 26. Behaviour of two (A, B) females of *C. rapunculi* observed at the nest entrance in the SE wall on 24.VII. 1974. For explanations see Fig. 25.

period, making circuit flights between. (4) The same pollen load was intact all the time. (5) The bee made short flights and came back immediately, watched with its head at the entrance, and then turned and assumed a typical sleeping position with its abdomen about 5 mm inside the nest. The weather became cloudy but the sky cleared after 14.15. The nest was checked at 15.25 and 18.00 and the bee was away.
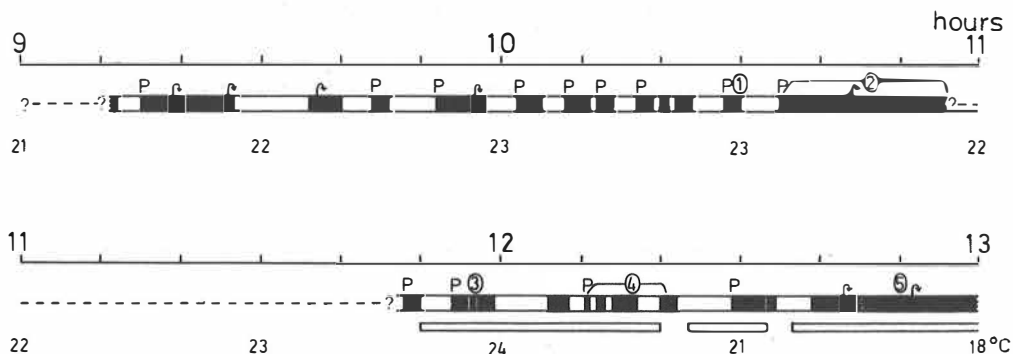
Fig. 27. Behaviour of one *H. truncorum* female observed at the nest entrance in the SE wall on 5.VIII. 1974. For explanations see Fig. 25.

Fig. 28. (1) The observation period began at 7.30. At 8.06 the bee came out, basked in the sun for about 4 min and started to study cavities in the wall, basking for short periods in between. (2) The bee went in and out at short intervals, facing forewards as well as backwards; in most cases no material was seen to be carried out. Besides cleaning the purpose of this behaviour is probably also to test the suitability and size of the cavity. (3) The bee went in head first, after a while it turned at the entrance and backed in. It stayed about 14 min with its head at the entrance, after which it turned and assumed a sleeping position with its abdomen outwards. (4) The behaviour pattern of the previous day was repeated before the bee settled for the night. (5) Rain until 14.30. (6) The bee was facing outwards and sometimes came half out. (7) When the bee worked its abdomen out, a *C. maxillosum* male tried three times to copulate with it. (8) The nest was finished. (9) A *Stelis phaeoptera* female visited the nest three times when the resident bee was away. When the bee arrived next time, it was caught and the pollen load was removed.

Searching for a suitable nest cavity is an easily recognized behavioural pattern. The bee flies slowly around the wall facing it. It investigates and often enters, the holes and then continues its flight.

Cleaning the nest cavity follows the acceptance of a hole, which seems to happen quite abruptly. Litter is carried out in the mandibles; the bee makes a short flight, drops the litter and goes back into the cavity. No orientation flights were observed while cleaning a new nest cavity. The occupation of a newly made nest by another female was observed twice: once
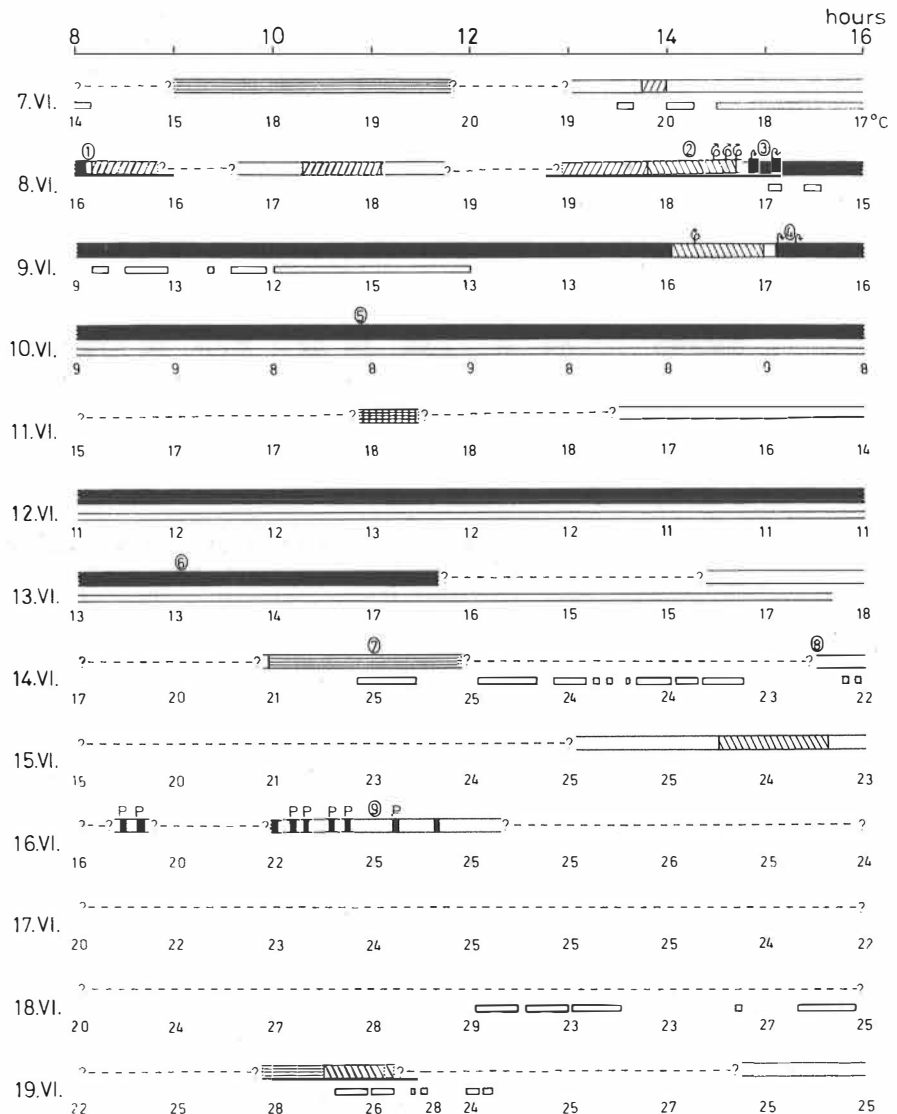
Fig. 28. Behaviour of one *O. tuberculata* female observed at the nest en-
trance in the SE wall in 1974. For explanations see Fig. 25. This individ-
ual was caught and marked on 5.VI. at 11.25. On 6.VI at 9.00 it was caught
when coming with a pollen load, and the load was removed. It was not seen
again that day.

in *C. maxillosum* and once in *H. truncorum*. In both cases the females pushed
out pollen from a nest that had apparently belonged to one of their own
species, judging from the pollen , which in the former case was of *Ranunculus*

and in the latter of mixed *Achillea* and Liguliflorae type. The nests prob-
ably lacked end plugs, the resident females having died before the nest
was finished. No fights were observed between females. Similar nest raid-
ing has been reported by MATTHEWS (1965) in *Heriades carinata* and by EICK-
WORT (1973) in *Hoplitis anthocopoides*.

Duration of foraging trips (Fig. 29). The longest trips were those of
C. maxillosum. There are no observations during the most abundant flower-
ing of *Ranunculus* to show whether these long trips were caused by a short-
age of suitable pollen. The very short foraging trips of *H. truncorum* can
be explained by the abundance of pollen offered by its food plants, most
probably *Matricaria inodora* and *Leontodon autumnalis*. In *C. rapunculi* and
O. tuberculata the foraging trips mostly lasted around 10 min. The times
reported for the foraging trips of solitary bees vary very much. In Mega-
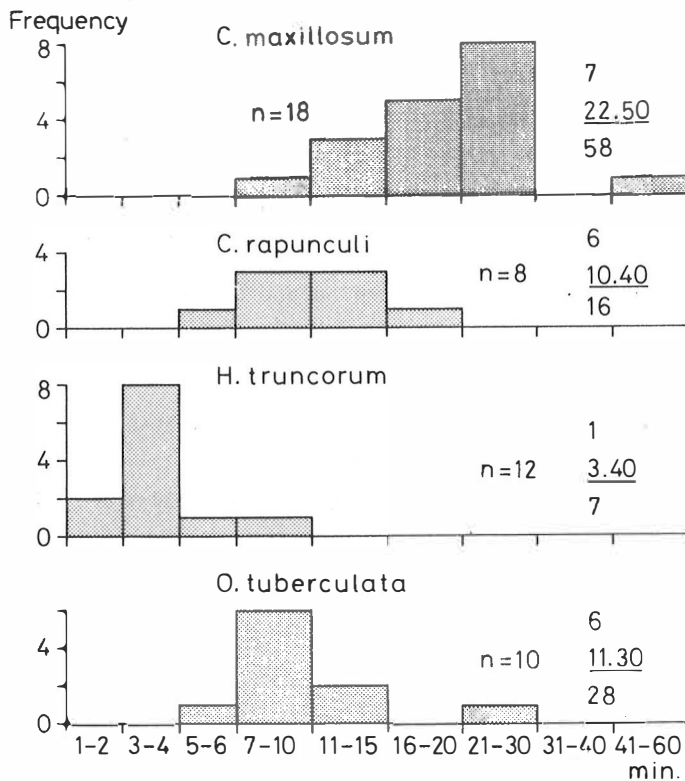
Fig. 29. The length of pollen foraging trips. The numbers on the right show
the mean (min.sec.) and the shortest and longest foraging trips.

chilidae the average duration varied from around 10 min   (MICHENER 1953, MATTHEWS 1965, KLOSTERMEYER & GERBER 1969, TASEI 1976) to about one hour (HASENKAMP 1974).   The foraging trips of other solitary bees vary within the same range (ORDWAY 1966, BATRA 1966, MÜNSTER-SWENDSEN 1968, LIND 1968, MOHAMED 1973b and c).   The duration evidently depends on the availability of pollen. The behaviour of a female returning from a foraging trip with a pollen load is usually as follows. The bee goes in head first, backs out after a while, turns at the nest entrance and backs in. After a pause the bee's head reappears at the nest entrance and the bee makes a new foraging trip. This shows that the nectar load is emptied first, after which the pollen load is brushed off with the hind legs. The nest cavity is too narrow for the bee to turn inside. The same sequence of events has been reported with *Osmia coerulescens* (TASEI 1976) and *Heriades carinata* (MATTHEWS 1965). If some exceptionally big values are omitted, the dur- ation of this sequence of events is fairly constant within a species (Table 7.). In the material of *O. tuberculata* only the shorter times (up to 2 min) are included. Two other times recorded were 10 and 17 min. In *Osmia coerulescens* the emptying of a nectar and pollen load took about 1 min (TASEI 1976).

Table 7. Time spent in emptying pollen loads and probably also nectar loads (mean and range, min:sec). A. Time from entering head first to turning at nest entrance. B. Time from turning and backing in to leaving nest.

	A	B	mean A+B	n
C. maxillosum	2:50 (1:00-6:00)	3:20 (1:30-8:00)	6:10	19
C. rapunculi	1:00 (0:30-1:55)	1:30 (0:30-4:00)	2:30	9
H. truncorum	0:25 (0:06-1:16)	2:20 (1:30-4:00)	2:45	11
O. tuberculata	?	?	1:30	5

The pollen loads carried in the abdominal scopae seem to be dry and chemical analyses gave negative results for sugar. Five sugar determina- tions were made on the pollen loads of both *C. maxillosum* and *C. campanula- rum*, three on those of both *C. rapunculi* and *H. truncorum*, and one on a load of *O. tuberculata*.

Making the end plug and transverse partitions. Much shorter working periods in the nest and flights outside were required to make a transverse
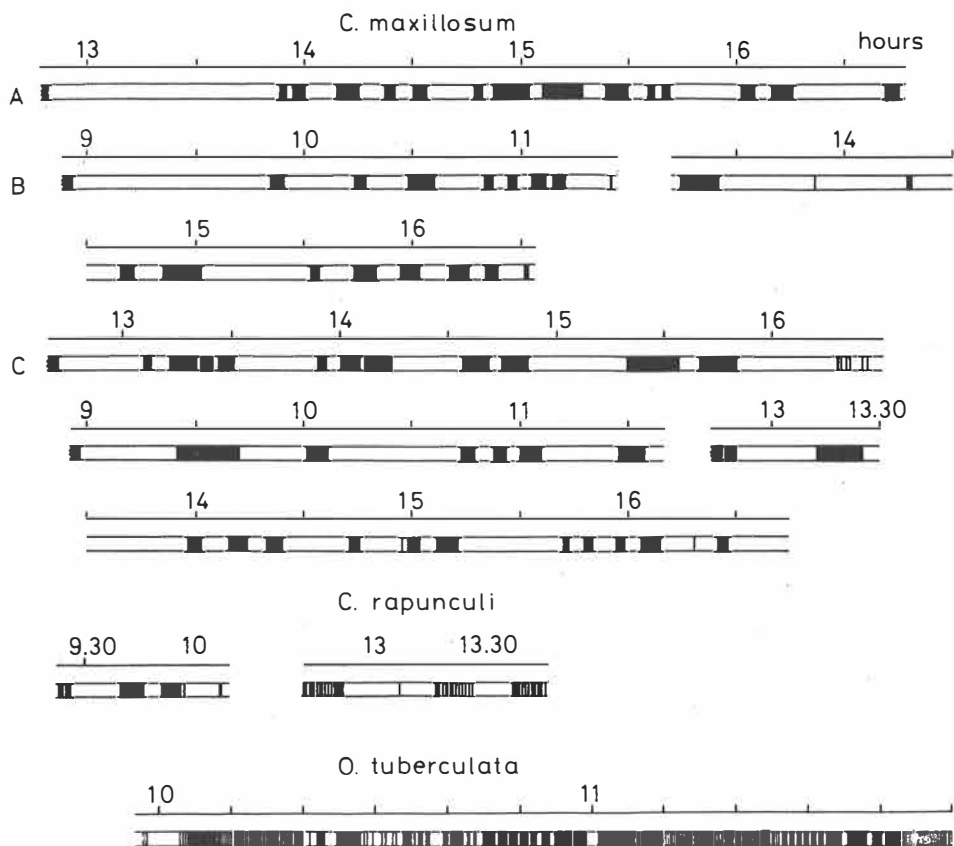
Fig. 30. Detailed observations of the making of an end plug. A, B and C
= different individuals of *C. maxillosum* (cf. Fig. 25). The observations
on *C. rapunculi* concern the individual B in Fig. 26. The observations on
O. tuberculata are from 14.VI.1974 (cf. Fig. 21). Black = bee working in
nest, white = bee out on flight. Note that the scales for the species are
not the same.

partition than to make an end plug (Fig. 24, comment 2, Fig. 30). Making
an end plug is a laborious task. In the three individuals of *C. maxillosum*
(Fig. 25), it took 4 - 5, 8 and 13 hours. The last number is equivalent to
one and a half normal days of activity. When constructing an end plug, *C.
rapunculi* makes a series of very rapid flights. This is followed by a long-
er flight, probably to collect nectar. In *C. maxillosum* both the flights
and the working periods in the nest are longer. This difference may be due
to the much bigger loads of earth carried in its extremely long mandibles;
dry earth taken from the mandibles of *C. maxillosum* was found to weigh 1.5

mg and *C. rapunculi* has to make several trips to carry the same amount. The longest flights in *C. maxillosum* are probably made to gather nectar.

