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## On the Biology of the Ivy-Bee *Colletes hederæ* Schmidt & Westrich, 1993 (Hymenoptera, Apidae)<sup>1</sup>

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**Abstract.** The biology of *Colletes hederæ* Schmidt & Westrich, 1993, a bee species oligolectic on ivy (*Hedera helix*), was studied in late summer 2003 at a nesting aggregation in Dirmstein near Grünstadt (Pfalz), Germany. We analysed the diurnal foraging rhythm, pollen carrying capacity, rate of reproduction, nest architecture, requirements on the nesting habitat and dependence on climatic parameters. In addition, the distribution of *C. hederæ* is revised and represents an adriato-mediterranean distribution type. All known localities of this species fall within the distributional area of *Hedera helix*. *Colletes hederæ* seems to prefer inclined and southward exposed nest sites in sand or loess soils. The females of *C. hederæ* started their first trip on average at 9.52 h in the morning, made 5.5 provisioning trips and returned from their last trip at 17.09 h. The mean duration of all provisioning trips was 60 minutes but the first flight in the morning was significantly longer (90 min) than the subsequent trips of the day. This is interpreted as additional adult feeding on nectar after a night in the nest. The duration of provisioning trips decreased with increasing temperature. The oligolecty of *C. hederæ* was confirmed. *Colletes hederæ* collected on average 0.5 million grains per pollen load and the cells contained 2.8 million grains. Four nests were excavated; the main burrow ran between 7 and 12 cm horizontally into the steep face and the first cells occurred at a depth of 30–45 cm. Beyond a depth of 60 cm no cells were found. Between four and eight cells branched off the vertical part of the main burrow; side burrows were only found in one nest. During the extraordinarily warm and dry season of 2003, the females completed up to 18 cells.

**Key words.** Distribution, diurnal foraging rhythm, pollen carrying capacity, reproduction rate, nest architecture

### 1. INTRODUCTION

*Colletes hederæ* was described as a new species only in 1993 (SCHMIDT & WESTRICH 1993), based on specimens collected in Germany and Croatia (Fig. 2). The species appears to be uncommon and is known from few localities. This species is also recently recorded from Great Britain, Luxembourg, The Netherlands, Belgium and Spain (FEITZ 2001, PEETERS et al. 1999, PETIT 1996, RATHJEN 1998). *Colletes hederæ* was probably recognized as a distinct species so recently because all species of *Colletes* are morphologically very similar and it particularly resembles *C. succinctus* (Linnaeus) and *C. halophilus* Verhoeff. Furthermore, *C. hederæ* is active in autumn when most other bees have finished their life cycle and ivy was not considered as an attractive pollen source for bees before.

In the past 20 years important new data on the biology of bees were gathered and published. In Germany, Paul WESTRICH (1989) set the standard for many other subsequent books dealing with the biology of bees (BELL-MANN 1995, SCHMID-EGGER et al. 1995, MÜLLER et al. 1997). Taking a more global view, "The bees of the World" by Charles D. MICHENER (2000) set a milestone in the history of literature on bees at the beginning of the millennium. Nevertheless, exact data on the biology of many of the more than 16,000 species worldwide or

about the 550 German species of solitary bees are scarce or not available. Likewise, the biology of the newly described *Colletes hederæ* is largely unknown. Biological data are needed to support taxonomic decisions as in the case of *C. hederæ*, *C. halophilus* and *C. succinctus*, but also to understand the mechanisms of speciation. Lastly, good knowledge of the biology and habitat requirements of the species facilitates conservation measures.

The aim of the present study was therefore to investigate the biology of *Colletes hederæ* including the diurnal foraging rhythm, pollen carrying capacity, rate of reproduction, nest architecture, requirements on the nesting habitat and dependence on climatic parameters. Furthermore the current distribution of the species is reviewed.

### 2. MATERIALS AND METHODS

#### 2.1. Study area

The study area is located in southwestern Germany near the city of Grünstadt (Pfalz) in a village called Dirmstein (49°34'04"N, 08°14'22"E). The nest aggregation of *C. hederæ* was discovered in 1994 (NIEHUIS pers. comm. Bonn 2003, SCHMID-EGGER 1997) and is situated on a steep face of loess below a vineyard. The steep face has a total length of approximately 150 m and is exposed southwards. The climate is sub-oceanic with mild winters, a summer maximum of precipitation (59–71 mm per m<sup>2</sup> and year) and an annual mean temperature of 10.2° C.

