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Foraging Strategy and Pollen Preferences of *Andrena vaga* (Panzer) and *Colletes cunicularius* (L.) (Hymenoptera: Apidae)

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Abstract.—*Andrena vaga* (Panzer) and *Colletes cunicularius* (L.), both vernal ground nesting bees, were studied in the years of 1996–1999 in a lowbush heath near Cologne, western Germany. Both species are solitarily but nest gregariously and sometimes form large aggregations with thousands of nests. They are reported to feed strictly oligolectic on the genus *Salix*. We observed the daily foraging rhythms of both species and compared their foraging strategies. *Colletes cunicularius* started provisioning trips earlier in the morning, made more trips per day than *A. vaga*, and finished nest provisioning later in the evening. *Colletes cunicularius* burrowed even in the dark after 08.00 p.m. *Andrena vaga* collected pollen and nectar on different days each. One pollen day included 1 to 5 pollen trips. There was no clear correlation between the number of pollen trips and the occurrence of a subsequent nectar day. We found also no correlation between the occurrence of nectar-provisioning trips and weather conditions. Pollen loads of both species were analyzed qualitatively and quantitatively with a cell counter and two different hand-counting systems. *Andrena vaga* collected nearly twice as much pollen as *C. cunicularius* during one foraging trip. Cells and pollen loads of *C. cunicularius* contained large portions of other pollen types, mostly Rosaceae such as *Prunus, Sorbus* and *Pyrus* or *Acer, Quercus* and *Ilex*. Thus, *C. cunicularius* is not oligolectic as described in the literature. The percentage of pollen types other than *Salix* increased at the end of the flowering period of *Salix*, which indicates a resource restriction at the end of the season. The reproductive success of *C. cunicularius* measured by nest provisionment exceeded that of *A. vaga*, because of longer activity per day and digging activity in the evening.

Andrena vaga (Panzer 1799) and *Colletes cunicularius* (L.) are univoltine, vernal solitary bees which are distributed throughout the entire Paleartic Region. They prefer to nest in sandy soils and often form large aggregations (Friese 1923, Moeschler 1938, Vleugel 1947, Westrich 1990). Both species are reported to be specialized on *Salix* as a pollen resource for their larvae (Westrich and Schmidt 1987). Being specialized on the same host-plant, their seasonal activity strongly overlaps (Westrich 1990). Therefore, we investigated the diurnal activity pattern and foraging strategy of both species. Several studies have dealt with diurnal activity patterns and the impact of weather conditions on a number of mostly Nearctic bee species (cf. Batra 1999, Lind 1968, Michener and Rettenmeyer 1956, Schönitzer and Klinksik 1990, Stephen 1966), but precise data on the life cycle of European species of *Andrena* and *Colletes* are very scarce (Gebhardt and Röhr 1987, Malyshev 1927, Witt 1992).

By analyzing thoroughly the daily activity patterns, niche differences between two species may be shown. Levermann et al. (2000) investigated the diurnal cycle and niche differentiation of *Dasypoda hirtipes* (Fabricius) and *Panurgus calcaratus* (Scopoli). They demonstrated that apart from weather conditions, body mass and pollen-collecting apparatus are important factors

determining the diurnal activity cycle. Regarding solitary Hymenoptera, female size appears to have a great influence on provisioning- and reproductive success (Alcock 1979). *Colletes cunicularius* is larger than *A. vaga* and has more hairs, especially on the thorax. Therefore, we hypothesized that better thermoregulatory abilities allow *C. cunicularius* an earlier start to provisioning activity in the morning.

Apart from the different sizes of the two species, the specific pollen-collecting apparatus suggests differences in their pollen collecting efficiency. Although both species have trochanter-femur-baskets, floccus and thoracic pollen basket of *A. vaga* is more strongly developed than in *C. cunicularius*. In a number of bee genera, the size and the type of pollen-collecting apparatus results in different amounts of pollen transported (Braué 1916, Friese 1923, Michener et al. 1978, Pasteels and Pasteels 1979, Westerkamp 1987, 1996, Westrich 1990). Thus, we examined the number of collected pollen grains in both species.

Although both species are regarded as strictly oligolectic on *Salix* (Vleugel 1947, Westrich and Schmidt 1987, Westrich 1990), anecdotal observations reviewed by Mader (1999) suggest that *C. cunicularius* visits also flowers other than *Salix*. A clear evaluation about oligolecty in a bee species can only be made by a quantitative analysis of pollen loads or cell provisions.

The aims of this study were to analyze niche differentiation of two synchronous and syntopic bee species on the basis of activity patterns and the use of host plants, to asses the degree of oligolecty, and to compare their pollen collecting efficiency.

The study area is part of the so-called "Wahner Heide", a large 5000 ha heathland, east of the river Rhine near Cologne. Since 1961 the heathland has been a military training area for NATO and was designated a Nature Reserve in 1968. Due to the presence of Quaternary gravel, sand and overlaying quicksand, soils are mostly sandy, permeable, and poor in nutrients. The climate is humid-oceanic with an annual mean temperature of 9.5 °C and an annual mean precipitation of 804 mm. Due to drainage and loss of traditional agricultural use, grass and bushland dominate great areas of the heathland (Interkommunaler Arbeitskreis Wahner Heide 1989). The investigated aggregations of *C. cunicularius* and *A. vaga* lie on sandy inland dunes.

METHODS

Field work.—To study their diurnal activity, individual female bees were marked with opalith-plates. A total of 238 females of *C. cunicularius* in 1996 and 174 females of *A. vaga* in 1997 were marked. Corresponding nests were identified by a colored nail of the same number as on the opalith-plate of the female. To record the exact departure and return times of the females, several nests were covered with preserving jars (cf. Witt 1992).

Climatic parameters were measured with data loggers (Orion Tiny Logger Manager OTLM Tinytalk©). Soil temperatures of all years were recorded 20 cm below the surface, and air temperature and atmospheric humidity in a portable weather station were measured at a height of 2 m in 1997–1999. Data from the Cologne/Bonn airport weather station were also used. The data on the activity and the nectar trip frequency of the bees were tested for possible correlation against various climatic parameters (daily hours of sunshine, mean daily temperature, mean daily atmospheric humidity, humidity of soil and minimal daily soil temperature).

Since the activity of most of the bees is extremely influenced by weather conditions (Larsson 1991, Lind 1968) we created a measure for the bees activity independent from weather conditions (cf. Müller 1994), which we referred to a so-called "bee day" (= BD). Such a measure makes it also easier to compare different years.