Osmia tuberculata makes the end plug in a very different way. No long trips are made, only very short and rapid flights (4 - 5 per min). It was seen collecting pieces of rotten wood from the lowest logs of the barn, or small stones from the ground beside the barn or from the road. It collected the same material for 10 - 25 min and then changes to other material. Occasionally the bee stayed longer in the nest arranging the material. The longer periods in the nest followed the longest flights which were made to collect masticated pieces of leaves.

Orientation flights. On leaving the nest a bee sometimes circled a few times at increasing distances from the nest, and in increasingly wider arcs, before flying away. When hovering like this, the bee faced the wall. Very similar behaviour has been described in many other solitary bees (e. g. ORDWAY 1966, MÜNSTER-SWENDSEN 1968, MOHAMED 1973c). Orientation flights have been reported to occur mostly at the first departure in the morning, but according to my observations they were made irregularly during several different working periods.

5. Copulation sites

Copulation or attempted copulation was seen relatively infrequently, but together with the observations on male patrolling behaviour, the records give a rough picture of the copulation sites, or rendezvous places (BARROWS 1976b).

C. maxillosum. At the beginning of the flight season, large swarms of males were seen at the barn. They flew at a distance of 10 - 20 cm from the wall, facing it and going up and down like a swarm of mosquitoes. Up near the the eaves was the most popular place. As soon as females appeared they were grasped by the males. These contacts generally lasted 1 - 2 sec or less, and were not successfull copulations. In most cases attempts at copulation were strongly resisted by the females. In some cases the contact was prolonged and the couple fell to the ground. Patrolling flights along the walls of the barn were also made by single males.

Swarms of males patrolled by the hazel bushes near the barn and several attempts at copulation were seen on the leaves. Males and females often rested on the leaves, basking in the sun.

The third type of copulation site is the flowers of *Ranunculus*, where males were regularly seen patrolling. Only one copulation or attempted

copulation was actually seen. It lasted about 1 sec and the couple then
fell to the ground and disengaged. Apparent patrolling flight was also
seen by flowers of *Geranium silvaticum*.

When patrolling flowers, the males never form swarms but always fly singly.
They go slowly from flower to flower, remaining a few centimeters from the
flower, without alighting. Now and then they interrupt their flight, to rest
on flowers or leaves, or suck nectar from several flowers at a time. Pa-
trolling flights were not restricted to any particular part of the day, but
were performed throughout the daily activity period. Patrolling males
frequently met each other, but aggressive behaviour was never seen. Nor do
they seem to have any precisely defined routes. The patrolling of *C. maxil-
losum* is thus of non-sequential type, according to the terminology of BARROWS
(1976a).

One case was seen of repeated attempts at copulation with a female of a
different species (Fig. 28, comment 7). Male bees have been reported to
grasp females of different species or even non-living particles of about
female size (BATRA 1966, ROBERTS 1969, BARROWS 1975). Males patrol both
flowers and nesting sites throughout their flight season, but towards the end
of the season they are seen much more frequently by flowers (Table 8).

Table 8. Sex ratio of *C. maxillosum* at barn and at flowers during different
parts of flight season in 1970. Males were found more frequently at flowers than
at barn. In the earlier period this difference is not significant (χ^2 = 1.60),
but in the latter period the difference is very significant (χ^2 = 104.4, P <
0.00001).

	11.-13.VI.		16.-27.VI.	
	barn	flowers	barn	flowers
♂♂	143	10	16	75
♀♀	254	10	322	113
♂♂ : ♀♀	0.56	1.00	0.05	0.66

C. rapunculi. No copulation was seen in this species. Evident patrolling
flight was seen several times by flowers of *Campanula* and once by flowers of
Malva moschata.

C. campanularum. Males were regularly seen patrolling by flowers of *Cam-
panula* . One copulation was seen in a flower of *Campanula rapunculoides* on
the hairy pollen-bearing part of the style. The male was above the female.

It lasted about 1 1/2 min, after which the couple fell into the grass and I lost sight of them. Another time a male was seen upon a female on a style of the same flower species, but the sexual organs were not united. They remained in this position for 13 min after which I stopped observing them. In both cases another male tried to grasp the female at the same time. The males sometimes seemed to be patrolling the barn, but no attempts at copulation were seen there. The occurrence of males of this species by the barn reaches its peak in the afternoon (Fig. 13), and they may be searching for suitable holes in which to spend the night (see next sect.).

Heriades truncorum. Copulation or attempted copulation was observed twice. On 6.VII.1974 at 15.15 a very small male grasped a female on the wall. The female tried to get rid of the male by shaking her abdomen and pushing him with her hind legs. Finally she went into the nest cavity and the male had to let go. The whole event lasted about 10 sec. On 16.VI.1974 at 10.05, a female entered a nest cavity and a male tried to copulate with her while her abdomen was protruding. On 6.VII.1973 I saw two males apparently searching for females around the flowers of *Arctium minus*.

BARROWS (1976b) made an extensive study of the copulation sites (or rendezvous places as he terms them) of bees. They are generally flowers but may be the nesting sites, or in some cases both. Other parts of plants than flowers are also frequently reported, and hazel leaves were observed in the case of *C. maxillosum* in this study.

The present observations agree with reports in the literature (MICHENER 1953, CROSS & BOHART 1960, BATRA 1966, SHINN 1967, ROBERTS 1969, EICKWORT 1973, BARROWS 1975), that actual copulation is rarely seen, but attempted copulation more often. These attempts are mostly violently resisted by the females. Females probably copulate only immediately after emergence, as has been demonstrated by KRUNIC (1971) in the laboratory with *Megachile rotundata*.

In this study no sign was observed of the territoriality behaviour reported in some other Megachilidae (VLEUGEL 1952, HAAS 1960, JAYCOX 1967).

6. Sleeping and resting

Before going to sleep in a nest cavity, the bee usually backs in, and stays some time with its head at the entrance of the hole. It then turns in the entrance and assumes the sleeping position (Fig. 25, comments 3 and 5, Fig. 26, comment 5, Fig. 27, comment 5, Fig. 28, comment 3). In the typical sleeping position the abdomen is near the nest entrance (Fig. 31). A similar
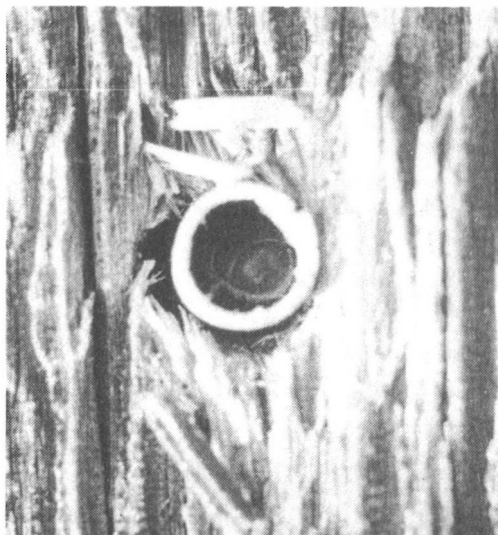
Fig. 31. A female of *C. rapunculi* in a typical sleeping position in a trap nest. Photo M. Käpylä.

position has been reported in *Heriades carinata* (MATTHEWS 1965) and another megachilid bee (EICKWORT 1973). It is not known whether the bee goes further in during the night, but this is not probable, because bees were found in the same position early in the morning. When the temperature approaches the threshold value in the morning, the bee turns in the nest entrance and stays in the nest cavity facing outwards (Fig. 25, comment 7). The start of flight is sometimes preceded by a short period spent basking in the sun near the nest entrance (Fig. 28, comment 1).

The bees rest and sleep in flowers as well (Table 9). Observations are few, but it seems that in *C. maxillosum* females spend the night in holes in wood, preferably their own nest cavity, whereas males spend the night in flowers. This may also be true of *C. rapunculi*. In *C. campanularum* both sexes spend the night in cavities in wood or in flowers of *Campanula*. The use of bell-flowers as sleeping places in this species is well known (e.g. FREY-GESSNER 1908-1912: 8, BENOIST 1946). *H. truncorum* was always found sleeping in cavities in wood. *O. tuberculata* females spend the night in holes in wood, and there are no observations about the sleeping behaviour of the males of this species.

In some cases small sleeping or resting aggregations were found. The five males of *C. campanularum* found resting in *Ranunculus* were all in the same flower; two males of *C. rapunculi* were found in a flower of *Campanula persici-folia*; one flower of *Campanula rapunculoides* contained two males and one female

Table 9. Observations on sleeping and resting places. The numbers mean individuals.

	C. max.		C. rap.		C. camp.		H. trunc.		O. tub.
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Cavities in wood	21	-	1	-	1	11	4	3	3
Flowers									
- *Campanula*	1*	1*	-	10	5	9	-	-	-
- *Ranunculus*	-	2	-	-	-	5*	-	-	-
- *Geranium silvaticum*	-	1*	-	-	-	-	-	-	-
- *Potentilla argentea*	-	-	-	-	-	-	-	5*	-
- *Chrysanthemum leucanthemum*	-	-	-	-	-	-	-	1*	-
- *Leontodon autumnalis*	1*	-	-	-	-	-	-	-	-

* Daytime during bad weather.

of *C. campanularum*, and another flower contained a male and female of the same species.

A sleeping female of *C. maxillosum* was once found hanging by her mandibles from a leaf margin in the lime tree beside the barn. This behaviour has been reported in some other solitary bees (FRIESE 1923: 62, SCHREMMER 1956, LINSLEY 1962b, SHINN 1967).

7. Contamination of flowers with foreign pollen by wind and insects

7.1. Introduction

The pollen loads of the bees often contained small amounts of pollen from many plant species, while the bulk of the load was mostly from one plant species or genus (see next sect.). The occurrence of these subsidiary pollen types can be explained in two ways:
(1) The bees have visited these flowers during their foraging trips.
(2) The collected pollen has been contaminated with pollen from other plant species, either by the wind or by flower-visiting insects.

It was decided to study the amount of contamination and its possible causes. Although neglected earlier, this question is important in interpreting analyses of the pollen loads of bees. FREE & WILLIAMS (1972) assumed that 'foreign' pollen found on the body hairs of honey-bees had mostly been received as the bees brushed against each other in the hive.

7.2. Methods

Flowers or capitula were collected by hand and put into a test tube. The tube was partly filled with a mixture of alcohol and water, and shaken. The flowers were then removed, and the contents centrifuged and decanted. The sample was further treated by the method described in sect. 8.1.1. The amount of foreign pollen in these samples from flowers may be expected to be bigger than in the pollen loads collected by bees. Bees mostly collect pollen directly from anthers, while these samples contain pollen from the whole flower or capitulum. The proportions of the different types of foreign pollen can be assumed to be the same.

During the days preceding the collecting of flowers the air in the same area was sampled for pollen with a specially designed apparatus (Fig. 32). Two of these samplers were placed at the height of the top of the vegetation. The apparatus turned freely, the collecting surface always facing the wind. The collecting tape was smeared with a thin layer of vaseline. The collecting period was 12 or 24 hours, during which time the tape did not become overloaded. The tape was removed and placed under a cover glass. Mounting
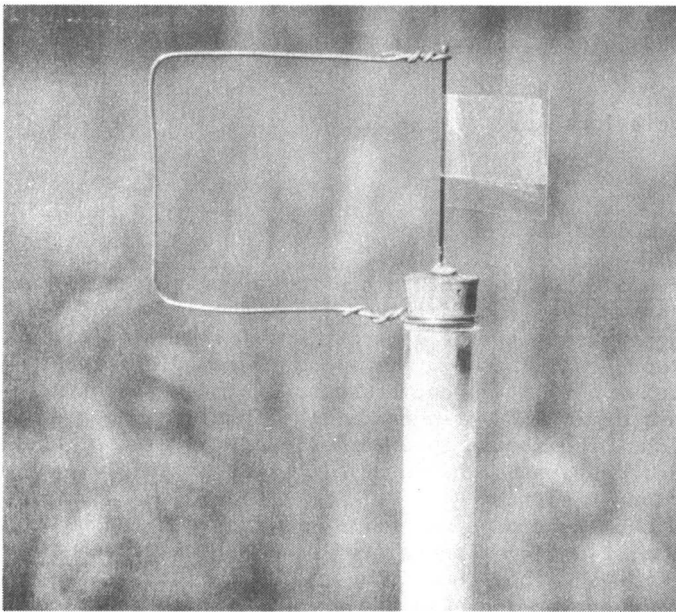
Fig. 32. The apparatus used to sample air-borne pollen. The collecting tape is supported by an insect pin, which turns freely in a narrow glass tube. The wind vane is made of a cover glass 20 by 20 mm. Photo M. Käpylä.

material, gelvatol, was placed on both sides of the tape. The width of
the collecting surface was 1 mm, which should be suitable for particles of
the size range of pollen grains (HARRINGTON *et al*. 1959, RAYNOR 1972).