<sup>1</sup> In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

## 2.2. Abiotic parameters

Climatic parameters were measured with data loggers (Orion Tiny Logger Manager OTLM Tinytalk®). The soil temperature was taken half-hourly at a 20 cm depth on the steep face, air temperature and atmospheric humidity were recorded every quarter of an hour in a portable weather station at a height of 2 m. Data of the “Deutscher Wetterdienst – Station Mannheim” were also used. The soil type was characterized using a soil particle size analysis and we determined the soil density. Furthermore we calculated the inclination of the steep face. The host plant *Hedera helix* LINNAEUS was mapped in a radius of 500 m around the nesting aggregation.

## 2.3. Ethological observations

We observed the behaviour of 16 different females for five days during September 2003. Marking tests at the beginning of the season showed that the females were very sensitive to this interference (cf. BISCHOFF et al. 2003) and consequently we decided to mark only the nests of the respective females. Nests were marked with coloured toothpicks. We recorded the time of first departure, number of foraging trips, last return and digging activity. A total of 168 data sets were documented. Since the activity of most bees is extremely influenced by weather conditions (BISCHOFF et al. 2003, LARSSON 1991, LIND 1968) we created a measure for the bees' activity independent from weather conditions (cf. MÜLLER 1994) which is referred to as a so-called “bee-day” (BD). One bee-day corresponds to a day with optimal weather conditions, which females could use completely for provisioning activities. The observed flying activity on days with optimal conditions was 8 hours. The mean temperature at those optimal days amounted to 17°C and the duration of sunshine was between 8 and 10 hours.

## 2.4. Pollen analysis

For pollen analysis, 15 females of *C. hederæ* were captured and transferred in vials with 70% ethanol. To remove the complete pollen load from the bees, all body

parts (legs and sometimes thorax without wings) were sonicated in vials filled with a liquid medium (cf. BUCHMANN & SHIPMAN 1990). Furthermore we excavated 20 cells of *C. hederæ*, removed the cell lining, larva and stored the pollen load in ethanol. The number of grains per pollen load or cell was determined using an electronic particle counter (Casy® cell counter and Analyser). To calculate the mean number of pollen grains per pollen load and cell, only particles between 20 and 30 µm were considered since they represent the grain size of *Hedera helix*. All pollen load and cell samples were qualitatively checked with a scanning electron microscope. The pollen samples were treated with Diethylether to remove pollen cement and with 1,1,1,3,3,3,-Hexamethyldisilazam to avoid deflation.

## 2.5. Nest excavations

Only nests with observed female activity were excavated at the end of the season. Due to the high inclination, nests could not be poured out with plaster. We excavated the nests by following the main burrow from the nest entrance and removed with a spoon the soil layers very carefully until the first cell appeared.

## 3. RESULTS

### 3.1. Abiotic characteristics

The observed nesting aggregation extended over a breadth of 8 m of the steep face. The height of the steep face amounted to 8.65 m at the studied aggregation. The base of the steep face ran with an inclination of 130° up to a height of 2.65 m and above this height the angle was nearly 90°. At a height of 2 m a line of natural grass cover could be identified and a total of 30% of the studied aggregation was covered with vegetation.

The mean values of air temperature, soil temperature, humidity and hours of sunshine at the study area (onsite measurements) and from the nearest weather station are documented in Table 1. No significant differences between our data and the data of the local weather station at Mannheim were found.

**Table 1:** Mean climatic parameters measured during five field days in September 2004 (DWD = local weather station at Mannheim)

	Air temp. (°C)	Soil temp. (°C)	Humidity	Hours of sunshine
On-site data	22.76 ± 4.42	21.48 ± 2.70	39.53 ± 11.90	
DWD	21.70 ± 3.58		39.38 ± 11.88	9.71 ± 1.06

The mean soil density amounted to 1.18 g/cm<sup>3</sup> (n = 6) and the grain size analysis revealed a typical loess soil comprising 78% silt, 15% clay and 7% sand.

### 3.2. Distribution of *C. hederæ*

*Colletes hederæ* has been recorded from the following localities in nine countries of southern and western Europe (Fig. 1):



Fig. 1: Distribution area of *Hedera* (shaded) (after MEUSEL 1978) and records of *Colletes hederæ*.