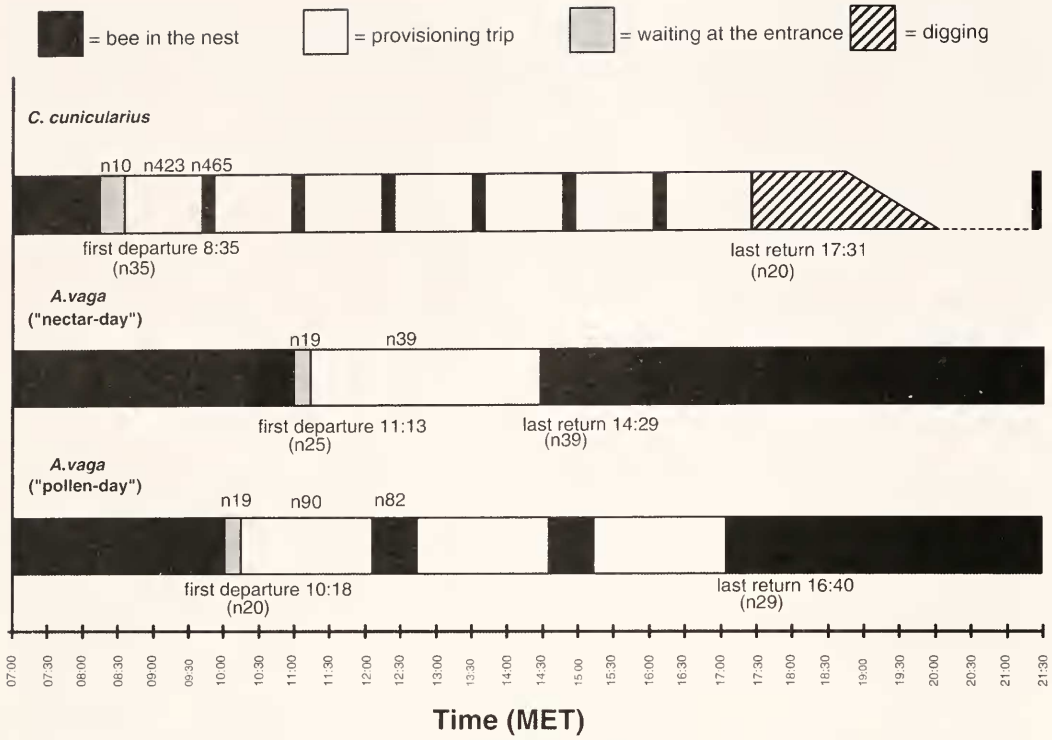

Fig. 1. "Ideal ethogram". Time schedule of provisioning behavior of *A. vaga* and *C. cunicularius* (dotted line = end of burrowing unknown). Further information's see text.

One bee day corresponds to a day with optimal weather conditions, which females could use completely for provisioning activities. A bee day for *C. cunicularius* had between 8–9 hours. The measure for these 8–9 hours was the observed flying activity at such an optimal day. Other days with less optimal flying conditions were defined as follows:

1.0 BD = flying activity of 8–9 hours
0.75 BD = flying activity more than ½ of one BD
0.25 BD = flying activity less than ½ of one BD
0 BD = no flying conditions the whole day

The classification of the bee day of *A. vaga* was more difficult because of the greater variance in activity time, in spite of good weather conditions:

1.0 BD = flying activity of 8–11 hours
0.75 BD = flying activity more than ½ of one BD
0.25 BD = flying activity less than ½ of one BD
0 BD = no flying conditions the whole day

Nectar- and pollen days of A. vaga.—To assess a pattern between *A. vaga's* nectar- and pollen-provisioning trips, we analyzed the number of pollen days as well as the number of pollen trips between nectar trips. One nectar trip corresponds to one nectar day and the patterns of pollen trips between nectar trips occurs over a period days since pollen and nectar are collected on different days. We obtained complete observations of pollen trips between nectar trips of 7 different females.

Pollen analysis.—For pollen analysis we excavated 10 cells of *C. cunicularius* in 1996 and 6 cells in 1998. The cells could not be attributed to a specific nest or time of com-

pletion. Additionally, females were captured to analyze pollen loads. This was necessary for *A. vaga* because cells could not be excavated without destruction and partial loss of the pollen mass. A total of 38 pollen loads of A. vaga and 28 pollen loads of *C. cunicularius* were analyzed (see Table 1). 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 and Shipman 1990). For a comparison of grain numbers, only pollen loads with nearly 100% *Salix* were used because the number of pollen grains varies with their size (see also Silveira 1991, Tasei 1973). For 10 pollen samples of *C. cunicularius* also volumetric percentages of the different pollen types were considered (cf. Buchmann and O'Rourke 1991). Pollen grain dimensions of *Salix*, *Quercus robur* and *Prunus padus* were measured for 10 grains of each species under a scanning electron microscope (SEM). The average size of the grains of Acer pseudo-platanus were taken from Crompton and Wojtas (1993).

The number of pollen grains in cells and pollen loads was counted by different methods:

a) Ratio-counting with *Lycopodium* spores: For this quantification, pollen was acetolyzed (Erdtmann 1960, Moore et al. 1991). During acetolysis a tablet with a known number of *Lycopodium* spores was added (Stockmarr 1971). In a subsample all pollen grains and spores were counted on a slide under a microscope. The total number of pollen grains in the sample was estimated from the equation:

$$\text{total number of grains} = \frac{\text{added Lycopodium spores}}{\text{counted Lycopodium spores}} \times \text{counted grains}$$

b) Cell counter: Most of the samples were additionally analyzed using a cell counter (Casy® 1 Cell counter and Analyser) and then checked with the SEM. Eight electronically counted samples for the years 1996 and 1998 were checked with the *Lycopodium* spores method described above. Between 500 and 1000 *Salix* grains were counted, respectively.
c) Hand-counting with a counting chamber: Samples from 1999 were counted with a Buerker counting chamber, a special slide with a cavity of a defined volume. To achieve an accuracy of 10 or 20 grains per µl, we determined the number of subsamples needed using the following formula (n = random sample, s = standard error, d = accuracy):

$$n \geq \left[\frac{1.96 \times s}{d}\right]^2$$

In this study, 6 to 14 subsamples had to be counted.

To calculate the number of provisioning trips for one cell, the average weight of food stored in the cell has to be divided by the average weight of the pollen load carried by the female (cf. Mohamed 1973). Therefore we determined the dry weight of the pollen load samples of the year 1996. The females were dried in a drying chamber, head and wings removed, and the rest weighted. Then pollen was removed from the body hairs and scopae with a sonicator. After removing the pollen, the thorax and abdomen were dried and weighed again. The difference corresponds to the weight of the pollen load.