7.3. Results

Foreign pollen was surprisingly abundant in all the flowers (3 - 28 %, Table
10) and its spectrum was rather similar in the different species, *Filipendula*
and *Galium* predominating.

Many more pollen types were found in flowers than in the air (Table 11).
When a pollen type was much more frequent in the air, it was assumed to be
transported mostly by wind. When it was much more frequent in flowers, it
was assumed to be transported mostly by insects. Gramineae and *Urtica* are
typical wind-pollinated plants, seldom visited by insects. The presence of
their pollen in flowers must be due solely to transport by wind. The pollen
of *Filipendula* and *Galium* is transported by both the wind and insects, the
former more by wind, the latter more by insects. Insects, probably mostly
unspecialized flies, wasps and beetles, are mainly responsible for the con-
tamination of flowers with pollen of *Caryophyllaceae*, the *Achillea* type,
Hypericum, Potentilla, Cirsium, Cruciferae, *Lotus* and Umbelliferae. Similar
but less certain conclusions can be reached with the other species.

8. Flower relationships

8.1. Methods

8.1.1. The study of pollen loads

Taking the sample. A bee returning from a foraging trip was caught with an
insect net and slightly narcotized with ether. It was taken between thumb
and forefinger, ventral side upwards, and its pollen load was removed with
a minute brush, and placed in a small numbered glass tube. Successive sam-
ples were taken with different brushes. Before reuse the brushes were washed
carefully and dried. The fingers of the sampler were also cleaned between
each sampling. The sample tube was filled with glacial acetic acid, which
preserves and dehydrates the material , and can safely be used with sulphuric
acid in further treatment.

Dry bees on insect pins were first moistened a few hours in a glass jar
containing moist paper. The pollen load was then brushed into a glass funnel,
from which it was washed down to a centrifuge tube with a mixture of concd.
sulphuric acid and acetic acid anhydride. With the samples from dry bees,
preparation for the microscope was started from point 3 in the following sec-
tion.

Making the microscope preparation: This procedure is a modification of the
method most commonly used by palynologists (ERDTMAN 1952: 7).

Table 10. Foreign pollen contamination in flowers. The numbers are percentages of foreign pollen grains.

	Achillea millefolium	*Campanula patula*	*C. persicifolia*	*C. rotundifolia*	*Cirsium arvense*	*Leontodon autumnalis*	*Matricaria inodora*	*Ranunculus repens*
Filipendula	44	13	48	29	46	20	66	14
Galium	30	30	4	8	14	5	12	13
Caryophyllaceae	2	21	8	10	2	3	1	34
Achillea type	-	7	10	3	25	12	-	3
Hypericum	-	3	11	3	5	14	2	21
Potentilla	0.5	2	0.5	29	4	11	5	10
Gramineae	11	12	7	4	2	2	7	3
Cirsium	3	3	7	4	-	7	-	-
Cruciferae	1	2	0.5	2	-	3	2	3
Urtica	0.5	2	-	4	1	0.5	-	-
Lotus corniculatus	-	-	-	-	-	7	-	-
Umbelliferae	3	1	-	-	-	1	1	-
Ranunculus	-	2	-	0.5	-	3	-	-
Plantago	-	-	-	-	-	5	-	-
Tilia	-	-	2	1	0.5	-	-	-
Pinus	2	-	-	0.5	0.5	0.5	-	-
Chenopodiaceae	-	2	0.5	-	-	-	2	-
Lysimachia	-	1	-	-	-	2	-	-
Campanula	-	-	-	-	1	-	-	1
Melampyrum	-	-	-	-	-	2	-	-
Betula	-	-	-	0.5	-	-	-	1
Lathyrus	-	-	-	-	-	2	-	-
Lamium (?)	-	-	0.5	-	-	-	1	-
Centaruea jacea	-	-	-	-	-	0.5	-	0.5
Rumex acet.	1	-	-	-	-	-	-	-
Liguliflorae	-	-	-	0.5	-	-	-	-
Number of foreign pollen grains studied	200	200	200	200	200	200	100	200
Foreign pollen %	7.0	9.8	13.4	2.6	20.8	22.8	3.8	27.6

1. The sample tube filled with glacial acetic acid was shaken and its contents poured into a centrifuge tube with a tapering end.
2. The tube was centrifuged for 3 - 5 min. (about 2500 rpm) and the contents decanted.
3. A fresh mixture of acetic acid anhydride and concd. sulphuric acid (9:1)

Table 11. Comparison of pollen found in air with foreign pollen con-
tamination in flowers. The numbers are percentages. The percentages
are compared with the binomial t-test. The significance level is shown
by the following classes: 0) $P > 0.05$, 1) $P < 0.05$, 2) $P < 0.01$, 3) $P <$
0.001, 4) $P < 0.0001$, 5) $P < 0.00001$.

	AIR	FLOWERS	AIR + FLOWERS	t	P
Filipendula	43.8	33.1	39.4	6.49	5
Gramineae	27.7	6.1	18.7	16.41	5
Galium	10.2	13.9	11.8	3.40	3
Urtica	13.9	1.0	8.4	13.77	5
Caryophyllaceae	0.4	10.7	4.7	14.41	5
Achillea type	0.6	8.1	3.7	11.77	5
Hypericum	0.2	7.8	3.3	12.60	5
Potentilla	-	7.5	3.1	12.82	5
Cirsium	-	3.1	1.3	8.11	5
Chenopodiaceae	1.1	0.4	0.8	2.33	1
Cruciferae	-	1.5	0.6	5.75	5
Plantago	0.5	0.7	0.6		0
Lotus corniculatus	-	0.9	0.4	4.22	4
Umbelliferae	-	0.8	0.3	4.33	4
Lysimachia	0.2	0.4	0.3		0
Pinus	0.2	0.5	0.3		0
Ranunculus	-	0.7	0.3	3.79	3
Rumex acet.	0.3	0.1	0.2		0
Tilia cordata	-	0.5	0.2	3.32	3
Betula	0.1	0.2	0.2		0
Campanula	-	0.3	0.1	2.81	2
Melampyrum	-	0.3	0.1	2.81	2
Cyperaceae	0.1	-	0.1		0
Lathyrus	-	0.2	0.1		0
Lamium	-	0.2	0.1		0
Centaurea jacea	-	0.1	0.1		0
Liguliflorae	-	0.1	0.0		0
Corylus avellana	0.1	-	0.0		0
Unidentified pollen	0.6	0.8	0.7		0
Number of pollen grains studied	2094	1500	3594		

was poured into a centrifuge tube to fill half the tube. The tube was then
kept for 1 - 2 min. in a boiling water bath, while the contents were mixed
with a glass rod.
4. The sample was centrifuged and decanted.
5. The tube was filled with distilled water with a little alcohol and shaken.

6. The sample was centrifuged and decanted.
7. The pollen sample was mixed with the small amount of water left in the bottom of the centrifuge tube. A sample of this was sucked up with a glass capillary and a drop was placed on a microscope slide.
8. After most of the water had evaporated 1 - 2 drops of melted glycerine-gelatine jelly were placed on the sample with a glass rod. A cover glass (20 x 20 mm) was placed on top, and the slide was gently heated to spread the jelly under the glass. Next day the edges of the cover glass were sealed with lacquer.

8.1.2. Study of contents of guts

During nectar sucking, some pollen enters the honey stomach. Pollen may also be deliberately eaten by solitary bees (TANIGUCHI 1956, ORDWAY 1966). Preparation were made from dry individuals. Nectar sugar is crystallized in dry specimens and can be studied after any time period. In most cases the sugars (quantity and quality) and pollen (quality) were studied on the same specimens. The procedure is as follows.

1. The abdomen was checked for pollen under a binocular microscope, and an attempt was made to remove any pollen with a fine brush.
2. The abdomen was removed and put on a glass slide. It was then cut through lengthwise with a preparation knife and the pieces were put in a centrifuge tube with the knife.
3. A measured amount of distilled water (mostly 3 ml) was added to the tube, and the tube was kept 3 - 5 min. in a boiling water bath, while the contents were stirred with a glass rod.
4. The sample was centrifugated and the water poured into a test tube. After acid hydrolysis, the total amount of sugar was determined using 3,5-dinitro-salisylic acid as a reagent (see KÄPYLÄ 1978).
5. A microscope slide was made from the sediment by the method described above, starting from point 3. As there was a drop of water in the bottom of the tube, it was necessary to add the mixture of acetic acid anhydride sulphuric acid very carefully, drop by drop. This mixture dissolves most of the insect parts and all the pollen is liberated.

8.1.3. Pollen identification

The pollen identifications were confirmed with the aid of a large reference collection prepared by the same method. Perforated key cards made for every species or pollen type proved to be very useful. The textbooks of ERDTMAN et al. (1961) and FAEGRI & IVERSEN (1964) were also used.
    At least 200 pollen grains were counted on each slide, along traverses in several parts of the slide. In many preparations made from the contents of the abdomen, grains did not amount to 200. In these cases the whole slide was counted. The results are expressed as percentages.
    In most cases the pollen grains could be identified only down to genus (e.g. *Ranunculus, Campanula, Potentilla, and Vaccinium*). The only species of *Cirsium* growing abundantly in the study area was *C. arvence*, and the only species of *Lysimachia* was *L. vulgare*. Umbelliferae, Caryophyllaceae and Cruciferae were identified only to family. In some cases several genera had to be united within the same pollen type. These are listed below, all the important genera in Seili being mentioned.

- *Achillea* type: *Achillea, Matricaria, Chrysanthemum, Anthemis.*

- *Convallaria* type: *Convallaria majalis, Polygonatum odoratum.*
- Galeopsis type: *Galeopsis, Lamium.*
- Liguliflorae type: *Taraxacum, Hieracium, Leontodon, Crepis, Sonchus, Lapsana.*
- *Potentilla* type: *Potentilla, Fragaria, Comarum, Agrimonia.*
- *Vicia* type: *Vicia, Lathyrus.* In this group *Lathyrus vernus* could be identified.

8.1.4. Pollen and nectar presentation in flowers

The amount of nectar was studied in uncaged flowers, so that insects had already had an opportunity to suck nectar from them. The flowers were picked and placed in a test tube, where the nectar was dissolved in water. Sugar was measured with a spectrophotometer, using 3,5-dinitrosalisylic acid as a reagent. The details of the procedure and most of the results will be published elsewhere (KÄPYLÄ 1978).

Pollen presentation in *Ranunculus* was studied by periodically counting the anthers presenting pollen. In *Campanula* and Compositae, periodic counts were made of flowers that were newly opened and presenting pollen.

8.1.5. Discussion

Acetolysis is a somewhat laborious procedure, but it reveals the structures of the exine very clearly. Pollen grains with intact contents are much more difficult to identify. Furthermore most of the literature on pollen morphology deals with acetolysed pollen.

In the mixed pollen load of a bee, the pollen is often arranged in layers, as is easily seen in the multicoloured pollen balls of honey-bees (HODGES 1974: 33) and bumble-bees. Accordingly a small piece taken from an intact load (as in the method of PERCIVAL 1965: 211) will not be representative of the whole load, and the load should be mixed thoroughly before taking a sample (ANASIEWICZ & WARAKOMSKA 1969). Few writers mention how the sample was taken.

Contamination is a serious problem in palynological laboratories, occurring via the air, tap-water or laboratory equipment. In this study the samples were so big that a couple foreign pollen grains would not affect the results. As a further precaution, pollen species contributing less than 1 % of the sample were omitted from the results.

As the size of the pollen grains differs greatly between plant species, the percentages obtained from counts are not the same as the proportions of the different species in the total weight or volume of the load. Correction coefficients (TASEI 1973) were not used in this study, because in this case the pollen grains of the most important food plants are of rather similar size.

When the contents of the guts were studied some pollen from the surface of the bee was included, as it could not be completely brushed off. However, in these species removal of external pollen is facilitated by the baldness of the upper surface of the abdomen.

According to a review on digestion of pollen in honey-bees (STANLEY & LISKENS 1974: 100 - 102), pollen passes through the gut fairly rapidly, reaching the rectum about 2.5 hours after it is swallowed. If, as is probable, the same is true of the solitary species studied here, the pollen analyses of the gut contents reflect flower visits made a few hours before capture.

8.2. Terminology

In this study flower constancy means the behaviour of a bee that keeps to one plant species or genus during a foraging trip. It is identical to KUGLER's (1970: 118) term "Blümenstätigkeit", and concerns only individual trips or individual bees.

LINSLEY & MacSWAIN (1958) and LINSLEY (1958) used this term to mean any specialization in flower visits. They discriminated between two types of flower constancy. The first (without a special term) was the same as the flower constancy meant here. The second was the constancy shown by a species (or occasionally a higher taxon), and is dealt with in the text below.

As bee species were observed to be more specialized in pollen collecting than in nectar collecting, ROBERTSON (1925) introduced the terms oligolecty and polylecty to express the degree of specialization in pollen collecting of a bee species. LOEW's (1884) terms oligotropism and polytropism could then be retained in their original use: to deal with all flower visits together. A definition of oligolecty has been given by LINSLEY & MacSWAIN (1957, 1958), who also pointed out the relativity of the concept. There is a range intermediate cases between extreme oligolecty (monolecty) and extreme polylecty (e.g. the honey-bee). The terms oligolecty - polylecty are here used in the same way as by the authors cited above.