**Belgium:** Bassenge (PETIT 1996); **Croatia:** Lopar: Francelici/Matahlici, Rovinj: 2 localities; **France:** Ile-de'Oléron, Le Caylar, St. Chaptes, St. Jean-du-Gard (SCHMIDT & WESTRICH 1993), Bathernay, Buoux: Le Fort, Fontvieille, Lacoste, Maussane-les-Alpilles, Paradou, Pargny, Ratières, Rempoul: near St. Pol, Rustrel (WIERING 1999), Cherbourg Peninsula: north coast (EDWARDS & TELFER 2001), Avelmes, Corse: Caleraggio; **Germany:** Karlsruhe-Durlach (SCHMIDT & WESTRICH 1993), Alsheim, Bockenheim, Dirmstein, Flörsheim, Jockgrim, Monsheim, Nackenheim, Oppenheim (SCHMIDEGGER et al. 1995), Oestrich-Winkel (TISCHENDORF 1997), Burkheim (WESTRICH & DATHE 1997), Ihringen (SCHWENNINGER, pers. com.); **Great Britain:** Guernsey (Channel Island): 38 localities (SCHMIDT & WESTRICH 1993, EDWARDS & TELFER 2001, BWARS data base), East Prawle, Isle of Portland, Lulworth: 3 localities, Ringstead Bay, Swanage: 6 localities, Weymouth, Worth Matravers: 3 localities (CROSS 2002, BWARS data base), Branscombe, Corfe Castle, Herm (Channel Island), Jersey (Channel Island), Kimmeridge, Langton Matravers, Lihou (Channel Island), Osmington Mills, Preston Winslow, Sark (Channel Island): 4 localities, Ulwell: Godlingston Hill, Wareham, Wool, (BWARS data base); **Italy:** Bolzano, Isola del Gilio, Merano (SCHMIDT & WESTRICH 1993), Lazio: Albano (WIERING 1999), Calci, Mte. Gargano: M.S. Angelo, Sardinia: Alghero, Sardinia: Oliena,

Varenna; **Luxembourg:** Remerschen, Schwebsange, Stadtbredimus, Wintrange (FEITZ 2001); **Netherlands:** Maastricht, Botanical Garden Lichtenberg (LEFEBER 1998); **Slovenia:** Kras: Brje pri Komnu, Kras: Gorjansko (GOGALA 1991), Hrastovlje (GOGALA 1994); **Spain:** Girona: Les Preses (RATHJEN 1998); **Switzerland:** Biasca: near river Brenno, Châble-Perron: Cheseaux, Lalden: banks of river Rhone near Taleia, Peney, Russin: 2 localities, Sion, Yverdon-les-Bains (AMIET et al. 1999, CSCF data base), Les Bioux: Lac de Joux (AMIET pers. com.).



Fig. 2: *Colletes hederæ* male (drawing by Florian Thümmel).

The distribution of *C. hederæ* extends from central Italy, Sardinia and northeast Spain in the south, to south-west Germany, Netherlands and the southern parts of Great Britain in the north. The east-west range is from Slovenia to the English Channel. On the whole *C. hederæ* represents an adriato-mediterranean distribution type (LATTIN 1967). All known localities of this species fall within the distribution of *Hedera helix* but its range is much smaller than that of its host plant (Fig. 1). *Hedera helix* occurs from North Africa in the south to southern Scandinavia in the north and from the Canaries and United Kingdom in the west eastwards to the coast of the Black Sea (MEUSEL 1978).

### 3.3. General behaviour of males and females

The first males patrolling at the aggregation were observed on the 24<sup>th</sup> of August. The males often interrupted their searching flights with inspections of the nest entrances of the previous years. The first flight was repeatedly preceded by grooming at a nest entrance. On the subsequent days the males appeared successively earlier in the morning at the aggregation, e.g. on the 1<sup>st</sup> of September the first male was recorded at 8.30 h. An obvious correlation between male activity and sunshine was observed. When the sun disappeared, the activity of the males stopped immediately and recurred directly when the sun came out again.

The first females were discovered on the 1<sup>st</sup> of September, but it was a matter of only a few individuals and the ivy was not yet in bloom. Only five days later, on the 6<sup>th</sup> of September, several hundred females were recognised. An emerging female was pounced upon at once by several males trying to mate and they formed a characteristic copulation cluster. The copulation cluster frequently tumbled down to the base of the steep face where mat-

ing with one male took place. Females that had already mated were mostly ignored by patrolling males. This behaviour could be observed directly after copulation. The phase of copulation lasted only from the 6<sup>th</sup> to 10<sup>th</sup> of September.