Statistics.—Mean values of all departures and returns or other activities were used to construct an "ideal ethogram". Except in cases when data were not normally distributed, the median was used. The compari-

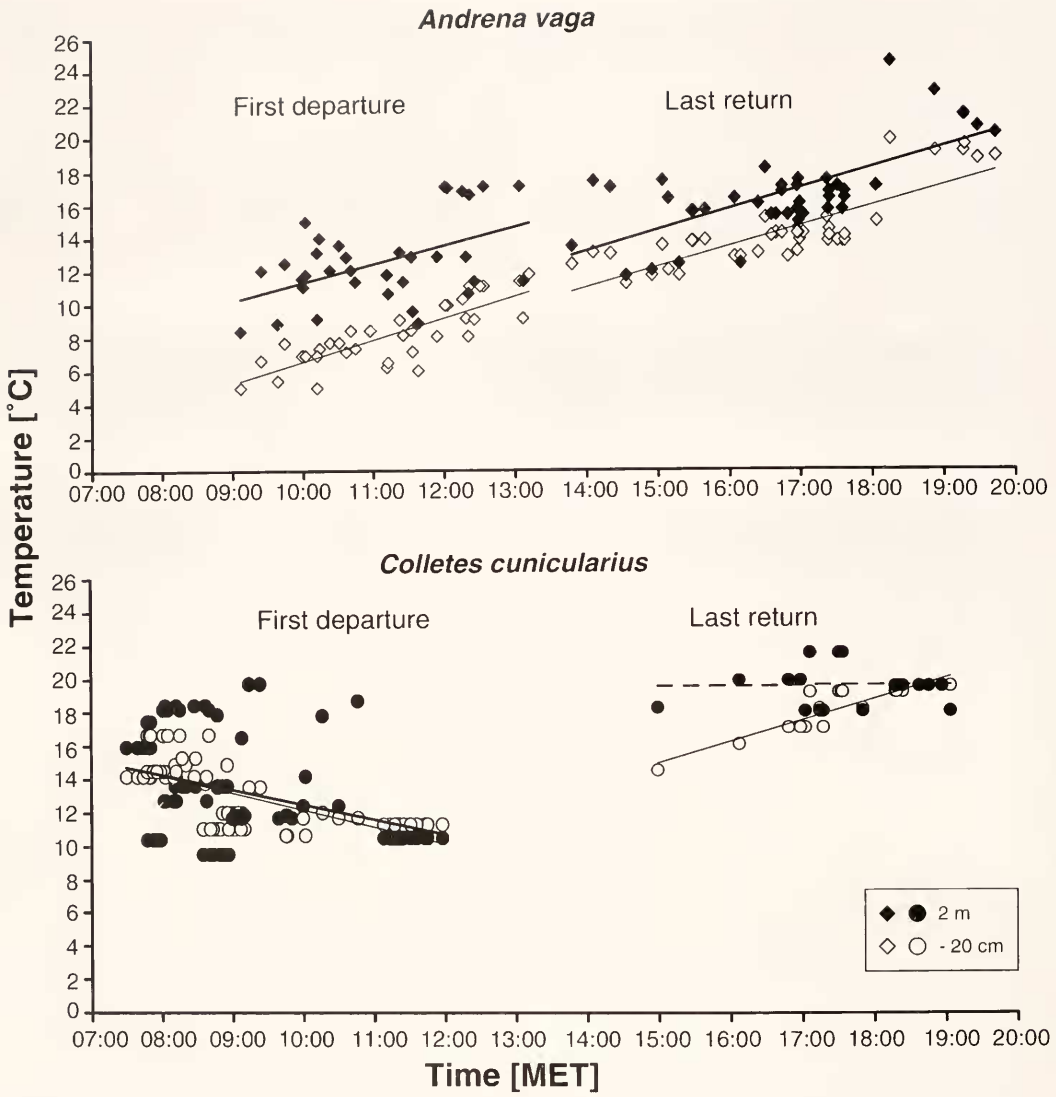

Fig. 2. Correlation of time of first departure and last return of *A. vaga* and *C. cunicularius* with temperature at 2 m height (BC = black circle; BS = black square) and 20 cm below soil surface (WC = white circle; WS = white square). (First departure: BS y = 26.49x+0.21, r = 0.48, n = 36; WS y = 30.92x−6.38, r = 0.82, n = 38; BC y = −21.57x+21.45, r = 0.36, n = 78; WC y = −24.56x+22.37, r = 0.71, n = 78; Last return: BS y = 29.94x−4.31, r = 0.68, n = 42; WS y = 29.35x−6.16, r = 0.81, n = 42; BC y = 0.34x+19.25, r = 0.01, n = 20; WC y = 30.12x−3.88, r = 0.89, n = 20).

son of mean values of activity data was presented in boxplots. These independent samples were analyzed with the t-test. Data of pollen samples were treated likewise. Mean values of non normally distributed data (number of pollen grains per pollen load and soil temperatures) were compared using the Man-Whitney U-test. The relationship between activity data and climate and mixed pollen cells and the blooming time of Salix were tested by Pearsons's correlation analysis.

RESULTS

Foraging strategy—diurnal cycle.—A comparison of the "ideal ethogram" (Fig.