With flower relationships I mean all visits for different reasons together.

8.3. Results

8.3.1. Occurrence of different pollen types in pollen loads and in guts

The pollen analyses are presented in two ways (Fig. 33, Table 12). About one third of the results for both *C. rapunculi* and *O. tuberculata* come from other parts of SW Finland. Field observations have been used to complete the picture (Table 13), but in the field it often remains uncertain whether a bee collected nectar, pollen or both or visited a flower for some other reason. Individuals found with pollen loads are classifield as pollen collectors, but pollen collectors mostly collect nectar at the same time (see sect. 9) and in some cases the wrong record may be made without

	C. maxillosum			C. rapunculi			C. campanularum			H. truncorum			O. tuberculata		
	♀♀ pollen loads	♀♀ stom-achs	♂♂ stom-achs	♀♀ pollen loads	♀♀ stom-achs	♂♂ stom-achs	♀♀ pollen loads	♀♀ stom-achs	♂♂ stom-achs	♀♀ pollen loads	♀♀ stom-achs	♂♂ stom-achs	♀♀ pollen loads all	♀♀ pollen loads Seili	stom-achs
Achillea type										74.0	83.4	83.2			
Anemone nemorosa															
Campanula				99.6	97.4	76.2	96.2	91.4							
Caragana arborescens															
Caryophyllaceae															
Centaurea jacea															
Cirsium															
Convallaria type															
Cruciferae															
Filipendula															
Galeopsis type															
Galium															
Geranium															
Geum															
Hypericum															
Lathyrus vernus															
Liguliflorae type															
Lotus corniculatus															
Lysimachia															
Potentilla type															
Ranunculus	97.9	92.8	83.6												
Rosa															
Rubus															
Tilia cordata															
Umbelliferae															
Vaccinium															
Veronica															
Vicia type															
Viola															
Others															
n	105	37	4	18	7	6	69	29	9	66	28	6	16	10	2

≡ 0.2 % scale
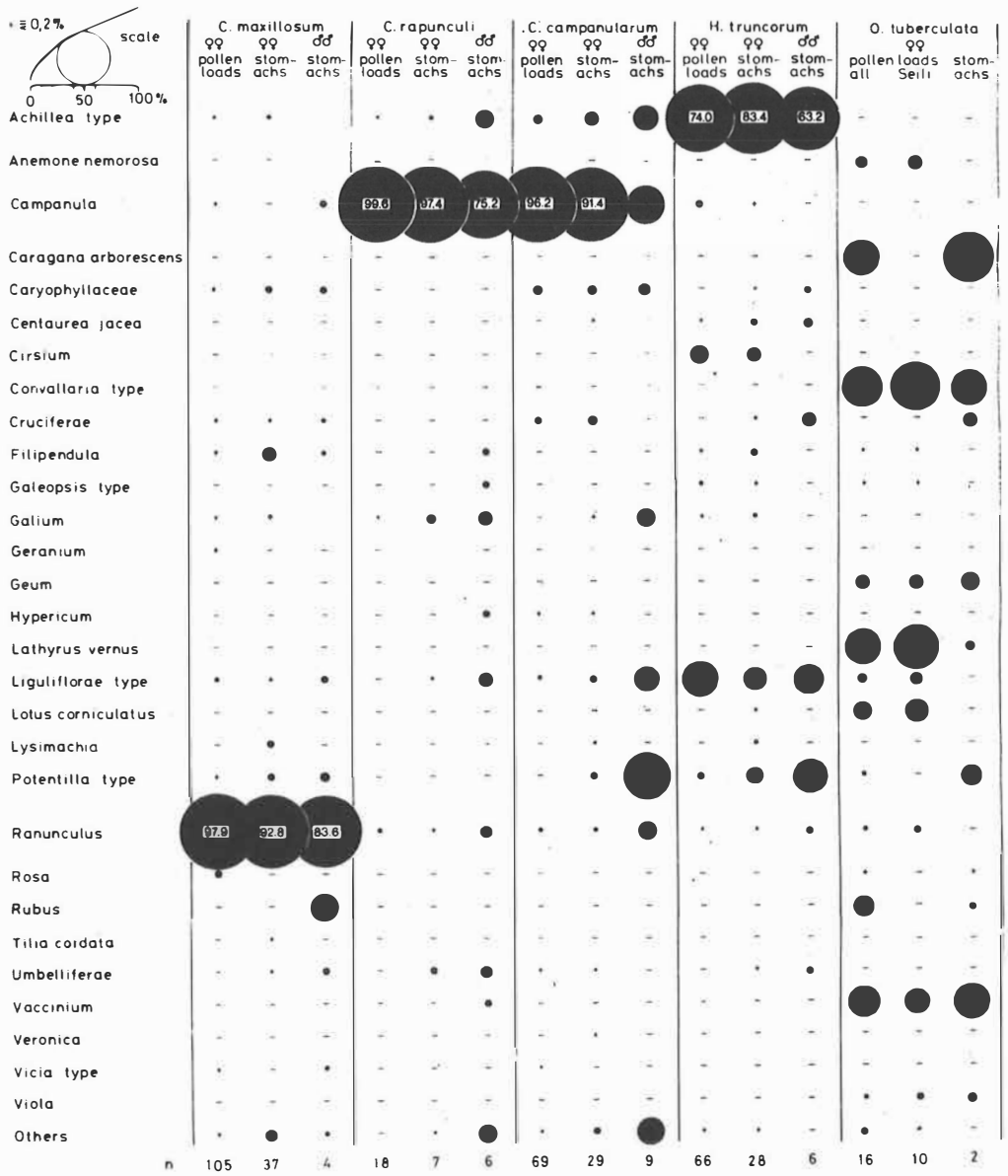0   50   100 %

Fig. 33. Percentages of different pollen types found in pollen loads and in guts (stomachs).

microscopical analysis of the pollen load (Table 14).

C. maxillosum is clearly specialized to *Ranunculus* species in both pollen and nectar collecting. It seems to visit all the available *Ranunculus* species equally readily. The bulk of the load was *Ranunculus* pollen in all but

Table 12. Results of the analyses of the pollen loads: the numbers of pollen loads in which the pollen species are found in different amounts.

C. maxillosum (n=105)

	100	91-99	71-90	31-70	11-30	3-10	1-2%
Ranunculus	82	17	4	1			
Liguliflorae type					1	1	4
Achillea type					1		2
Rosa majalis	1						
Caryophyllaceae				1			3
Geranium					1		2
Campanula					1	1	
Potentilla type					1		
Vicia type							2
Filipendula							1
Cruciferae							1
Galium							1
Unidentified							3

C. rapunculi (n=18)

	100	91-99	71-90	31-70	11-30	3-10	1-2%
Campanula	14	4					
Ranunculus						1	1
Galium							1
Achillea type							1

C. campanularum (n=69)

	100	91-99	71-90	31-70	11-30	3-10	1-2%
Campanula	30	36	1	1	1		
Achillea type						10	13
Liguliflorae type						2	9
Cruciferae				1		1	
Caryophyllaceae		1					
Ranunculus					1	2	
Umbelliferae						1	1
Melampyrum						1	
Vicia type						1	
Hypericum							2
Calluna							1
Unidentified						1	

H. truncorum (n=66)

	100	91-99	71-90	31-70	11-30	3-10	1-2%
Achillea type	14	25	7	7	5	3	4
Liguliflorae type	1	5	4	7	3	4	5
Cirsium		1	1	2		1	6
Potentilla						5	4
Campanula						7	11
Galeopsis						1	2
Centaurea jacea						1	1
Filipendula							7
Galium						2	
Vicia type							2
Ranunculus							5
Calluna							1
Unidentified						1	

O. tuberculata (n=16)

	100	91-99	71-90	31-70	11-30	3-10	1-2%
Convallaria type		1	2	1	2	4	1
Vicia type			4				2
Caragana arborescene	1	2				1	
Vaccinium		2		1		1	
Rubus		1			1		
Lotus corniculatus			1				1
Anemone nemorosa					1		
Liguliflorae type					1	1	1
Geum					2		
Potentilla type					1		
Viola						1	1
Rosa							2
Ranunculus						1	
Galeopsis							1
Filipendula							1
Unidentified						1	2

one case, where the load was 100 % *Rosa* pollen, most probably collected from a bush of *Rosa majalis* beside the barn. There was also one evident case of pollen collecting from *Stellaria graminea* (Table 14). The pollen possibly collected fortuitously included *Taraxacum* (29 % of one load), *Campanula* (16 % of one load), *Geranium* (20 % of one incomplete load) and the *Achillea* type (18 % of one incomplete load). The main subsidiary nectar sourses are yellow Compositae belonging to the subfamily Liguliflorae (especially *Taraxacum, Hieracium, Sonchus), Geranium silvaticum, Stellaria graminea* and *Tilia cordata*. The occurrence of pollen of many other species, especially *Filipendula, Galium, Potentilla,* and *Lysimachia* is probably due to contamination of the flowers (see sect. 7 and Tables 10 - 11). Pollen of *Geranium* was found fairly often but mostly composed less than 1 % of the load. The pollen grains of this species are very big, and thus rarely enter

Table 13. Field observations on flower visiting for food. When a bee visited several flowers of the same species in succession, this was treated as one observation. Underlined numbers represent pollen-collecting, the other numbers nectar-sucking. Observations from other parts of SW Finland are included.

	C. max. ♀♀	C. max. ♂♂	C. rap. ♀♀	C. rap. ♂♂	C. camp. ♀♀	C. camp. ♂♂	H. trunc. ♀♀	H. trunc. ♂♂	O. tub. ♀♀
Achillea millefolium	-	-	-	-	-	-	$\underline{1}$+3	-	-
Aegopodium podagraria	-	-	-	1	-	-	-	2	-
Anthemis tinctoria	-	-	-	1	-	-	$\underline{1}$+1	-	-
Arctium minus	-	-	-	-	-	-	-	2	-
Aster sp.	-	-	-	-	-	-	$\underline{2}$	-	-
Campanula glomerata	-	-	-	-	$\underline{1}$+2	3	-	-	-
C. patula	-	-	1	3	$\underline{2}$+4	5	-	-	-
C. persicifolia	-	-	$\underline{1}$+2	7	$\underline{4}$+6	9	-	-	-
C. rapunculoides	-	-	$\underline{4}$	1	1	2	-	-	-
C. rotundifolia	-	-	2	2	-	-	-	-	-
Caragana arborescens	-	-	-	-	-	-	-	-	$\underline{3}$
Centaurea jacea	-	-	-	-	-	-	1	-	-
Chamaenerion angustifolium	-	-	5	4	2	-	-	1	-
Chrysanthemum leucanthemum	-	-	-	-	-	-	$\underline{1}$	1	-
Cirsium arvense	-	-	-	-	-	-	1	-	-
Crepis tectorum	-	-	-	-	-	-	$\underline{1}$+1	-	-
Geranium silvaticum	1	1	-	1	-	-	-	-	-
Hieracium pilosella	1	-	-	-	-	1	-	3	-
H. umbellatum	2	-	-	-	10	2	-	-	-
Knautia arvensis	-	-	-	1	-	-	-	-	-
Lapsana communis	-	-	-	-	-	-	$\underline{1}$	-	-
Leontodon autumnalis	-	-	-	-	2	1	$\underline{9}$+2	2	1
Malva moschata	-	-	-	1	-	-	-	-	-
Matricaria inodora	-	-	-	-	-	-	$\underline{4}$+2	3	-
Potentilla argentea	-	-	1	-	1	2	3	3	-
Ranunculus acris	2	1	-	-	-	-	-	-	-
R. auricomus	1	9	-	-	-	-	-	-	-
R. polyanthemos	$\underline{6}$+8	10	-	-	-	2	-	-	-
R. repens	$\underline{5}$+1	1	-	-	-	-	-	-	-
Sonchus arvensis	1	-	-	-	1	-	-	-	-
Stellaria graminea	$\underline{1}$	-	-	-	-	-	-	-	-
Tilia cordata	2	-	-	-	-	-	-	-	-
Veronica chamaedrys	-	-	-	-	-	1	-	-	-
Viola arvensis	-	-	-	-	-	-	-	-	1
No. of species	10	5	6	10	9	10	11	8	3
No. of observations	31	22	16	22	36	28	34	17	5

Table 14. Cases in which the pollen load was from another plant species
than the one on which the bee was caught. In these cases *C. maxillosum* was
classified as a pollen-collector, the others as nectar-collectors.

Bee species	Place and date	Flower species on which the bee was caught	Size of pollen load	Pollen types in the load	Nectar load
C. maxillosum	Seili 16.VII.1974	*Stellaria graminea*	Short	*Ranunculus* 66% Caryophyllaceae 32 (10)% *Galium* 1% Others 1%	0.7 mg
C. rapunculi	Seili 8.VII.1973	*Chamaenerion angustifolium*	Short	*Campanula* 100%	Not studied
C. campanularum	Seili 8.VII.1973	*Chamaenerion angustifolium*	Short	*Campanula* 100% *Chamaenerion* <1%	Not studied
C. campanularum	Seili 3.VIII.1974	*Hieracium umbellatum*	Full	*Campanula* 98% Others 2%	None
H. truncorum	Forssa 11.VII.1968	*Potentilla argentea*	Small	*Achillea* 61% Liguliflorae type 24% Umbelliferae 8% *Potentilla* 7 (8)%	0.3 mg
H. truncorum	Seili 5.VII.1970	*Potentilla argentea*	Full	*Achillea* type 98% *Potentilla* 1 (10)% *Filipendula* 1%	None

the honey stomachs.

Field observations suggest that males are even more specialized to
Ranunculus than females. The same trend is evident in NIEMELÄ's (1934)
material.

C. rapunculi females show strong specialization to *Campanula*. Other
pollen types are probably only found because of contamination of flowers.
The most important subsidiary nectar source seems to be *Chamaenerion*
angustifolium. The pollen grains of this plant rarely enter the stomach,
because they are big and connected with threads, and it is possible that
this and related bee species are unable to collect this peculiar pollen.
Males seem to visit many more plant species than females. The same trend
is evident in NIEMELÄ's (1934) material.