Shortly after having mated the females started to dig and provision a nest. Many females apparently chose old nests and expanded the old burrows. Other females favoured to dig a new nest, mainly at places that were hidden behind grass or other vegetation. Traces of digging activity could be observed sometimes in the morning at the nest entrances, which meant that the females continued with nest construction after their last foraging trip on the previous day. The females did not close the nest entrance after leaving. Usually they found the entrance immediately when they returned from a provisioning trip. However, changes to the last detail (e.g. marking with a toothpick) were followed by orientation flights in the shape of increasing zigzag flights. If the next approach was not successive, the females rested in the surrounding area and searched on the ground with their antennae, or rested on neighbouring vegetation and started a new approach after a few minutes. None of the observed females constructed a second nest at the observed aggregation. No parasites were observed at the aggregation.

### 3.4. Diurnal foraging rhythm and reproduction

The females started their first trip at 9.52 h in the morning, after waiting and trilling with their antennae a few minutes at the nest entrance. The earliest observed flight started at 09.07 h and the latest at 12.19 h. On average *C. hederæ* made 5.5 provisioning trips and returned from its last trip at 17.09 h. The earliest return was at 16.19 h and the latest at 17.53 h (Fig. 3). The mean du-

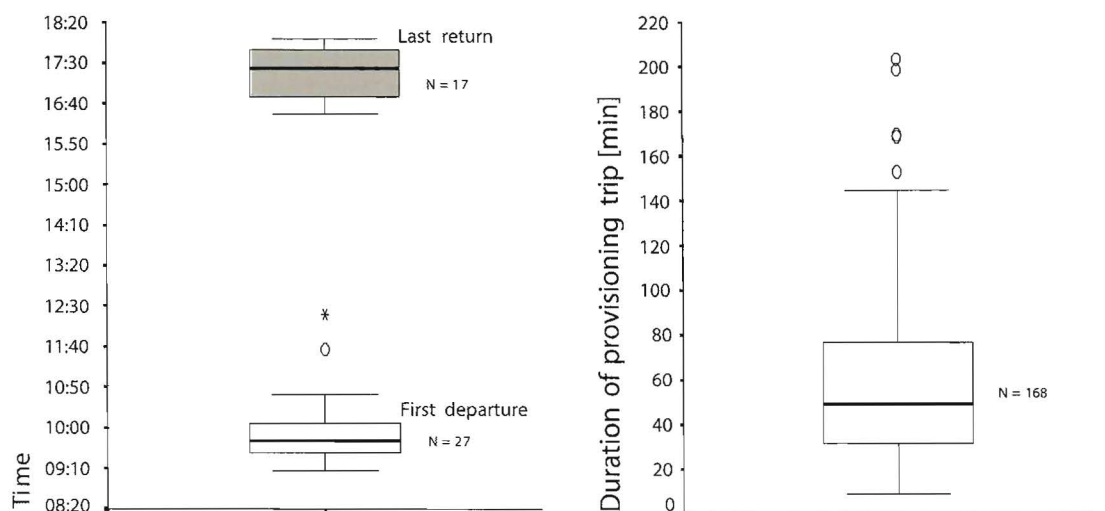


Fig 3: Time range of main activity data as the departure for the first trip, the last return to the nest and the duration of provisioning flights.