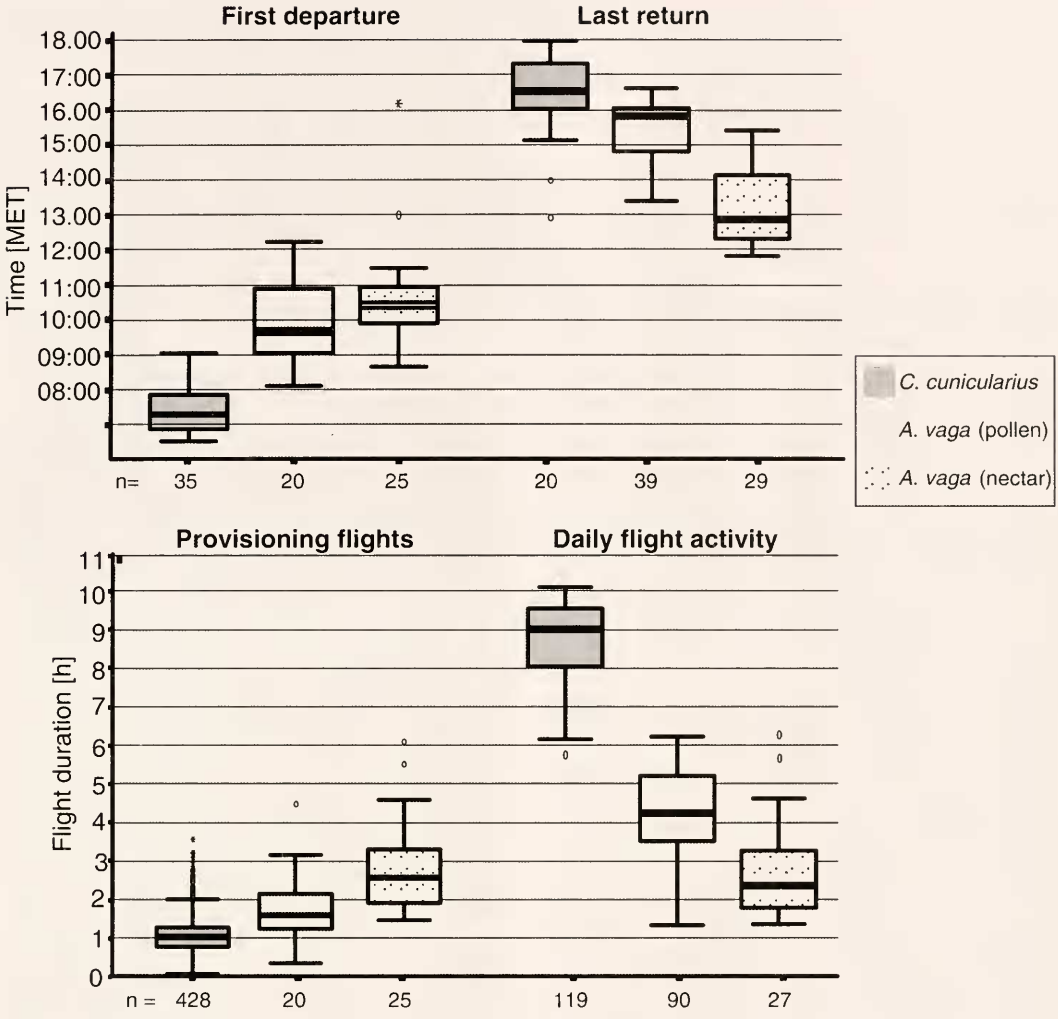

Fig. 3. Variance and difference in time of first departure, last return, time of provisioning trips and hours of daily activity of *A. vaga* and *C. cunicularius*.

1) shows a different diurnal cycle of *A. vaga* and *C. cunicularius*. For *A. vaga* two separate cycles are shown since it collects pollen and nectar on different days and this is represented by different flight patterns.

Colletes cunicularius started its first trip at 8:37 in the morning, after waiting about 20 minutes at the entrance. It made seven provisioning trips and returned from its last trip at 17:34. It did not interrupt its foraging cycle by digging or other activities in the nest, as indicated by short durations of presence in the nest (six minutes on average). In the evening, after the last return to the nest, many females began burrowing and continued even in the dark (Fig. 1). *Colletes cunicularius* showed lower variation in the number of trips per day than *A. vaga*. The first departure and the last return of *C. cunicularius* correlated with the soil temperature (Fig. 2). The females started earlier when soil temperatures were higher and returned later from their last trip when temperature was still high. The correlation of the last return with the air temperature was not significant. The soil temperature at the aggre-

Table 1. Number of excavated cells and collected pollen loads (C. c. = *C. cunicularius*, A. v. = *A. vaga*).

Year	Cells C.c.	Pollen loads C.c.	Pollen loads A.v.
1996	10	9	7
1998	6	1	14
1999		18	17

gation of *C. cunicularius* was significantly higher ($U = 88698$, $p < 0.001$) than the soil temperature of the location of *A. vaga's* aggregation, though the year 1996 was much colder than 1997 (Bischoff 2000). Thus, lowest soil temperature during first departure of *C. cunicularius* (11 °C) differed highly from soil temperature in the aggregation of *A. vaga* (5 °C). The temperature threshold for the first trip of *C. cunicularius* was 9.5 °C; the mean temperature of first departure was 12 °C.

On pollen days *A. vaga* made three trips on average. After remaining a while at the entrance, it started its first trip at 10:32. The females stayed on average half an hour (median 0.33) in the nest between two provisioning trips and no digging activity was observed during these periods. At 16:17 it came back from its last trip and closed its nest entrance. On nectar days, females emerged not before 11:30 and returned at 14:29. In the evening no intense digging activity as observed for *C. cunicularius*, occurred. The last return of the females was influenced by the temperature; a significant correlation of the time of the last return both with soil temperature and air temperature was found. The first flight in the morning, which started much later than that of *C. cunicularius*, seems not to be influenced by the temperature at all since a positive correlation was found (Fig. 2). The temperature threshold for the first trip of *A. vaga* was 8 °C, the mean temperature of first departure was 12 °C.

To summarize, the females of *C. cunicularius* started their provisioning behavior earlier in the morning, made more but shorter trips a day, remained for shorter periods in the nest, returned later in the evening (Fig. 3) and burrowed after dark. *Andrena vaga* started its first trip later in the morning but the temperature threshold for the first trip was lower than that of *C. cunicularius*.

Nectar and pollen days of A. vaga.—*A. vaga* made 1 to 9 pollen trips between two nectar trips (mean: 4 trips, Table 2). Two groups of flight patterns seem to exist: the first group of bees makes 1 to 4 pollen trips between two nectar trips, and the second group makes 7 to 9 pollen trips between each nectar trip.

The activities of *A. vaga* females at different bee days are shown in Fig. 4. There was a high percentage of inactive females on 0.25 BD's, i.e. days with less than 5.5 hours of good flying conditions. On days with good flying conditions (1.0 BD), more females made pollen trips than nectar trips. Yet, this relation was also found on 0.25 BD's. Furthermore we compared the percentage of nectar trips with the bee day status of the preceding day. After a 0 BD (no flying conditions the whole day), females made significantly more often a nectar trip ($r = -0.471$, $p = 0.031$, $n = 21$).

We also tried to correlate the percentage of nectar trips of *A. vaga* with climatic parameters of the same day and the preceding day (Table 3). At days with more hours of sunshine females made more often a nectar trip but the correlation was not very strong. Otherwise no significant

Table 2. Number of observed pollen trips between two nectar trips of *A. vaga*.

Pollen trips	1	2	3	4	5	6	7	8	9
Frequency	2	3	2	1	0	0	2	2	1

Table 3. Correlation (Pearson) of the percentage of nectar trips (of all active females of *A. vaga*) with climatic parameters of the day of the nectar trip (a) and of the preceding day (b) (n = 20).

	Hours of sunshine		Mean temperature		Mean humidity		Minimum temperature	
Day	a	b	a	b	a	b	a	b
r	−0.578	−0.169	−0.86	0.76	0.308	0.244	0.302	0.113
p	**0.008	0.476	0.719	0.751	0.186	0.300	0.196	0.636

correlations with climatic parameters were found.

Composition of pollen loads.—In 1996, 40% of all analyzed cells of *C. cunicularius* contained more than 20% of pollen types other than *Salix*. Since only percentages of foreign pollen types lower than 5% (Westrich 1990) are considered as contamination, we decided to analyze more cells of *C. cunicularius* and pollen loads of *A. vaga*. In subsequent years, high percentages of non-*Salix* pollen were identified in the cells of *C. cunicularius*. In fact three of six excavated cells in 1998 and one of 10 cells in 1996 respectively, contained no *Salix* pollen at all. Only three cells of both years were pure (>90% Salix) and 9 cells were mixtures of Salix and other grain types. The remaining pollen types in the cells of 1996 were mainly composed of various Rosaceae (Table 4). Apart from Rosaceae, only *Quercus* and *Sambucus* occurred in higher percentages. *Ilex* pollen dominated one pollen load sample of *C. cunicularius* of 1996.