C. campanularum is also specialized to *Campanula*. There are some cases
of pollen collection from other species: one load was 92 % Caryophyllaceae
pollen, probably *Stellaria graminea:* one contained 33 % Cruciferae pollen,
and one load 12 % *Ranunculus* pollen. Fortuitous nectar-sucking mainly
occurs in Compositae, Caryophyllaceae, Cruciferae, and *Potentilla*.

According to both field observations and pollen analyses, males show

only weak specialization, visiting many more plant species than females.
Besides *Campanula* they prefer *Potentilla* and Compositae. The occurrence
of *Galium* pollen is probably caused by contamination by insects and air
currents. *Ranunculus* is used as a resting place and a source of nectar.

H. truncorum is specialized to the family Compositae, visiting many
species within this family. The most important pollen type in both the
pollen loads and guts was the *Achillea* type, followed by the Liguliflorae
type. Many of the loads contained both types mixed. The plants with these
pollen types include many common species, which this bee has been observed
to visit. Pollen is also occasionally collected from *Cirsium arvense*.
In Forssa I observed pollen collecting on cultivated *Aster* and NIEMELÄ
(1934) reported a preference for cultivated *Erigerons*. *Centaurea* is often
mentioned as a preferred food source (e.g. SCHMIEDEKNECHT 1930: 823), but
this was not the case in Seili, although this plant was abundant in the
study area. There was only one clear case of pollen collection from *Centaurea
jacea*. This species is probably used as a nectar source, because its pollen
was often found in guts. One load was 18 % pollen of *Lamium* or *Galeopsis*,
but this bee cannot obtain nectar from the long corolla tubes. This same
pollen type was also found in two other pollen loads and in one stomach.
Its presence may be due to contamination of flowers.

Eighteen of the 66 loads contained small amounts of *Campanula* pollen,
but it was rarer in the stomachs. The most probable explanation is contami-
nation of flowers, because there are no field observations of the use of
bell-flowers as resting places or nectar sources.

Of the non-composite flowers, *Potentilla* is most often visited for nec-
tar, being especially favoured by males. Otherwise males visit roughly
the same plant species as females.

O. tuberculata visits many plant species. In Seili the most important
pollen (and nectar) plants were *Lathyrus vernus, Polygonatum odoratum,
Convallaria majalis, Vaccinium, Lotus corniculatus, Geum rivale* and *Anemone
nemorosa*. The preferred pollen sources from other parts of SW Finland were
Caragana arborescens, Vaccinium and *Rubus idaeus (?)*. The high proportion
shown for *Caragana* is due to three individuals caught in Raisio.

8.3.2. Composition of the pollen loads at different times in the flight
seasons

The material of three species was big enough to allow the study of the change

in the composition of the pollen loads during the flight seasons (Fig. 34).

   C. maxillosum. At the beginning of the flight season there may a shortage of *Ranunculus* pollen, and the loads contained a fairly large proportion of
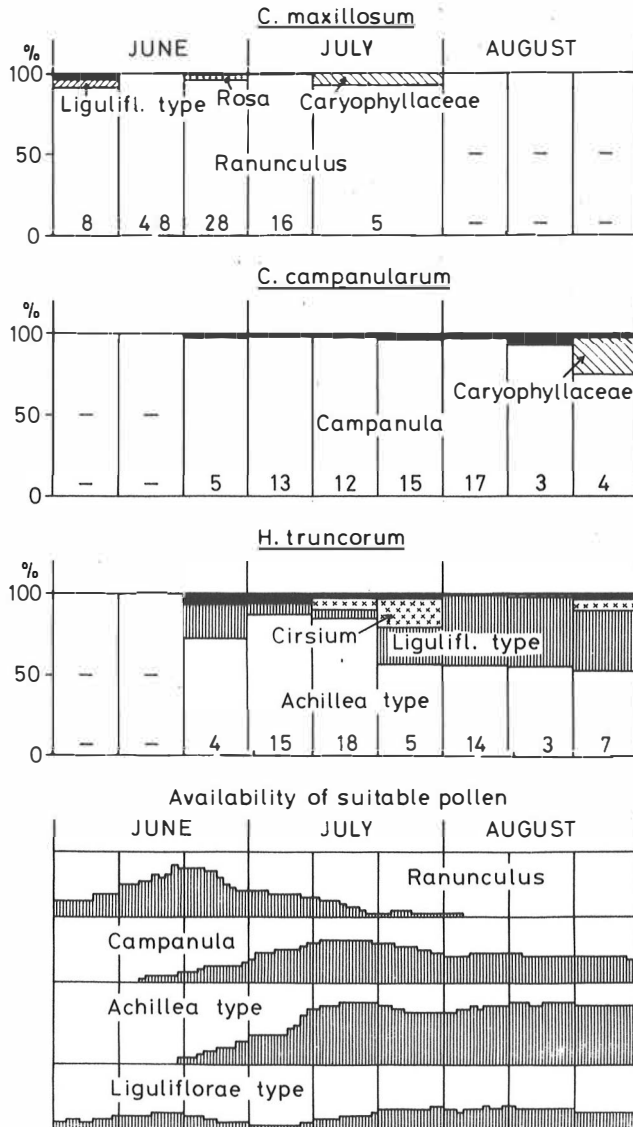

Fig. 34. The composition of pollen loads and the availability of suitable pollen at different times in the flight seasons. Analyses of pollen loads from all the study years in Seili combined. Numbers of loads studied shown in base of columns. The diagram of pollen availability is based on the flowering intensity values of the plant species belonging to each pollen type (see Fig. 8).

Liguliflorae-type pollen, probably *Taraxacum* and *Hieracium pilosella*.
With its small flowers, *Ranunculus auricomus* is a poorer food source than
the bigger *Ranunculus* species, which start their flowering later on.
The peak of the flight period coincides well with the main flowering period
of *Ranunculus* (Figs. 5-8). From 11.VI to 10.VII there was very little
foreign pollen in the loads, apart from one exceptional load (Rosa 100 %).
Towards the end of the flight season, *Ranunculus* pollen may become increasing-
ly scarce, but there are also fewer competitors for it. At the end of the
flight period there was only one load with a considerable amount of other
pollen than *Ranunculus*. Either there was not actual shortage of *Ranunculus*
pollen or this species does not change to another pollen source even during
a shortage of suitable pollen.

   C. campanularum. As the amount of foreign pollen in the loads was about
the same during most of the flight season, suitable pollen was evidently
available throughout this period. In the last third of August there was one
exceptional pollen load (92 % Caryophyllaceae).

   H. truncorum. The amount of Liguliflorae-type pollen present in the loads
differed during the flight season and was correlated with the availability
of this pollen, which is poor early in July. In August Liguliflorae-type
pollen constituted nearly half the contents of the loads. At that time the
favoured food plant, *Leontodon autumnalis*, was in full bloom. The occur-
rence of *Cirsium* pollen in the loads was highest at the beginning of the
flowering of this species (Fig. 7 - 8). In August, when *Leontodon* came into
full bloom, *Cirsium* was largely abandoned as a pollen source.

8.3.3. Diurnal pattern of pollen and nectar presentation in the most import-
ant food flowers

Ranunculus. There seems to be no difference in the availability of nectar,
between the forenoon and afternoon (Fig. 35). The anthers of *R. repens* open
throughout the day but the peak is in the late forenoon (Fig. 36, PERCIVAL
1965: 74 - 75). The opening of the anthers proceeds from the outside in-
wards, a single row of anthers opening every day. According to observations
made in Seili in 1974, in a single flower of *R. polyanthemos* (n = 2) or
R. repens (n = 3) anthesis lasts 6 days.

   Campanula. The availability of nectar does not seem to vary during the
daytime (Fig. 35). The anthers dehisce before the flowers open. The
stigma grows through the united anthers and the pollen is caught by the
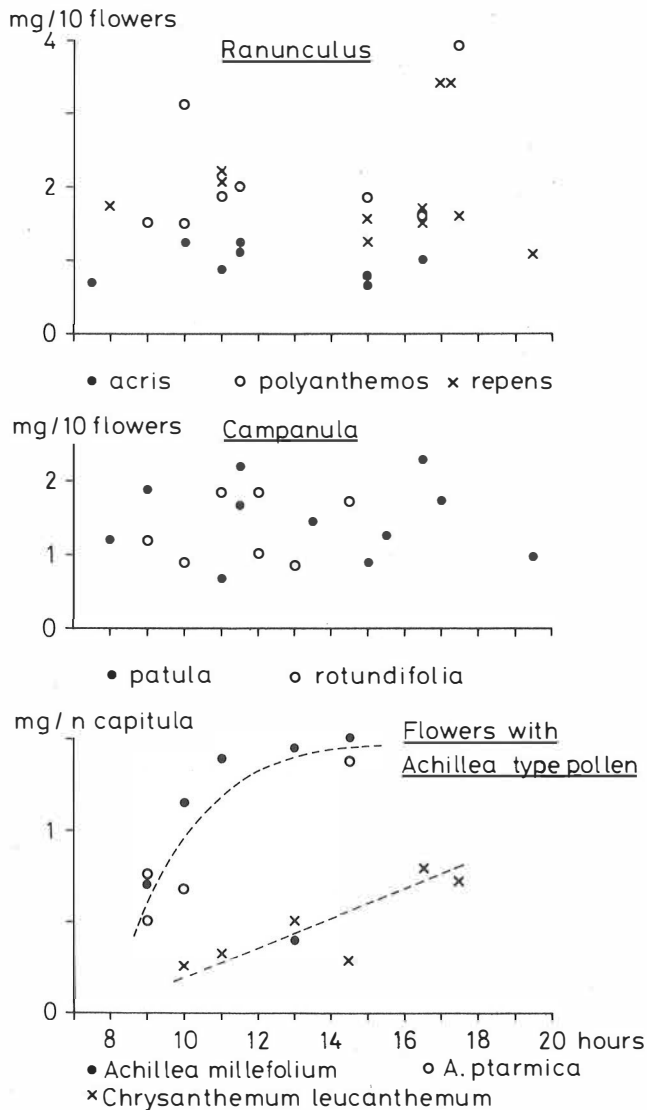hairy layer on the style. As soon as the flower opens, pollen is available

Fig. 35. Diurnal pattern of nectar supply in the most important food plants. In *Achillea millefolium* the unit is the contents of 100 capitula, in *A. ptarmica* of 10 capitula, and in *Crysanthemum leucanthemum* of one capitulum. The lines are fitted by eye. In *Chrysanthemum* the amount of nectar increases significantly towards afternoon (r = 0.85, P < 0.05). In flowers with *Achillea* type pollen the increase is not significant (r = 0.60, P < 0.1, log transformation of the time variable).

for bees. The stigma lobes start to open and curve outwards about 10 hours later, by which time very little pollen is left on the style, because the pollen bearing hairs have withered. In *C. persicifolia* the long stigma
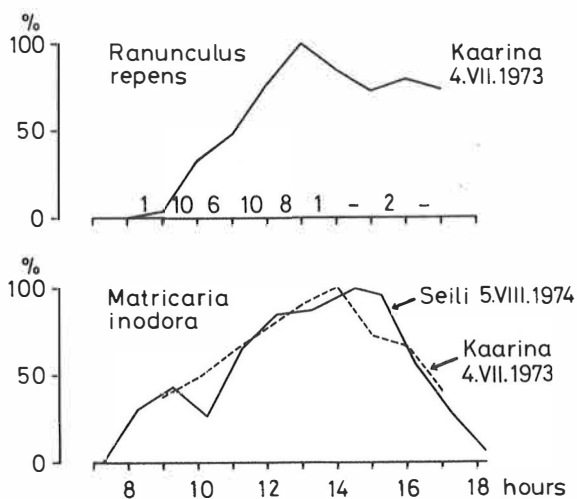
Fig. 36. Pollen presentation in *Ranunculus repes* and *Matricaria inodora*.
Five flowers or capitula were used in each series of observations. In
Ranunculus the numbers indicate the amounts of anthers that opened within
each hour. In this case pollen remained on the anthers for some time,
because there were few insect visitors to collect it.

lobes are already apart in the bud, but their tips are curved inwards and
their inner surface looks very different than in the obviously receptive
stage next day.

Newly opened flowers are thus best for pollen-collecting bees. The
opening of the flowers was studied by periodically checking marked plants.
Before the day of observation the flower buds were checked at about. 20.00.
In all the species there is a peak opening period in the forenoon, opening
proceeds slowly throughout the day and night (Table 15). The pollen pre-
sented in the forenoon can be collected by the bees until the evening.