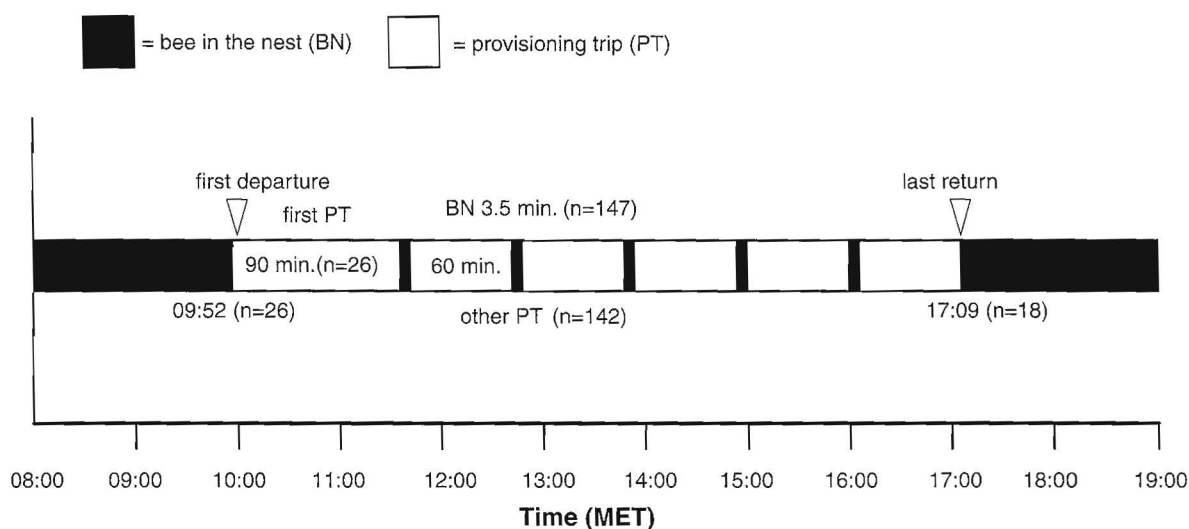


Fig. 4: Ethogram of an average daily foraging cycle of *C. hederae*.

ration of all provisioning trips was  $60.3 \pm 39.9$  min ( $n = 169$ ). However, the first flight in the morning was significantly longer (90 min) than the other trips of the day (Wilcoxon-test:  $Z = -2.767$ ,  $p = 0.006$ ,  $n = 16$ ). The activity in the nest after one provisioning trip amounted to  $3.5 \pm 1.7$  min ( $n = 165$ ). No significant correlation between the activity in the nest and the preceding provisioning trip could be detected. A scheme of the average foraging behaviour of *C. hederae* is documented in an ethogramm (Fig. 4).

The estimation of the time that the bees used for provisioning behaviour independent of weather conditions revealed 12 complete and 12 half = 18 BDs. Assuming five provisioning trips for one cell (see below), *C.*

*hederae* could approximately complete between 12 and 18 cells during the season of 2003.

### 3.5. Dependence on climatic parameters

We correlated the different activity data (departures, length of provisioning trips and nest activity) with climatic parameters. The results are presented in Table 2. A highly significant negative correlation between the duration of provisioning trips and temperature was found: the higher the temperature, the shorter the provisioning trip (Fig. 5). The correlation between the time of first departure and temperature represents only the increasing number of starting bees with time, parallel to the increasing temperature and humidity with time.

Table 2 : Correlation of activity data with climatic parameters (pt = provisioning trip)

	Temperature (2m)	Soil temperature	Humidity
<b>Duration of pt</b>			
n	99	99	99
r	-0.290	0.089	0.155
p	0.004*	0.379	0.126
<b>Time in nest</b>			
n	146	146	146
r	0.101	0.001	-0.167
p	0.223	0.986	0.044*
<b>Time of 1<sup>st</sup> trip</b>			
n	26	26	27
r	-0.783	-0.042	-0.894
p	<0.001*	0.492	<0.001*

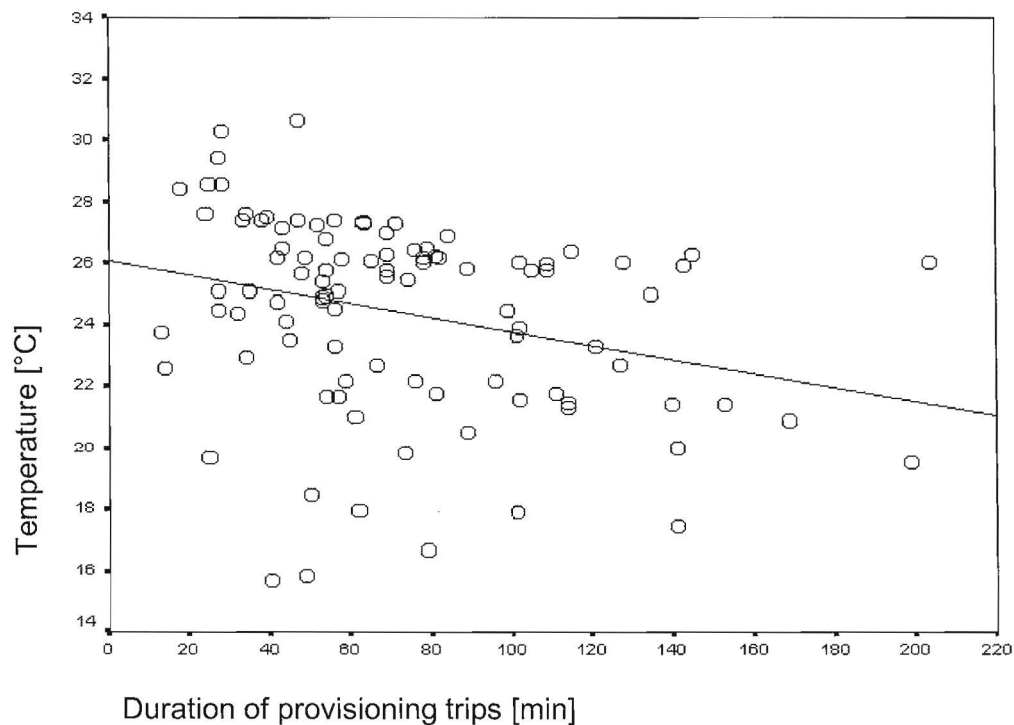


Fig. 5: Correlation (Pearson) between the duration of foraging trips and temperature.