Percentages of other pollen types were also found in pollen loads of *C. cunicularius* of the years 1998 and 1999. The loads of two females (captured on 29.4. and 7.5.1999) contained only grains of *Acer* sp., one load (also from 7.5.1999) contained *Acer* and *Ilex* grains in a ratio of 1:1, and two pollen loads contained exclusively *Quercus* pollen. Regarding also the volume of the different pollen types (10 samples of 1999), *Salix* grains represent even a smaller proportion of the diet of *C. cunicularius*, since *Acer pseudo-platanus*, *Prunus padus* and *Quercus robur* grains are much larger than *Salix* (Fig. 5). Percentages of other pollen types in pollen loads of *C. cunicularius* (in the year 1998) increased significantly with time, i.e. with the end of the blooming of *Salix* (r = 0.731, p = 0.01, n = 14).

In the graphs of the cell counter (Fig. 6), mixed loads of mainly two pollen types (*Salix* and various Rosaceae) could be recognized as two separated peaks. These graphs are counts from *C. cunicularius* cells of 1999. They show three clearly separated peaks. The first peak represents particles smaller than 10 μm and can be interpreted as pollution. The second peak (15–22 μm) represents the *Salix* grains. The third peak (25–35 μm) shows bigger grains, e.g. Rosaceae. The broad distribution of grain sizes as displayed in the counter graph corresponded to different pollen types detected under the light microscope. However, results of the hand countings differed often from percentages given by the counter. All results of the counter had to be checked at least qualitatively by microscope, because one peak could represent pollen types other than *Salix*.

The cell counter calculated a mean number of 1512901 (± 720715 SD) pollen grains per pollen load for *C. cunicularius*. Only 7 out of 18 pollen loads counted by the cell counter were pure *Salix* loads. In *A. vaga*, electronic counting determined 2058692 (± 737197 SD) grains per pollen load. *Andrena vaga* collected on average one and a half more pollen on one provisioning trip than *C. cunicularius*. This difference is highly significant (t-test, $p < 0.001$).

A comparison of the results using different counting methods is displayed in

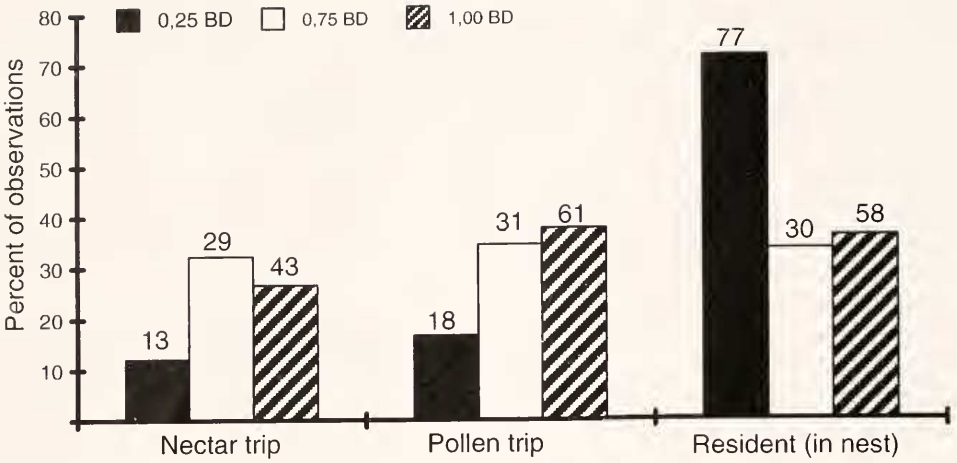

Fig. 4. Activities of *A. vaga* females at a bee day of the category 0,25 (< 5,5 hours good flying-conditions), a bee day of the category 0,75 (> 5,5 hours good flying conditions) and the category 1 (8–11 hours good flying-conditions) (number of total observations = 360).

Table 5. Ratio counting with *Lycopodium* spores showed greater divergence from cell counter results than counting with the counting chamber. Counting chamber results revealed a mean difference of 255728 (± 192194) grains in comparison to the cell counter. Regarding *Lycopodium* ratio counting, one half of the results exceeded the cell counter calculations and the other half was below the cell counter calculations. The mean difference between *Lycopodium* spores ratio counting and cell counter was 498713 (± 675670) grains.

The pollen loads of *A. vaga* contained fewer foreign grains than those of *C. cunicularius*. In five (13%) of 38 loads, we found percentages of other pollen types ranging from 1 to 7% and consisting mostly of *Rosaceae*, *Quercus* and *Betula* grains.

DISCUSSION

Diurnal cycle—foraging strategies.—In this study, *C. cunicularius* started its provisioning cycle much earlier than *A. vaga*. The specified activity times are probably dependent on weather conditions. This earlier departure may have been caused by higher soil temperatures. However, the departure time is not known from the other study site at the Fliegenberg. The investigated aggregation of *C. cunicularius* is exposed southward, has a strong slope and the soil is only sparsely covered with vegetation. The exposition of *A. vaga's* ag-

Table 4. Classification of pollen types other than *Salix* in the cells of *C. cunicularius* in 1996.

Family	Genus or species	Percentage [%]
Rosaceae	*Sorbus aucuparia, Prunus padus, Prunus laurocerasus, Prunus* sp., *Pyrus* sp., *Malus* sp.	5–92
	Filipendula sp.	<1
Fagaceae	*Quercus* sp.	2–10
Caprifoliceae	*Sambucus niger*	7
Ranunculaceae	*Ranunculus* sp.	0.2–3.3
Celastraceae	*Euonymus europaeus*	2
Aceraceae	*Acer* sp.	<1

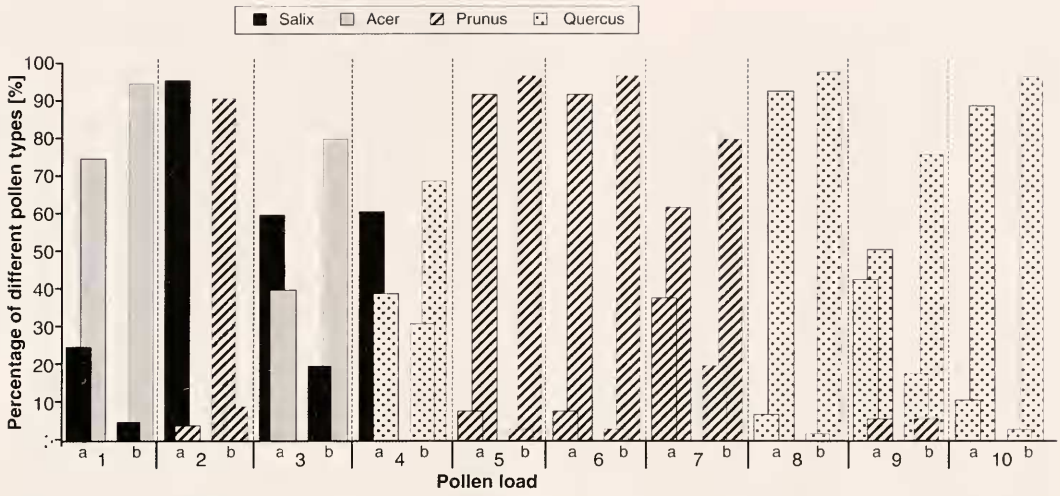

Fig. 5. Numerical (a) and volumetric (b) percentage of *Salix* pollen and other pollen types in excavated cells of *C. cunicularius* in the year 1996 and 1998.

gregation is south-eastward, slope is lower than in the *C. cunicularius* aggregation and the sand path is covered with grass. The surrounding site of *A. vaga's* aggregation has also more and higher vegetation cover. Thus, higher soil temperature at the *C. cunicularius* aggregation may be caused by these local differences of exposure, slope and vegetation cover (cf. Bischoff 2000). Ideally, the diurnal cycle of *C. cunicularius* should be investigated at aggregations close to *A. vaga's* aggregation, i.e. with similar conditions of soil, exposure, slope and vegetation cover.