Compositae. The nectar production of *Achillea* species and *Chrysanthemum*

Table 15. Opening times of the flowers of *Campanula* studied in Seili 1974.

hours	-7	7-9	9-11	11-13	13-15	15-17	17-19	n
C. patula (8. and 10.VII.)	9	19	22	12	1	1	-	64
C. persicifolia (7.-8.VII.)	2	1	-	1	-	1	-	5
C. rapunculoides (7.-8.VII.)	2	2	2	4	-	-	-	10
C. rotundifolia (5.VIII.)	9	2	5	7	3	1	1	28
	22	24	29	24	4	3	1	107

leucanthemum is highest in the afternoon (Fig. 35). *Matricaria inodora* (Fig. 36) presents pollen throughout the day with a peak in early afternoon. *Leontodon autumnalis* (Fig. 37) presents pollen for a short time in the fore- noon. As in *Campanula* the style in Compositae grows through the united anthers and pollen is presented on hairs of the style. If the pollen is not collected by insects, it is blown away by wind within two hours, since the pol- len-bearing hairs wither. That is why Compositae pollen is regularly found
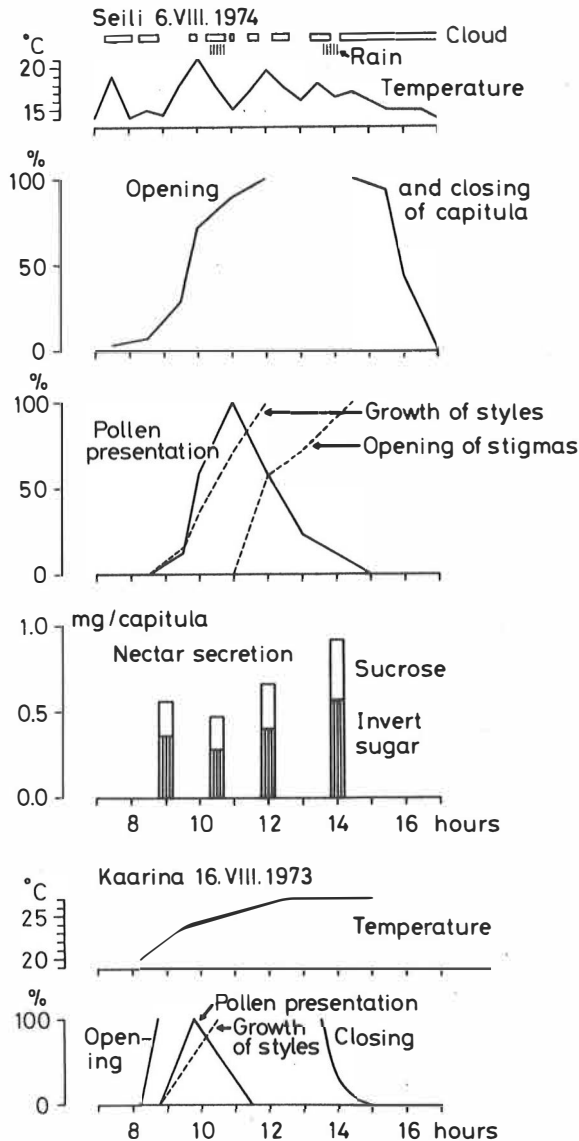
Fig. 37. Pollen and nectar presentation in *Leontodon autumnalis*.

in the air (Table 11, KÄPYLÄ & KOIVIKKO 1975). The anthesis of *Leontodon autumnalis* on Seili on 6.VIII.1974 was somewhat delayed because of cold unsettled weather. The observations made in Kaarina on 16.VIII.1973 are more representative of the normal situation on a warm sunny day. The stigma lobes open slightly in the afternoon, at which time the nectar production seems to be highest. Next morning the stigmas are more widely open and seem to be receptive.

8.3.4. Pollen collecting at different times of the day

Measured with the percentage of females returning to their nests with pollen loads, pollen collecting activity is slightly higher before than after noon (Table 16). In *C. maxillosum* the difference is not significant ($t = 1.79$, $P < 0.1$), in *C. campanularum* ($t = 2.12$, $P < 0.05$) and *H. truncorum* ($t = 2.33$, $P < 0.02$) it is fairly significant. In *C. rapunculi* the activity was higher after noon ($\chi^2 = 3.15$, $P < 0.1$), but this result is doubtful because the material is very small.

In *C. maxillosum* and *C. campanularum*, pollen-collecting activity corresponds well with the pollen presentation rhythm of their food plants (Fig. 36 Table 15).

For *H. truncorum*, pollen availability is also slightly better noon, because in the forenoon both *Leontodon* and *Matricaria* present pollen, in the afternoon only *Matricaria*. This is clearly reflected in the composition of the pollen loads of *H. truncorum* at different times of the day (Fig. 38).

Table 16. Pollen-collecting activity of the bees at different times of the day. N = number of females caught, P % = the percentages of females with pollen loads.

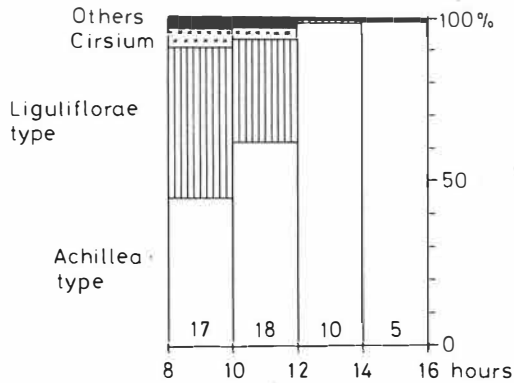| hours		6-8	8-10	10-12	12-14	14-16	16-18
C. maxillosum	N	18	315	516	273	312	134
	P%	33	23	13	14	13	16
C. rapunculi	N	-	6	9	16	8	2
	P%	-	0	0	31	25	0
C. campanularum	N	-	79	105	128	62	1
	P%	-	29	30	22	16	100
H. truncorum	N	-	39	68	68	27	-
	P%	-	49	47	32	30	-

Fig. 38. The composition of pollen loads of *H. truncorum* at different times of the day. Numbers of loads studied shown in base of each column.

8.3.5. Flower constancy and oligolecty

Pollen analyses may be used to express flower constancy numerically, but one drawback is that many pollen types cannot be identified down to species level. On the other hand, genera such as *Ranunculus* and *Campanula* are probably one "species" for bees. A good criterion of flower constancy is the proportion (%) of pure or almost pure loads in the total pollen loads studied. The definition of a pure pollen load is necessarily subjective, but it may be taken to include pollen loads with 95 % or more of one pollen type. This excludes pollen derived from contamination of the flowers. The following flower constancy percentages were obtained:

C. maxillosum	94 %
C. rapunculi	100 %
C. campanularum	86 %
H. truncorum	62 %
●. tuberculata	44 %

Another good measure of flower constancy is the mean number of pollen types (frequency ≥ 5 %) per load (Table 17).

The best way to express the degree of oligolecty numerically is to take the proportion (%) of the most important pollen type in all the pollen loads studied or in the nest provisions. The following percentages were obtained (the most important pollen type is shown in brackets):

Table 17. The numbers of pollen loads with different amounts of pollen types expressed as actual numbers and percentages. The content of pollen types is calculated at two accuracy levels: the amount of pollen types that constitute ≥ 1 %, or ≥ 5 % of the pollen load.

		Number of pollen types in a load							
≥ 1%	n	1	2	3	4	5	6	7	Mean
C. maxillosum	105	85	15	5	-	-	-	-	1.24
%		81	14	5	-	-	-	-	
C. rapunculi	18	14	4	-	-	-	-	-	1.22
%		78	22	-	-	-	-	-	
C. campanularum	69	36	20	11	2	-	-	-	1.70
%		52	29	16	3	-	-	-	
H. truncorum	66	19	24	13	6	3	-	1	2.30
%		29	36	20	9	5	-	1	
O. tuberculata	16	3	5	4	2	-	1	1	2.88
%		19	31	25	13		6	6	
≥ 5%									
C. maxillosum	105	99	6	-	-	-	-	-	1.06
%		94	6	-	-	-	-	-	
C. rapunculi	18	18	-	-	-	-	-	-	1.00
%		100	-	-	-	-	-	-	
C. campanularum	69	61	7	1	-	-	-	-	1.13
%		89	10	1	-	-	-	-	
H. truncorum	66	42	22	2	-	-	-	-	1.39
%		64	33	3	-	-	-	-	
O. tuberculata	16	7	5	3	-	-	1	-	2.00
%		44	31	19	-	-	6	-	

C. maxillosum	97.9 % (Ranunculus),
C. rapunculi	99.6 % (Campanula),
C. campanularum	96.2 % (Campanula),
H. truncorum	74.0 % (Achillea type),
O. tuberculata	24.4 % (Convallaria type).

Very high oligolecty is shown by the *Chelostoma* species. Naturally they must also show high flower constancy. *Heriades truncorum* is widely oligolectic; it is specialized to one plant family. Compositae pollen constituted 98.0 % of all the pollen grains in the pollen loads. The constancy to Compositae on individual pollen-collecting trips was 86 % (limit ≥ 95 %). *O. tuberculata* is narrowly polylectic. Four pollen types each constitute over 15 % of the

pollen in the loads. These belong to three plant families (two to Legu-
minosae). *O. tuberculata* showed very little constancy; the majority of
the pollen loads were mixed.

9. Weights of bees and their nectar and pollen loads
9.1. Methods

The bee, caught in an insect net, was put alive in a small glass tube and
taken to the laboratory within one hour. In the laboratory the animal was
killed with chloroform in the same tube. Any pollen scratched off by the
bee could be observed in the tube. The bee was first weighed with its pol-
len load, after which load was brushed into a centrifuge tube for analysis
and the bee was weighed again. The difference between the results gave the
weight of the pollen load. The sugars in the gut were then determined by
the method described in sect. 8.1.2. The concentration of nectar in the
honey stomach was not measured. The concentration of nectar in flowers
with open or partly concealed nectar mostly varies between 30 and 50 %
(BEUTLER & SCHÖNTAG 1940, PERCIVAL 1965: 89). After secretion the concen-
tration of nectar increases because of evaporation, until it reaches hygro-
scopic balance with the surrounding air (SHUEL 1955, HUBER 1956). Bees are
known to evaporate water from nectar by exposing it between their extended
mouthparts (ROBERTS 1969, SZABO & SMITH 1972, EICKWORT 1973). Accordinly,
the concentration of the nectar in the honey stomachs was assumed to be
50 % and the dry weight of the nectar sugars was multiplied by two to obtain
the approximate weight of the nectar load. The weight of the bee was ob-
tained by subtracting the weight of the pollen and the nectar load from the
gross weight.

9.2. Results and discussion

The weight of the bees varied widely (Fig. 39), being greatest in *C. maxil-
losum*. The largest nectar loads (Fig. 40, Table 18) can be assumed to be
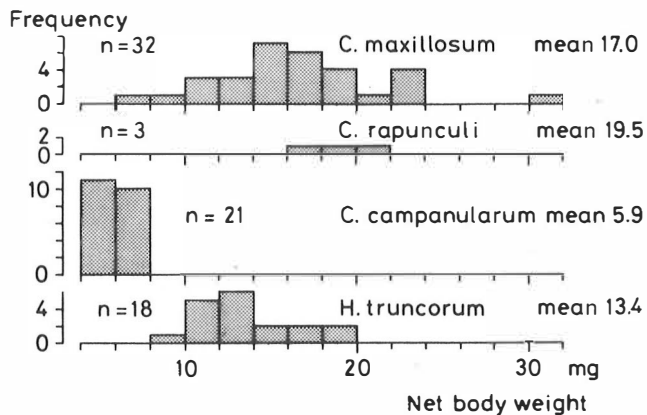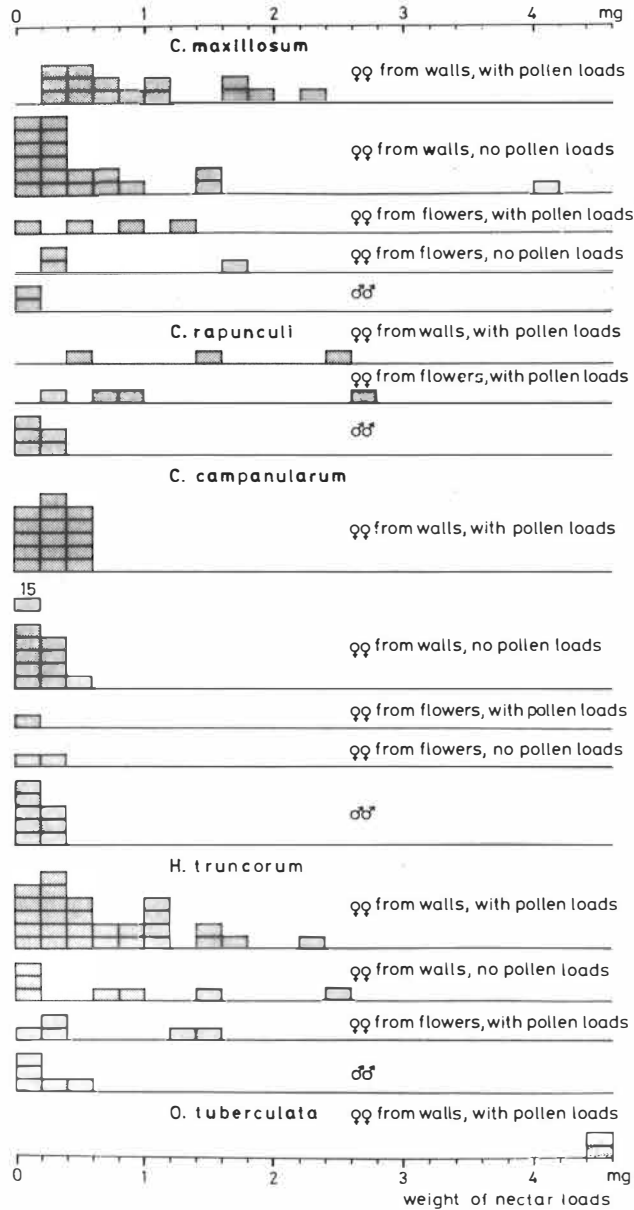

Fig. 39. Weight variation of the female bees.