### 3.6. Pollen

In all pollen loads and cells only pollen of *Hedera helix* (Fig. 6) was found. The mean longitudinal diameter of the pollen grains measured  $38 \pm 1.3 \mu\text{m}$  ( $n = 20$ ), the equatorial diameter was  $23 \pm 1.3 \mu\text{m}$  ( $n = 20$ ).

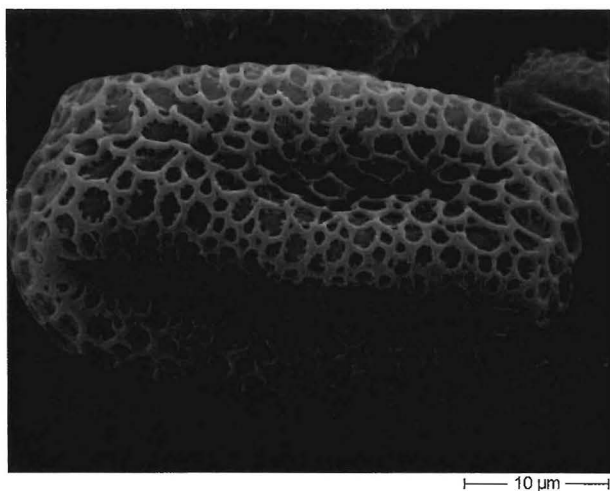


Fig. 6: SEM-Photograph of a pollen grain of *Hedera helix*.

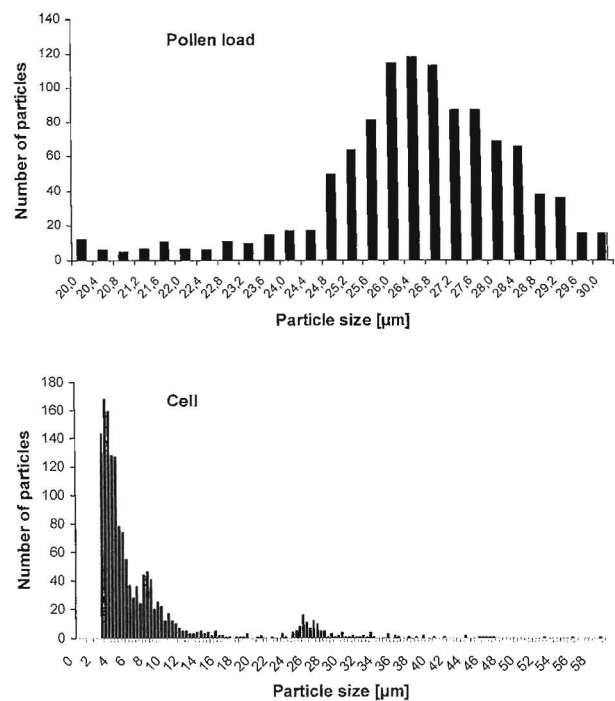


Fig. 7: Grain size distribution of one pollen load (only particles between 20 and 30  $\mu\text{m}$ ) and one cell (all particles) of *C. hederae* counted with an electronic particle counter in a volume of 1100  $\mu\text{l}$ .

*Colletes hederæ* collected on average  $518103 \pm 346639$  ( $n = 15$ ) grains per pollen load and the cells contained  $2811816 \pm 1843170$  ( $n = 20$ ) grains. Thus, the females had to make approximately 4 or 5 (5.4) provisioning trips to complete one cell. The grain size distribution of one pollen load and cell is documented in Figure 7.

### 3.7. Nest density and architecture

Most nests were found on sunny parts of the steep face, often covered by small tufts of grass. At the vertical part of the steep face more nests were located than at the base. Most females dug their nests above a level of 1 m. The mean number of nests was as high as 20 nests per  $m^2$  in areas of the aggregation without vegetation cover, and up to 300 nests per  $m^2$  in areas covered with grass.