Several authors have found correlations between the behavior of bees and weather conditions (e.g. Linsley 1958, Michener and Rettenmeyer 1956, Willmer 1983). Temperature thresholds for the bee's activities depend on weather conditions and the season in which the species occurs. Many vernal bees begin flight activity at 10 °C and they are less influenced by cloud cover or wind. Flight activity temperatures reported for other European early spring species of *Andrena*, for instance *A. barbilabris* (Kirby), *A. cineraria* (Linnaeus), *A. clarkella* (Kirby), and the Nearctic species *A. erythronii* Robertson, *A. viburnella* Graenicher, and *A. vicina* Smith range from 10 to 16 °C (Gebhardt and Röhr 1987, Johnson 1981, Michener and Rettenmeyer 1956, Miliczky and Osgood 1995, Stephen 1966, Witt 1992). For vernal species of *Colletes* like *C. inaequalis* Say and *C. validus* Cresson, similar temperature thresholds are known (Batra 1980). In our study, the two species began flight activity at 8–9.5 °C air temperature. Similarly, Schönitzer and Klinksik (1990) recorded flight activity at a temperature of 8 °C for *A. nycthemera* Imhoff. Due to unstable weather conditions in spring, vernal species have to use days with good weather conditions very efficiently. To illustrate, on days with optimal weather conditions provisioning activity of *A. clarkella* is completed in 4 or 5 days (Friese 1923). Late summer species such as *Panurgus banksianus* (Kirby) and *Dasypoda hirtipes* (Fabricius) often need temperatures $>$ 20 °C to start their first trip (Lind 1968, Münster-Swendsen 1968). Though the flight of *A. vaga* may already start at 8 °C, time of its first departure is later than that of many of the other species of *Andrena* mentioned above. This may be caused by local and seasonal differences in temperature compared to the other studies mentioned above. In the present study the required temperature threshold of 8 °C

at the investigated aggregation of *A. vaga* was not reached before 09.00 a.m. This fact may explain the strange correlation of the first departure of *A. vaga* with the temperature, which represents in fact no correlation with the temperature. The bees can start their first trip at a temperature threshold of 8 °C and the regression represents only the increasing number of starting bees with time.

Apart from differences in soil temperature, the beginning of flight activity of the two species may be influenced by their respective thermoregulatory abilities. Larger bees are more likely to achieve flight temperatures at low ambient temperatures (Michener and Rettenmeyer 1956, Stone et al. 1988, Stone and Willmer 1989, Stone 1993a, b, Stone 1994, Stone et al. 1995, Wolda and Roubik 1986). *Colletes cunicularius* is one of the largest bees in Germany, having a mean heating rate of 7.35 °C per minute (Stone and Willmer 1989). These authors investigated the heating-rate among *A. clarkella* and *A. fulva* (Müller). These two species are comparable to *A. vaga* in body size, hairiness and flight season, and differ only in color from *A. vaga*. Mean heating rate of these two species of *Andrena* is about 4 to 6.2 °C per minute, respectively. Although *C. cunicularius* is larger and more hairy than *A. vaga*, the abdomen of the latter is deep black and passive heat absorbency may be increased. Nevertheless, body size is probably more important for warming up in the morning and may enable *C. cunicularius* to begin earlier with daily activity. After sunset, this species may also benefit from its larger size.

Most of the flights of *A. vaga* took between 1 and 2.5 hours on pollen days, and between 2 and 3.5 hours on nectar days. The known duration of provisioning trips of other species of *Andrena* ranged from 20 minutes to 4 hours, and the number of provisioning trips per day showed a transition from 1 to 5 (Gebhardt and Röhr 1987, Michener and Rettenmeyer 1956, Miliczky and Osgood 1995, Schönitzer and Klinksik 1990).

A second reason for the marked difference in daily activity of the two investigated species could result from *A. vaga's'* prolonged stay in the nest. It could not be clarified whether *A. vaga* uses these periods in the nest for digging, since no new sand was pushed to the surface. The occurrence of sand output depends of the sequence of nest construction. When the bee first digs the main burrow and constructs the cells regressively (i.e., the lowest one is built first and each subsequent one is at a higher level), it can fill the inferior main burrow with the material of the side burrows. Thus no new sand needs to be pushed out. This has been described by Malyshev (1927) for *C. cunicularius* and also by Rajotte (1979) for *C. validus*. Yet, *A. vaga* constructs its nest conversely, subsequent cells lie deeper and the oldest cell is nearest to the surface. Side burrows of *A. vaga* are also filled with sand and in order to fill the first side burrow of a completed cell, the bee may use the material of a second side burrow. This was also assumed by Michener and Rettenmeyer (1956) for *A. erythronii*. Our (Bischoff 2001) and Malyshev's (1926) description of *A. vaga's* nest architecture are contradictory to the descriptions and figures of Friese (1882, 1923), in which the last cell is located at the lowest level. Michener and Rettenmeyer (1956) suggested that Friese's nest figure with cells close along the main burrow like a cluster of grapes resulted from a mixture of different nests lying very close together.

In many species, digging of side burrows and new cells has been described to take place in the afternoon (Lind 1968, Münster-Swendsen 1968, Gebhardt and Röhr 1987, Michener and Rettenmeyer 1956, Witt 1992). However, our results do not confirm these findings for *A. vaga*, where even after the last provisioning trip, females did no intensive digging as observed in *C. cunicularius*. Yet, at the begin-

Table 5. Results of pollen counts with the electronic counter, the counting chamber and the Lycopodium-ratio-method (means of all counts of both species).

	Grain number/pollen load	Standard deviation	Mean difference to electronic counter
Electronic	1053796	722183	
counter	1777806	626778	
Counting	798069	711542	255728
chamber			
Lycopodium-	1850200	515579	498713
ratio-counting			

ning of the season, when the aggregation of *A. vaga* develops, new tumuli could be found early in the morning. Thus, we assume that the construction of these tumuli took place at night or early in the morning, because sand often was still moisted and no sand output was observed in the late evening of the previous day. *Andrena erythronii* digs in the late afternoon and even in the dark (Michener and Rettenmeyer 1956). Nocturnal digging activity has been reported from other Nearctic species of *Colletes* (Batra 1980, Rajotte 1979). Since *C. cunicularius* constructs its cells regressively as described above, no large sand output should occur after the construction of the main burrow. Digging activities in the evening can be interpreted as constructions of new nests, since *C. cunicularius* makes 2 or 3 nests in its life. *Colletes cunicularius* defers the construction of new nests to the evening time, thus it can use the whole day for provisioning trips and can increase the number of constructed nests.