Fig. 40. Weights of nectar loads. Each small rectangle means one observation.

closest to the normal loads for several reasons. (1) During catching or killing, the bees sometimes regurgitated a drop of nectar, and some scratched pollen off from their loads. (2) Most of the bees caught on flowers cannot

Table 18. The heaviest loads compared with the weight of the bee (mg).
In case of dried bees, the weight of the pollen load was estimated by
comparing it with fresh pollen loads, and the mean net weight of the spe-
cies was used. The figures for these cases are provided with question-
marks.

			gross weight	pollen load	nectar load	loads together	net weight	loads as % of net weight
C. maxillosum								
Seili	3.VII.1974	W	21.0	-	4.0	4.0	17.0	24
"	3.VII.1974	W	25.3	2.9	1.8	4.7	20.6	23
"	15.VI.1974	W	28.4	2.7	2.4	5.1	23.3	22
"	15.VI.1974	W	17.0	1.9	1.1	3.0	14.0	21
"	2.VII.1974	W	21.8	2.3	1.0	3.3	18.5	18
"	23.VII.1974	W	22.2	2.5	0.6	3.1	19.1	16
"	5.VII.1973	W	21.4	0.9	1.9	2.8	18.6	15
"	11.VII.1974	W	12.5	1.5*	0.3	1.8	10.7	17
C. rapunculi			(* lump of earth)					
Seili	16.VII.1974	W	24.5	2.4	1.6	4.0	20.5	20
"	2.VII.1974	C	19.1	0.3	2.6	2.9	16.2	18
"	19.VII.1972	W	?	1.0?	2.1	3.1?	19.5?	16?
C. campanularum								
Seili	7.VII.1974	W	7.5	1.1	0.5	1.6	5.9	27
"	9.VIII.1974	W	?	0.5?	0.6	1.1?	5.9?	19?
"	3.VIII.1974	W	6.2	0.4	0.5	0.9	5.3	17
"	5.VII.1973	W	6.9	0.4	0.4	0.8	6.1	13
"	14.VIII.1974	W	?	0.5	0.4	0.9	7.4	12
H. truncorum								
Seili	5.VII.1973	W	16.4	2.1	1.8	3.9	12.5	31
Säkylä	19.VII.1967	W	?	1.5?	1.6	3.1?	13.4?	23?
Seili	16.VII.1970	W	?	1.5?	1.5	3.0?	13.4?	22?
"	22.VIII.1974	W	23.3	1.6	2.4	4.0	19.3	21
"	23.VII.1974	W	14.4	1.4	1.0	2.4	12.0	20
"	7.VII.1973	W	12.1	1.0	1.0	2.0	10.1	20
"	16.VII.1970	W	?	-	2.4	2.4	13.4?	18?
"	5.VII.1973	W	10.1	0.7	0.7	1.4	8.7	16
"	7.VII.1973	W	14.3	1.7	0.2	1.9	12.4	15

have had a full load. The following conclusions can be made from these results.
In *C. maxillosum* full pollen loads weigh 2 - 3 mg, probably depending on
the size of the bee. The same evidently applies to *C. rapunculi*. In
C. campanularum, full pollen loads weigh 0.5 - 1 mg, and in *H. truncorum*

1.5 - 2 mg or slightly more.

Bees returning to their nest from a foraging trip may carry only nectar or pollen, or both nectar and pollen, the last alternative being found in most cases. Similar observations were made by TANIGUCHI (1956), BATRA (1966), and ORDWAY (1966).

The combined weight of the heaviest nectar and pollen loads was generally 20 - 30 % of the net weight of the bee, an individual obviously does not carry a maximum nectar load and a maximum pollen load at the same time. The individuals with the largest pollen loads had small nectar loads and vice versa.

I have not found any other observations about the weights of the nectar loads carried by small solitary bees. According to POUVREAU (1974), in bumble-bees the nectar loads average about 50 % of their weight, and in individual cases constitute up to 90 % of their weight. Honey-bees can also carry nectar loads nearly as heavy as themselves, but the load in mostly less than half the weight of the bee; combined pollen and nectar loads are on the average only slightly heavier than pure nectar loads. (FUKUDA et al. 1969).

10. Discussion of the main results

10.1. Flower visits for food

The populations of the *Chelostoma* species studied were more specialized in their pollen collecting than could be expected from flower records in the literature.

Chelostoma maxillosum favours buttercups *(Ranunculus)* as both a pollen and nectar source. It occasionally sucks nectar from several other flowers, especially *Geranium* and yellow Compositae (cf. NIEMELÄ 1934). Reports of pollen collecting from *Geranium sanguineum, Leontodon autumnalis* (POPPIUS 1903), and *Hieracium pilosella* (NIEMELÄ 1934) are probably erroneous. Bees may have gone to these flowers to such nectar with a load of *Ranunculus* pollen. Workers in other countries report that *C. maxillosum* favours *Ranunculus*, and in addition *Veronica* (JØRGENSEN 1921:82), *Taraxacum,* and *Rubus* (STOECKHERT 1933: 195, DYLEWSKA 1962). It is probable that in the other European countries, too, flowers other than buttercups may be visited only for nectar.

C. rapunculi and *C. campanularum* are almost identical in their flower preferences. Their specialization to bell-flowers (Campanula) is confirmed by observations from Finland (NIEMELÄ 1934) and other countries (FREY-GESSNER

1908 - 1912: 7 - 8, JØRGENSEN 1921: 81 - 82, SCHMIEDEKNECHT 1930: 823, STOECKHERT 1933: 194, BENOIST 1946, DYLEWSKA 1966, PESENKO 1971). According to the same authors, other important food plants are *Malva*, *Echium vulgare* and *Jasione montana*. NIEMELÄ (1934) reported occasional pollen collecting by both species from *Chamaenerion angustifolium*, *Malva moschata*, and *Echium vulgare*. These observations are probably erroneous, for the reasons given earlier. *Malva* and *Echium*, are rare in Finland and are thus more frequently visited in Central Europe. A more detailed study is needed to ascertain whether, as seems likely, these flowers are visited only for nectar. Both species frequently visited *Chamaenerion angustifolium* for nectar and favourite nectar sources of *C. campanularum* were yellow Compositae (cf. NIEMELÄ 1934). In both species males sucked nectar from many more flower species than females.

My observations of the flower visits of *Heriades truncorum* support earlier reports that this species visits many species of the family Compositae (FREY-GESSNER 1908 - 1912: 5, SCHMIEDEKNECHT 1930: 823, STOECKHERT 1933: 193, PESENKO 1971). There seems to be no preference for a particular shape, size or colour of the capitula. Possibly certain scent chemicals common to these species are involved. Non-composite flowers were visited only for nectar.

O. tuberculata is a rare species in Europe, occurring in the Alps and the northern part (SCHMIEDEKNECHT 1930): 813). Observations on its biology are few. New flower records for this species in Finland are *Lathyrus vernus*, *Polygonatum odoratum*, *Convallaria majalis*, *Vaccinium*, *Caragana arborescens*, *Geum rivale*, *Anemone nemorosa*, *Rubus idaeus (?)*, *Leontodon autumnalis*, and *Viola arvensis*, i.e. most of the present records (cf. ELFVING 1968). Some pollen loads contained pollen of *Lotus corniculatus*. Visits to this flower species have been reported by several authors (FREY-GESSNER 1908-1912: 33, NIEMELÄ 1934, MÜLLER 1944).

This material supports ROBERTSON's (1925) generally accepted view that bees usually collect nectar from a larger selection of flowers than pollen. Actually this has been clearly demonstrated in only a few earlier publications (MICHENER 1953, BATRA 1966). In the present species, the main nectar and pollen sources were about the same and other flower species were visited occasionally for nectar.

Even in honey-bees a few pollen types may constitute the bulk of the provisions in local populations (McLELLAN 1976), but a bee species is oligolectic only if the major pollen source is the same in different populations

and areas. In this case only single populations were studied intensively, but flower records in the literature suggest that *Chelostoma maxillosum*, *C. rapunculi*, and *C. campanularum* are strictly oligolectic species, each specialized to a single plant genus. *Heriades truncorum* is more widely oligolectic, being specialized to a plant family. We might say that *O. tuberculata* is narrowly polylectic, because its choice of food plants is more limited than that of the extreme polyleges, honey-bees and bumble-bees.

A strictly oligolectic species naturally also shows high constancy during individual foraging trips. Even extremely polylectic species are known to show high flower constancy (CLEMENTS & LONG 1923, BRITTAIN & NEWTON 1933, MACIOR 1968, ANASIEWICZ & WARAKOMSKA 1969, FREE 1970). On the other hand the pollen loads of *Heriades truncorum* regarded as an oligolectic species, were often mixed. *Osmia tuberculata* showed very little constancy, the majority of the loads being mixed.

In many studies pollen loads have been classified only as pure or mixed (BRITTAIN & NEWTON 1933, MACIOR 1968, BEATTIE 1972). This is misleading, because in most cases mixed pollen loads are over 95 % pure (FREE 1970, HASLERUD 1974). The reasons for the existence of "foreing" pollen are (1) occasional visits for nectar to another flower species between pollen collecting (FREE 1970, Table 14 of this study), or (2) in a social species, contamination within the nest (FREE & WILLIAMS 1972), or (3) contamination of flowers (Table 10).

When pollen loads are clearly composed of two or more pollen types, a change from one flower species to another may have happened at some moment during the foraging trip (BATEMAN 1951, MICHENER 1953). In this case the pollen loads are formed of layers of different pollen. In the majority of the mixed loads of honey-bee studied by BETTS (1920), the two or more pollen types were mixed, and only a minority of the cases were they segregated in layers. In the present study it was not clear whether the mixed pollen loads were layered or not. The regular occurrence of mixed Compositae pollen loads in *Heriades truncorum* indicates that it visits many plant species with capitula of varying size and colour. I once followed the flower visits of this species in a flower patch of *Matricaria inodora* and *Lapsana communis* and observed that these very different looking flower heads were visited without distinction. Further field studies could be made to confirm this observation and to ascertain whether females of *Chelostoma* visit any *Ranunculus* (*C. maxillosum*) or *Campanula* (*C. rapunculi* and *C. campanularum*)

species available.

Honey bees discriminate between closely related species or subspecies if there are some distinct differences in the colour, shape or smell of the flower (MATHER 1947, GRANT 1949, 1950, BATEMAN 1951). The similarity of the flower is thus more important in flower constancy than taxonomic kinship. It is possible that the species of *Chelostoma* studied here are not able to differentiate between different species of *Ranunculus* or *Campanula*.

It is not known how the flower specificity of oligolectic bees is maintained from generation to generation. Preimaginal conditioning to pollen has been suggested by LINSLEY (1961) and THORP (1969). But the occacional use of the pollen of other flowers during a local shortage of the specific pollen has never been observed to cause changes in the next generation. Thus oligolecty is probably an inherited character operating through behavioural responses (CRUDEN 1972).

10.2. Adaptations associated with oligolecty

The most important adaptations in the bee are:
- Synchronization of the flight period with the flowering of the food plant.
- Morphological adaptation to collecting nectar and pollen and to carrying pollen from the particular flower type.

In this study the phenology of the flowers and bees showed good agreement ((cf. ROBERTSON 1929, MÜNSTER-SWENDSEN 1968, EICKWORT 1973). Also important is adaptation to the diurnal rhythm of pollen presentation and nectar secretion in the food plant. In bee flowers the maximum pollen presentation is generally at noon or in the late forenoon (PERCIVAL 1950, 1965: 74 - 75). The bees studied here were active from about 8.00 to 16.00 hours, during which time both pollen and nectar were available. The pollen collecting activity was somewhat higher in the forenoon, which accords with the pollen presentation of the main food plants.

The morphological adaptation most often associated with flower visiting is the length of the proboscis (e.g. LOEW 1884, HOBBS et al. 1961, TERÄS 1976, HEINRICH 1976). The hair structures associated with carrying and collecting pollen are probably also adapted to certain flower and pollen types (LINSLEY & MacSWAIN 1957, THORP 1969, PASTEELS & PASTEELS 1974). A study should be done on the hair structures of oligolectic bees and their adaptation to the pollen morphology of the food plants.

The evolution of the sense organs and morphology of bees and other insects has been considered responsible for the evolution of more and more complex flower types (LEPPIK 1957, 1969). LEPPIK (1957) wrote that pollinators tend to visit the most advanced flower type available and GRANT (1950) claimed that the development of concealed nectaries and other advanced characters in insect-pollinated flowers has been a necessary precondition for the development of flower constancy among insects. But these authors dealt principally with polylectic social bees, and their views do not hold with solitary bees and their food flowers, for the reasons given below (cf. also LINSLEY 1958). Moreover, in most areas solitary bees clearly outnumber social bees (LINSLEY 1958, HEINRICH 1976).

The nectar sources of oligoleges are usually scattered through the local familier of plants with entomophilous flowers (LINSLEY 1958) and no relationship is apparent with the level of specialization of the flower (PESENKO 1975). I do not see any morphological reason why the *Chelostoma* and *Heriades* species studied should be restricted to the flowers they visit, and yet they are oligolectic. The flowers visited have partly concealed nectaries, but the bees could reach nectar in deeper ones. The flowers are not dependent on these bees for their pollination, but are visited by several other insects.

Some cases have been described where the oligolectic bee and its food plant are poorly coadapted (POPOV 1958, LINSLEY et al. 1963, CRUDEN 1972, BARROWS et al. 1976). Oligolecty is common among more primitive bees with short proboscises (ROBERTSON 1925, NIEMELÄ 1934), whereas it seems that the most advanced bees with the longest proboscises are generally the most polylectic. When concealment of nectar and other structural specializations limit the amount of flower visitors, oligolecty is presumably not needed to reduce competition.

If two related bee species with the same food plant start to live sympatrically, slight differences may develop in their phenology and diurnal activity to reduce competition (LINSLEY & MacSWAIN 1959). Severe competition may even cause one of the species to turn to a different plant family (LINSLEY & MacSWAIN 1957, 1958, THORP 1969, CRUDEN 1972). This study did not show how *Chelostoma campanularum* and *C. rapunculi* reduce competition for their common food source. They have the same flight period, but pollen may be collected at different times of the day.

Differences in the chemical composition and nutritional value of different

pollen types may be an important factor in oligolecty, but this question has been studied very little. LEVIN & HAYDAK (1957) fed the larvae of *Osmia lignaria* artificially with pollen of different plant species. Only some pollen types gave proper growth and development of the larvae, although this species is relatively polylectic. It is not known whether oligolectic species can develop to adults with foreign pollen.

10.3. Competition for nest cavities

The dimensions that most often separate the ecological niches of solitary bees are (1) the selection of food plants and (2) the choice of nesting places. Habitat selection is evidently secondary (LINSLEY 1958). The seasonal and diurnal time of flight activity affect the degree of competition. Competition for the first resource has already been dealt with earlier in this discussion.