We excavated four nests and the architecture is shown in Figure 8. In all four nests the main burrow first ran between 7 and 12 cm horizontally into the steep face. The first cells occurred at a depth of 30–45 cm and beyond a depth of 60 cm no cells were found. Between four and six cells were attached to one nest but presumably the number is higher. All cells branched off the vertical part of the main burrow. Only one of the four nests exhibited side burrows. The most conspicuous character of the architecture was the successive arrangement of cells (up to 4 cells) without side burrows.

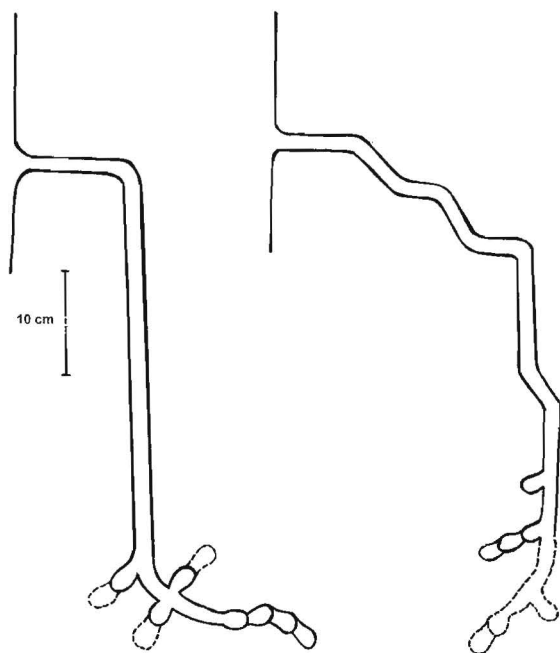


Fig. 8: Nest architecture reconstructed from four excavated nests of *C. hederæ*.

The cell size measured on average 1–1.5 cm long with a diameter of 0.5 cm. The cells showed a convex shape at the side orientated to the main burrow and the membrane projected the cell at that end which optimised the

successive arrangement of the cells. The fluid mixture of nectar and pollen filled approximately  $2/3^{rd}$  of the cell.

## 4. DISCUSSION

### 4.1. Distribution

The distribution pattern of *C. hederæ* can be interpreted as the result of the postglacial recolonization of parts of Europe from an Italian refuge (DE LATTIN 1967, HEWITT 1999). Its restricted distribution compared with the host plant may indicate a relatively recent origin of this species. The latter view is supported by the weak morphological differentiation of *C. hederæ* and its assumed closest relatives.

Numerous *Colletes* species are oligolectic and collect pollen on the flowers of only one plant family or even a genus (MÜLLER & KUHLMANN 2003). Among them *C. hederæ*, a member of the transpalearctic *C. succinctus* species group (sensu NOSKIEWICZ 1936) that comprises 12 taxa, is unique because it is the only known bee species that is a specialised visitor of ivy (*Hedera helix*) (SCHMIDT & WESTRICH 1993). Species of the *C. succinctus* group show a close morphological resemblance and are often hard to identify. The phylogeny of the species within this group is not yet clear but there is some evidence that *C. succinctus* and *C. halophilus* are the closest relatives of *C. hederæ*. Despite their close relationship, the flower visiting behaviour of the three species differs significantly. As far as known this is a unique case at least among the Old World *Colletes* and of special interest with respect to the understanding of evolution of oligolecty and speciation within the genus (KUHLMANN 2003). *Colletes halophilus* is a narrow endemic of coastal sites of the southern North Sea and English Channel and an oligolectic of Asteraceae. *Colletes succinctus* is widespread in the western Palearctic and known to be an oligolectic of *Calluna vulgaris* and *Erica* spp. (Ericaceae) (WESTRICH 1989), but in some populations of the British Isles exclusive pollen collecting on Asteraceae is documented (PERKINS 1945, EDWARDS & TELFER 2001). Phenology of all three species is similar, a single flight period in late summer / early autumn.