The third explanation for the difference in daily activity may be the different pollen carrying capacities of both species. Braué (1916) and Friese (1923) described the different pollen collecting apparatus of bees and inferred from these differences the systematic order of bee genera. Since these early studies, many authors worked on different pollen collecting apparatus (Grinfeld 1962, Michener et al. 1978, Pasteels and Pasteels 1979, Proctor et al. 1996, Thorp 1969, Westerkamp 1987). According to Braué (1916), *Andrena* is the genus that can carry home the largest amount of pollen with its hind leg brushes and parts of the thorax. Although both species have trochanter-femur baskets, the floccus and thoracic pollen baskets of *A. vaga* seem to be more strongly developed than in *C. cunicularius*. In the present investigation, *A. vaga* collected nearly twice as much pollen per load on average than *C. cunicularius*. Exact quantitative data on number of pollen grains per pollen load are scarce in the literature. In most cases, only percentages of different pollen types are presented, e.g. pollen loads of *Andrena* (Chambers 1946). Parker (1981) analyzed pollen loads of polylectic and oligolectic bee species quantitatively in order to determine the effectiveness of these species in pollinating sunflowers. He demonstrated that female oligoleges carried more pollen than did any other group of bees studied. In our study, species collected much more grains per load than in Parker's example; however, the number of carried pollen grains depends highly on the mean size of the grain type. Accordingly, our results can only be compared quantitatively to data of the same bee species, collecting the same pollen species. One possible factor as to why *C. cunicularius* pollen loads were smaller than *A. vaga's* is that *C. cunicularius* collects nectar along with pollen in each trip. From honey bees and bumble bees it is known that they can carry an amount of nectar from 50 to 90% of their body weight (Heinrich 1979). We

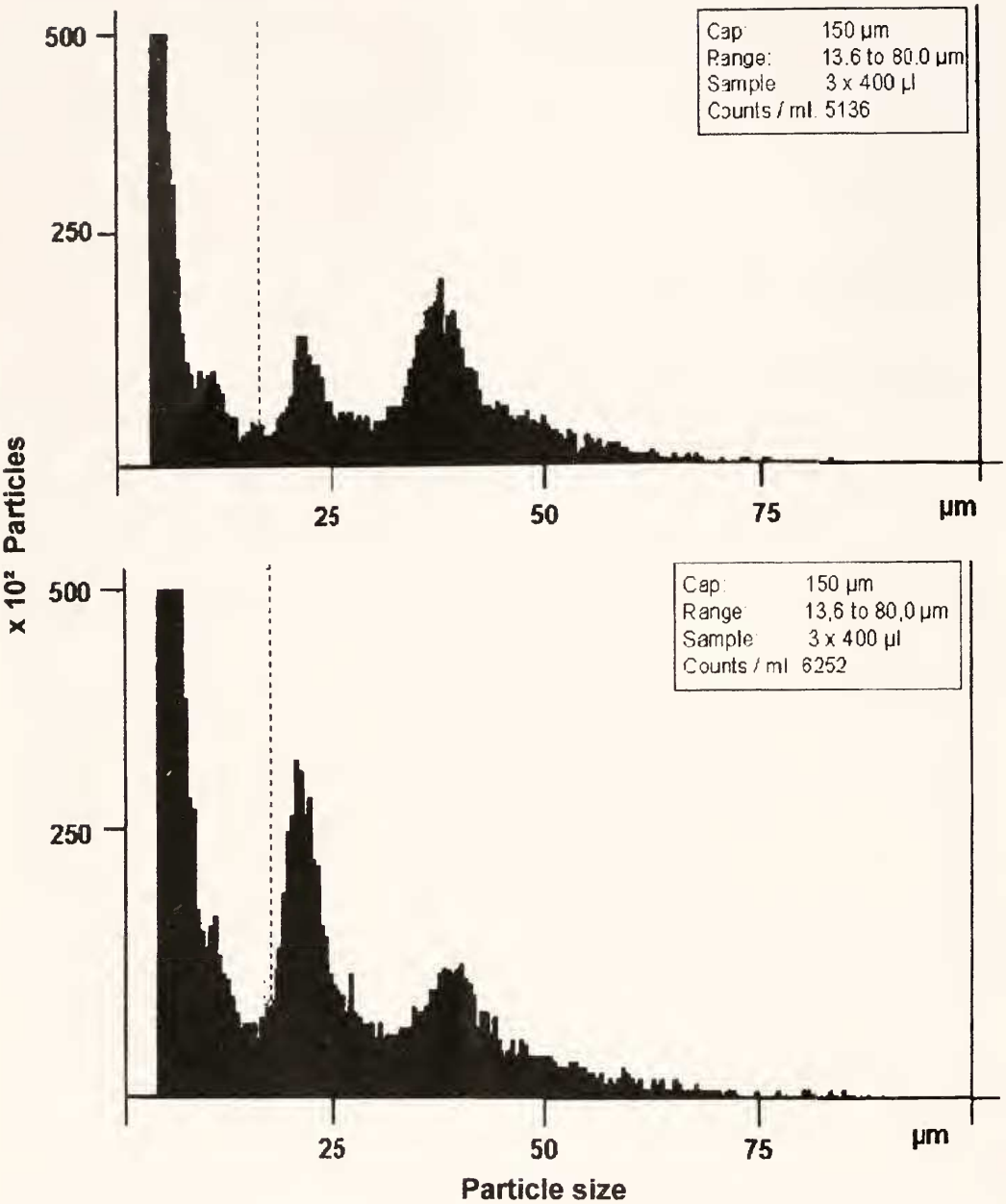

Fig. 6. Quantitative analysis of the pollen loads of *C. cunicularius* with the cell counter. Upper graph: 1. female, 23.04.99, below: 2. female, 27.94.99 (Cap = capillary, particles beneath dotted line = smaller than 10 µm, no pollen).

were unable to find precise data in the literature on the amount of nectar collected by solitary bees on one single trip, but for *C. cunicularius* it is reported that the provision in the cell is extremely liquid and though contains a lot of nectar (Malyshev 1936). Other bees like *Osmia rufa* (Linnaeus) make more dry provisions (Westrich 1990).