The species of bees studied use cavities already existing in wood (or straws, etc.) as nesting places. It may be supposed that the most important factor limiting population size is the amount of nest cavities available (cf. DANKS 1971 a, b), and this is also suggested by the very similar sizes of the bee populations in the two main study years.

The species divide the available cavities according to their size. *Chelostoma campanularum* does not compete with the others, because of its small size. Similarly, there is no competition with the biggest species, *Osmia tuberculata*. Three species *C. maxillosum, C. rapunculi,* and *Heriades truncorum* use nest cavities of about the same size. *C. maxillosum* nests in shady areas of the walls, while the other two use the sunny areas. MICHENER (1970) also found a sun-shade division of nest cavities among African stem-nesting bees. Competition probably exists between *C. rapunculi* and *H. truncorum*, and this may be the reason for the small amounts of *C. rapunculi* at the barn. This point should be studied further e.g. by examining the bee populations of many barns, or by experimentally eliminating one of the populations. Recent observations by CORREIA (1976 b) also point to nest competition between these two species; she found an inverse relationship in their abundance between successive years. If there is competition for nest cavities, this factor is probably limiting in most cases, and *C. rapunculi* and *C. campanularum* can coexist without dividing their common food source.

11. Summary

The following species of solitary bees have very similar nesting habits
using old cavities in wooden buildings: *Chelostoma maxillosum, C. rapunculi,
C. campanularum, Heriades truncorum*, and *Osmia tuberculata*. Their bionomics
was studied, an old log barn being chosen as the principal study place. The
emphasis was on flower relationships. The field work was mainly done during
summers 1970 and 1974.

    C. maxillosum and *O. tuberculata* are early summer species, the peaks of
their flight periods occurring in mid-June. *C. rapunculi, C. campanularum*
and *H. truncorum* are mid and late summer bees, with no clearly defined peaks
and rather long emergence periods. The phenology of the bees agreed well
with the phenology of the principal food plants.

    The sizes of the bee populations were very similar in 1970 and 1974, which
suggests that population size was limited by the amount of available nest
cavities. The sex ratio of *C. maxillosum* and *C. campanularum* was about 1:3
($\male\male:\female\female$), and that of *H. truncorum* about 1:1. The populations of *C. rapunculi*
and *O. tuberculata* were too small to determine this.

    Marking of individuals and the shape of the flight curves indicated that
the maximal life span was about 30 days for females and 20 days for males.
The death rate was studied in *C. maxillosum*. It seems to be fairly constant
throughout the flight season. The ageing of the population depends on the
amount of active (warm enough) days.

    All the species had about the same diurnal flight period from ca. 8.00 to
16.00 hours. Flight activity showed the highest correlation with light and
the next highest with temperature. It was best explained by temperature and
light thresholds. The temperature thresholds ranged from 16.5 to 19°C,
according to the species.

    Owing to their size, the smallest (*C. campanularum*) and biggest (*O. tuber-
culata*) species did not compete with the others for nest cavities, but the
three remaining species used nest cavities of about the same size. Of these,
C. maxillosum nested only in the shady parts of the walls, while the other
two used the sunny parts. *C. rapunculi* and *H. truncorum* thus probably compete
with each other for nesting sites.

    The liquid used to moisten the earth in the nest structures of *C. maxillo-
sum* and *C. campanularum* proved to be nectar. *O. tuberculata* used grains of
sand, pieces of decayed wood and pieces of masticated leaves to construct the
terminal plug.

    The length of a pollen foraging trip varied with the species from one
minute to one hour. On arrival, the bee enters the nest head first and pro-
bably empties the nectar load, then turns at the entrance and backs in to
remove the pollen load.

    Copulation was rarely seen. Copulation attempts were mostly violently
resisted by the females. Observation of male patrolling behaviour and
copulation attempts, indicates that *C. maxillosum* copulates at the nesting
place, on the leaves of bushes and in flowers of *Ranunculus, C. rapunculi*
and *C. campanularum* in flowers of *Campanula, H. truncorum* by the nesting
walls and in flowers of Compositae.

    The bees spend the night in nest cavities (females and males of *C. campa-
nularum* and *H. truncorum*), facing inwards with the abdomen near the entrance,
or in flowers (males of *C. maxillosum* and *C. rapunculi* and both sexes of *C.
campanularum*).

    The flowers visited for food were studied by pollen analysis of the pollen
loads and guts, methods being developed for this purpose. The results were
supplemented with field observations. All the *Chelostoma* species proved to

be oligolectic. *C. maxillosum* collected pollen of *Ranunculus*, *C. rapunculi* and *C. campanularum* collected pollen of *Campanula*. *H. truncorum* visited many species of the family Compositae and is thus widely oligolectic. *O. tuberculata* is polylectic, visiting flowers of many plant families. The main nectar sources were the same as the main pollen sources, but many other flower species were occasionally visited for nectar. The pollen loads regularly contained small amounts of many pollen types. This was because the flowers were contaminated with foreign pollen by wind and insects. The most important pollen types causing this contamination were *Filipendula*, *Galium*, Garyophyllaceae, *Achillea* type, *Hypericum*, and *Potentilla*. The pollen and nectar presentation of the main food plants coincided with the collecting activity of the bees.

All the species carry the pollen loads dry in their abdominal scopas. Bees on a foraging trip mostly collected both pollen and nectar, but also only pollen or only nectar. The biggest nectar loads were found in individuals with little or no pollen, and vice versa. The heaviest loads were about 1/4 - 1/3 of the weight of the bee.

Pollen analysis of the pollen loads and guts, and sugar analysis of the guts proved to be the most valuable tools in studies of the flower relationships of bees. Field observations alone are often inadequate. Drawbacks to pollen analysis are the difficulties encountered in pollen identification and contamination of flowers by foreign pollen. The present theories are opinions on the flower relationships of bees are discussed.

Acknowledgements

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Selostus

Tutkimuksessa selvitettiin yksityiskohtaisesti viiden Megachilidae-heimoon
kuuluvan mesipistiäislajin (*Chelostoma maxillosum* (L.), *C. rapunculi* Lep.,
C. campanularum (K.), *Heriades truncorum* (L.) ja *Osmia tuberculata* Nyl.)
ekologiaa pääpainon ollessa kukillakäyntien selvittämisessä. Tutkimukses-
sa pyrittiin myös kehittämään mesipistiäisten ekologian, etenkin ravinto-
ekologian tutkimiseen liittyviä menetelmiä.

Kaikki lajit pesivät latojen seinissä tai vastaavissa paikoissa vanhois-
sa kovakuoriaisten toukkakäytävissä. Käytävän naaras jakaa väliseinin pe-
räkkäisiin kennoihin, joihin se kerää medellä kostutetun siitepölykakun
toukan ravinnoksi. Lopuksi pesä suljetaan tulpalla.

Tutkimuspaikaksi valittiin vanha hirsilato ympäristöineen Seilin saa-
rella Nauvossa Turun yliopiston Saaristomeren Tutkimuslaitoksen välittömäs-
sä läheisyydessä. Em. laitoksessa tehtiin laboratoriotyöt. Työ tehtiin
pääosaksi kesinä 1970 ja 1974.

C. maxillosum ja *O. tuberculata* ovat varhaiskesän lajeja, joiden lento-
aikojen huiput sattuivat kesäkuun puoliväliin. *C. rapunculi*, *C. campanula-
rum* ja *H. truncorum* ovat keski- ja loppukesän lajeja, joilla on verrattain
pitkä kuoriutumisaika, eikä lentoajassa ole selvää huippua. Yksilöllises-
ti merkittyjen yksilöiden ja lentoaikakuvion perusteella naaraiden maksi-
maalinen elinaika oli noin 30 päivää, koiraiden n. 20 päivää. Populaation
kuolemisnopeutta selvitettiin tarkemmin *C. maxillosum*illa. Se oli riippu-
vainen lentoaktiivisuudelle tarpeeksi lämpimien päivien määrästä mieluum-
min kuin todellisesta iästä.

Kaikkien lajien päivittäinen lentoaika oli suunnilleen sama, n. klo 8-
16. Lentoaktiivisuus oli parhaiten korreloitunut valaistukseen, seuraa-
vaksi parhaiten lämpötilaan. Lentoaktiivisuus voitiin parhaiten selittää
valaistuksen ja lämpötilan kynnysarvoilla. Lämpötilakynnykset vaihtelivat
välillä 16.5 - 19° lajista riippuen.

Kokonsa vuoksi pienin (*C. campanularum*) ja suurin (*O. tuberculata*) laji
eivät kilpailleet pesäkoloista muiden lajien kanssa, mutta kolme muuta lajia
käyttivät suunnilleen samankokoisia pesäkoloja. Näistä *C. maxillosum* pesi
vain varjoisilla seinillä ja etelänpuoleisten seinien varjoisissa kohdis-
sa, etenkin räystään varjossa, kun taas *C. rapunculi* ja *H. truncorum* pesi-
vät vain aurinkoisilla seinillä. Kahden viimeksi mainitun lajin välillä
vallitsee mahdollisesti kilpailu pesäpaikoista. *Chelostoma*-lajit rakensi-
vat pesiensä väliseinät ja tulpan maasta. Ainakin lajit *C. maxillosum* ja
C. rapunculi käyttivät mettä maan kostuttamiseen rakentamisen yhteydessä.
O. tuberculata rakensi pesätulpan pikkukivistä, lahopuun paloista ja pures-
kelluista lehtien paloista. *H. truncorum* käytti pesänrakennuksessa pihkaa,
johon oli toisinaan sekoitettu hieman maata tai puun purua.

Yhden siitepölynkeruumatkan kesto vaihteli eri lajeilla yhdestä minuutis-
ta yhteen tuntiin. Saapuessaan pesälle kuorman kanssa naaras menee ensin
pää edellä sisään tyhjentäen todennäköisesti mesikuorman, kääntyy sitten
pesäaukolla, peruuttaa sisään ja raaputtaa takajaloillaan siitepölykuorman
pois takaruumiin alapinnan karvojen väleistä.

Paritteluja nähtiin harvoin, sen sijaan useammin parittelun yrityksiä,
joita naaraat voimakkaasti vastustivat. Nämä tapahtuivat paikoilla, joilla
koiraat suorittivat parveilulentoa tai naaraiden etsintälentoa. *C. maxillo-
sum*in koiraat suorittivat parveilulentoa pesäpaikalla ja pensaiden lehtien
yllä ja yksittäin naaraiden etsintälentoa leinikkien (*Ranunculus*) kukilla.
C. rapunculi- ja *C. campanularum*-koiraat suorittivat naaraiden etsintälen-
toa kellokukilla (*Campanula*), *H. truncorum* -koiraat ladon seinustalla ja
Compositae-heimon mykeröiden tuntumassa.

Yönsä mesipistiäiset viettivät osaksi pesäkoloissa tai vastaavissa puun-
koloissa (*C. maxillosum*in ja *O. tuberculata*n naaraat, *C. campanularum*in ja
*H. truncorum*in molemmat sukupuolet) tai kukissa (*C. maxillosum*in ja *C. rapun-
culi*n koiraat, *C. campanularum*in molemmat sukupuolet). Puunkoloissa yöpy-
essä takaruumis oli aina ulospäin kärki lähellä pesäaukkoa.

Ravinnonhakua kukista selvitettiin pääasiassa analysoimalla siitepöly-
kuorman ja suolen siitepöly. Tätä varten kehitettiin preparaatinvalmistus-
tekniikkaa. Edelleen kehitettiin menetelmä suolen sisältämän sokerin mää-
rän analysoimiseksi. Tuloksia täydennettiin maastohavainnoilla. Kaikki
Chelostoma-lajit osoittautuivat oligolektisiksi, mikä tarkoittaa sitä, että
ne ovat erikoistuneet keräämään siitepölyä vain yhdeltä kasvisuvulta. *C.
maxillosum* keräsi siitepölyä leinikeiltä (*Ranunculus*), *C. rapunculi* ja *C.
campanularum* kellokukilta (*Campanula*). *H. truncorum* käytti siitepölynläh-
teenä monia Compositae-heimon kasveja. Sitä voidaan pitää väljästi oligo-
lektisena. *O. tuberculata* on polylektinen, vieraillen moneen eri heimoon
kuuluvien kasvien kukilla. Tärkeimmät mesilähteet olivat samat kuin tär-
keimmät siitepölylähteet. Mettä kerättiin kuitenkin satunnaisesti paljon
useamman kasvilajin kukilta kuin siitepölyä. Koiraat kävivät mettä imemäs-
sä suunnilleen samoilla kasvilajeilla kuin naaraatkin. Usein siitepöly-
kuormat sisälsivät pieniä määriä vierasta siitepölyä. Osaksi tähän olivat
syynä satunnaiset vierailut muilla kukilla keruumatkojen yhteydessä. Osak-
si tämä voitiin osoittaa johtuvaksi siitä, että tuuli ja hyönteiset sekoit-
tavat vierasta siitepölyä kukkiin.

Kaikki lajit kuljettivat siitepölyn kuivana ns. vatsaharjassaan. Yhdel-
lä keruumatkalla naaraat keräsivät yleensä sekä mettä että siitepölyä, mut-
ta toisinaan vain siitepölyä tai vain mettä. Suurimmat mesikuormat tavat-
tiin yksilöillä, joiden siitepölykuorma oli pieni tai puuttui ja päinvas-
toin. Painavimmat kuormat olivat noin 1/4 - 1/3 yksilön painosta.

Siitepölykuorman ja suolen siitepölyn analysointi ja mesimahan sokerin
analysointi osoittautuivat arvokkaiksi menetelmiksi mesipistiäisten ravin-
toekologian tutkimisessa. Kenttähavainnoista pelkästään ei saa aivan luo-
tettavaa tietoa. Tärkeimmät vaikeudet siitepölyanalyysissä liittyivät vie-
raan siitepölyn kontaminaatioon kukissa sekä siitepölyn määritysvaikeuksiin.