### 4.2. Pollen

The oligolecty of *C. hederæ* was confirmed in this study. All 15 pollen loads and 20 cells contained only pollen of *Hedera helix*. The amount of grains per pollen load can only be compared with other species of the same genus since the pollen collecting apparatus varies much between different genera (BRAUÉ 1916; FRIESE 1923; GRINFELD 1962; PASTEELS & PASTEELS 1979) and such studies are rare. The only *Colletes* species for which such data are available is *C. cunicularius* (Linnaeus) (cf. BISCHOFF et al. 2003). *Colletes cunicularius*

collects on average three times as much grains per load as *C. hederæ*, but the latter species is much smaller than *C. cunicularius*. Furthermore these authors did not consider the percentage of particles out of the range of pollen grains, which must be subtracted. In the present study this percentage of "pollution" amounted to 60% even in the pollen loads. Furthermore the number of collected grains strongly depends on the grain size (SILVEIRA 1991; BISCHOFF et al. 2003). The grains of *Hedera helix* display approximately the same elliptical shape but are nearly twice as large as *Salix* grains. Only with volumetric calculations a comparison of the carrying capacity can be achieved. Therefore quantitative analyses of related species (which have the same size) and a volumetric comparison should be done.

#### 4.3. Nest site selection and nest architecture

Like other *Colletes* species, *C. hederæ* seems to prefer inclined and southward exposed nesting sites in sand or loess soils (cf. BISCHOFF 2000; MADER 1999). Likewise as with other congeners *C. hederæ* forms large aggregations. The nest architecture resembles that of *C. cunicularius* insofar as the short part of the horizontal main burrow is followed by a longer nearly completely vertical part and no real side burrows (K. FELTGEN pers. comm. Bonn 1997; MALYSHEV 1936). Nevertheless these authors did not mention a successive arrangement of several cells without side burrows. Only FRIESE (1923) figured a nest of *C. cunicularius* in which the cells were arranged successively. The successive arrangement of cells is also documented for *C. daviesanus* (Smith) (TISCHLER 1951; HAESELER 1972; MADER 1981; WESTRICH 1989). A comparison with the nest architecture of *C. halophilus* and *C. succinctus*, which remains to be discovered, would be interesting.

#### 4.4. Diurnal and seasonal rhythm and reproduction rate

Seasonally overlapping bee species living in the same habitat often differ in their diurnal foraging rhythm (LEVERMANN et al. 2000; BISCHOFF et al. 2003). *Colletes hederæ* is active in late summer and autumn when interspecific competition is reduced. This may have been one reason for a host switch to a late flowering host plant. The diurnal rhythm of *C. hederæ* allows an optimal use of days with good flying conditions. One apparent character of the life cycle of *C. hederæ* is the beginning of female provisioning behaviour shortly after mating without a resting period for oocyte maturation as reported in other species (cf. GEBHARDT & RÖHR 1987; MÜNSTER-SWENDSEN 1968; BISCHOFF 2001). *Colletes hederæ* made five provisioning trips on average per day but on days with optimal weather conditions we observed several females that made up to 10 trips and were active eight hours of the day. *Colletes cunicularius*, a vernal species, makes on average seven

trips per day and shows also flying activity between 8-9 hours on days with good flying conditions (BISCHOFF et al. 2003). Comparable to vernal species, autumnal species have to deal often with long periods of unfavourable weather conditions. Unlike the vernal *C. cunicularius*, *C. hederæ* started its provisioning activity at a temperature threshold of 14.5 °C. This value is between the values of vernal and summer species and is also dependent of size (BATRA 1980; LIND 1968; MÜNSTER-SWENDSEN 1968). *Colletes hederæ* is much smaller than *C. cunicularius*, one of the largest bees in Germany with a mean heating rate of 7.35 °C per min (STONE & WILLMER 1989). Furthermore the activity is not only influenced by temperature but also by light intensity. KLOSTERMEYER (1969) and GERBER (1969) reported that the flight activity of bees stopped under a limit of 15000 lux. We did not measure light intensity but the activity of males and females was reduced when it was cloudy.

The first trip of the females was significantly longer than the other trips of the day. This can be interpreted as additional adult feeding on nectar after a night in the nest. Another reason may be a temperature threshold since the duration of the flights correlated negatively with temperature.

The results of the quantitative pollen analyses revealed on average five provisioning trips per cell. Thus *C. hederæ* could provision one cell on an optimal day. A total of 18 bee days was estimated during which a female could provision by rule of thumb 18 cells. It has to be considered, though, that the summer and autumn were extraordinary warm and dry in 2003. Thus the females could not only use more days with optimal weather conditions for nest provisioning but also work faster because of high temperatures.

Summarising the results, the specialisation of *C. hederæ* on a late blooming host plant seems to minimise the competition for pollen resources as well as for nest site resources. The risk of parasitism may also be reduced. These advantages may compensate the disadvantages of bad weather periods in autumn. It would be worthwhile to study also the diurnal foraging cycle and reproduction rate of the closely related species *C. halophilus* and *C. succinctus*, who may follow different strategies.

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