Dividing the grain number of the pure

Salix cells for the year 1996 by the grain number of pure *Salix* pollen loads (same year), *C. cunicularius* had to make approximately nine provisioning trips per cell. In 1998, we had only one cell of *C. cunicularius*, containing only *Salix* grains. In this case, *C. cunicularius* had to collect seven pollen loads for completing one cell. If *A. vaga* had to gather approximately the same amount of pollen per cell, it would have to make only four trips per cells, because of its bigger carrying capacity per load. These assumptions agree well with the observed trips of both species during one day. Vleugel (1947) observed for *A. vaga* only 1 or 2 trips on days with good weather conditions. The foraging statistics for *Andrena complexa* visiting *Ranunculus* for pollen show a time of 1½ hours to complete a load, and a pollen foraging rate of three loads per day (Linsley and MacSwain 1959). Futhermore the amount of pollen per cell may depend on the sex of the offspring. Gerber and Klostermeyer (1970) provided evidence that females determine the sex of their offspring by fertilizing the egg or not. Males are often smaller than females and therefore the stored pollen mass for males is smaller (Helms 1994, Strickler 1982, Maddocks and Paulus 1987, Johnson 1988). Regardless of the sex of the offspring, it seems likely that *C. cunicularius* has to make more provisioning trips per cell, because of its smaller pollen carrying capacity. In conclusion, *A. vaga* can carry more pollen per collecting trip; however, due to its body size *C. cunicularius* is more independent of weather conditions and can be active for longer periods per day. Indeed, the last point is of considerable importance for vernal bee species, because weather conditions are often quite unfavorable during spring. Additionally, *C. cunicularius* uses the evening and perhaps the night for digging activity. Our investigations of daily collecting capacity as well as those of nest excavations (cf. Bischoff 2001) indicate a higher reproduction rate for *C. cunicularius* in comparison to *A. vaga*.

Nectar- and pollen provisioning trips.—We observed a rhythm of nectar and pollen provisioning trips and assumed that *A. vaga* collected first all the pollen for one cell, then added the nectar. Friese (1923) described exactly this type of behavior for *A. vaga*. *Dasypoda hirtipes, Andrena erythronii* and various species of *Anthophora* are also known to add nectar only after several pollen loads have been carried into the cell (Lind 1968, Michener and Rettenmeyer 1956, Müller 1884, Westrich 1990). Malyshev (1936) states that pollen predominates in the first load or even makes up the whole load and that the last load deposited in the cell usually consists mainly of honey. Other species clearly alternate nectar- and pollen provisioning trips, e.g. *Osmia adunca* (Panzer), *Osmia fulviventris* Panzer or *Chelostoma florisomne* (Linnaeus) (Brechtel 1986, Käpylä 1978, Westerkamp 1978, Westrich 1990). It is possible that digger bees and carpenter or mason bees differ with respect to this behavior. Miliczky and Osgood (1995) described four trips for *A. vicina* during which no pollen was collected (in comparison with 64 pollen-collecting trips) and interpreted them as adult feeding trips. Since we did not analyze quantity of nectar in *A. vaga's* cells, it cannot be definitely clarified whether nectar trips are adult feeding trips or nectar provisioning trips for the offspring. Assuming that *A. vaga* cells contain nectar, then there must be a rhythm between nectar and pollen provisioning trips. The two observed flight patterns may represent the different provisioning behavior for female and male cells. However, in order to prove this hypothesis, a longer series of provisioning trips of a greater number of females have to be documented and the mass of provisioned pollen has to be analyzed for sex specifically.

Another reason for the observed pattern of pollen and nectar trips may be the in-

fluence of weather conditions. Our underlying hypothesis was that females make a nectar trip after a particular hot and dry day to increase humidity inside the cell. In fact, Stephen (1966) noted that the temperature at which flight activity was initiated in *A. viburnella* was a function of weather conditions of the previous day. Yet, we did not find any correlation of occurrence of nectar trips to the climatic parameters of the previous day. On the contrary, after a bad weather day (no flying conditions the whole day) more females made a nectar trip. This may be caused by an increased energy consumption after one day in the nest. Probably females provide themselves with nectar during their pollen collecting trips (male *Salix* plants also produce nectar).

Oligolecty.—Qualitative comparison of collected pollen of both bee species indicated important differences in diet breadth between the two species: *A. vaga* collected almost pure *Salix* pollen, whereas *C. cunicularius* collected also a high percentage of other pollen types. The fact that whole cells contained exclusively other pollen types indicates that females of *C. cunicularius* systematically collect pollen from other host plants. Early flowering, tree-like Rosaceae in particular seem to be of great importance to this bee species. Mader (1999) listed a number of species of *Colletes* having a relationship to Rosaceae. In fact, the Nearctic *C. thoracicus* Smith and *C. nigrifrons* Titus are even specialized on Rosaceae. In our study, we found also pollen loads containing only *Quercus, Acer* or *Ilex* pollen, indicating that not only Rosaceae can replace missing *Salix* plants. On the Turkish coast, *C. cunicularius* females were observed foraging on *Pistacia; Salix* did not occur at this location. In Italy, *C. cunicularius* females were observed exclusively on Fabaceae (Kuhlmann in litt.). The whole complex of species, subspecies and their host-plants seems not yet clear. Mader (1999) cited several authors which observed *C. cunicularius* on many other flowers than *Salix,* but their reports contain no precise information whether these flower visits were for collecting pollen or nectar. In fact it is not proved at all that *C. cunicularius* is really oligolectic on *Salix.* Therefore it is not clear whether the collection of other pollen, as observed in this study, is a result of resource restriction. The correlation of increasing percentages of other pollen types in the pollen loads of *C. cunicularius* with the end of flowering time of *Salix* may be an indication for a resource limitation. We registered all *Salix* trees within a radius of 3 km, most of which were *S. caprea.* In the years 1996 to 1998, these trees were blooming very early and had ceased to flower before females of *C. cunicularius* and *A. vaga* began to collect pollen. Only several bushes of *S. aurícula* were available during nest provisioning time of both species. To prove whether *C. cunicularius* collects only other pollen when *Salix* is not available, comparative studies with resource quantifications at other locations from different years are needed.

In conclusion, *C. cunicularius* can not be regarded as an oligolectic species. The use of other, longer blooming host plants, which are more abundant in the study area, may increase the reproductive success of this species. In contrast to *C. cunicularius, A. vaga* seems not to be affected by the problem of long searching times for pollen sources, since it collected only *Salix* pollen. However, the activity time of *A. vaga* ceased approximately 4 weeks before that of *C. cunicularius* and the problem of pollen availability probably did not yet occur.

Niche differentiation.—*A. vaga* and *C. cunicularius* use the same host plant. This overlap may result in interspecific competition, if resources are limited. Since availability of specific pollen is one of the most relevant niche parameters for bees (Eickwort 1973, Strickler 1979), interspecific competition in case of a resource restriction seems very likely. Niche differ-

entiation is often the basis for the coexistence of competitors. There are a number of ways in which niches can be differentiated. In this case the niches of the two species seemed to be differentiated on the basis of conditions. This means that they use the same resource but their ability to do so is influenced by environmental conditions and they respond differently to these conditions (Begon et al. 1990). The two species show diurnal differences in their foraging behavior. This temporal separation is influenced by climatic parameters such as temperature.

Whether *C. cunicularius* uses other host plants because of resource restriction and/or competition with other species (besides *A. vaga* two other *Andrena* species specialized on *Salix* occur in the study area) or whether it is not oligolectic at all can only be proved with removal experiments and manipulation of the resource availiability.

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