

Analysis of Nesting Behavior Based on Daily Observation of *Andrena vaga* (Hymenoptera: Andrenidae)

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Abstract We present a study on nesting behavior of the gregarious solitary bee, *Andrena vaga* Panzer. Based on the daily observation of individually marked females, we constructed an ethogram, determined a sequence of behavioral elements within the provisioning cycle, estimated their length and computed the transition probability between the elements. We confirmed the existence of distinctive pollen and nectar days in *A. vaga* and showed apparent differences in the overall daily provisioning pattern in pollen and nectar days as well as in the probability of transition between some behavioral elements. Bees typically performed one provisioning trip and carried no pollen on nectar days, but they performed up to four pollen-provisioning trips on pollen days. The duration of one pollen trip depended on the number and sequence of the trip in a given day, with the shortest trip usually occurring last in the day.

Keywords Apoidea · andrenidae · *andrena vaga* · nesting behavior · ethogram

Introduction

Nesting behavior consists of various behavioral components such as nest and cell founding and closing as well as building, provisioning, and protection (Michener

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2007). This pattern is essential in the reproductive process of every species of bee, and thus, nesting behavior should be a well-studied scientific branch.

Although vast literature on nesting biology and foraging behavior of many bee species exists, detailed descriptions or analyses of nesting behavior are very rare. Many progressive studies of nesting biology include little information on nesting behavior but rather focus on descriptions of nest arrangement and larval morphology (e.g., Rozen and Buchmann 1990; Eickwort 1977; Bohart and Youssef 1976; Rozen et al. 2009). Other important studies describe the foraging behavior of various species, including daily foraging patterns, number of provisioning flights per day and flight length or rate of reproduction (e.g., Haeseler 1982; Bennett and Breed 1985; Danforth 1990; Neff and Danforth 1991; Stone 1994; Neff and Simpson 1997; Levermann et al. 2000; Bischoff et al. 2003; Klein et al. 2004; Giovanetti and Lasso 2005). Some studies also include information about the time and energy costs of provisioning based on offspring sex ratio or food availability (e.g., Alcock 1999; Danforth 1990; Giovanetti and Lasso 2005).

Comparative studies on nesting behavior, however, are quite unique. In one such study, Neff (2007) compared components of provisioning behavior in bees. This study includes a comprehensive review of nesting behavior publications and shows low comparability of published results. Ethograms summarizing and showing relationships between behavioral elements are useful tools for possible comparison among studied species. McConnell-Garner and Kukuk (1997) used an ethogram for characterization and comparison of social behavior using circle-tube arenas. This method has been widely used in subsequent studies, e.g., Packer (2000) and Boesi et al. (2009). Bogusch et al. (2006) constructed an ethogram on 'nesting' behavior of *Sphecodes* Latreille cuckoo bees during host nest visitation. Some of the *Andrena* Fabricius studies discussed below include detailed descriptions of nesting behavioral components, thus providing a comparison to studies that use an ethogram. However, ethograms often provide a more comprehensive description.

Only a few studies describe nesting behavior within the genus *Andrena* in detail (Malyshev 1926; Michener and Rettenmeyer 1956; Gebhardt and Röhr 1987; Schönitzer and Klinksik 1990 or Bischoff et al. 2003). The remaining investigated information about bee nesting is scattered across a number of articles.

Regarding nesting behavior, we found several behavioral elements described in different articles. Provision departure is preceded by sitting in the nest entrance with head and thorax outside in many, if not all, *Andrena* species (Malyshev 1926; Michener and Rettenmeyer 1956; Davis and LaBerge 1975; Osgood 1989; Schönitzer and Klinksik 1990; Batra 1990). This behavior is especially common on cold days and has been explained as an adaptation to the unstable conditions typical of early spring (Schönitzer and Klinksik 1990).

Many *Andrena* species close their nest entrances before departing for provisions (*A. vaga* Panzer—Malyshev 1926 and Vleugel 1947; *A. clarkella* (Kirby)—Gebhardt and Röhr 1987; *A. nycthemera* Imhoff—Schönitzer and Klinksik 1990) or at the end of the day (*A. rudbeckiae* Robertson—Neff and Simpson 1997; *A. prunorum* Cockerell—Miliczky 2008), whereas other do not close their nests at all (e.g., *A. cineraria* (Linnaeus) and *A. fuscipes* (Kirby)—Gebhardt and Röhr 1987; *A. dunningi* Cockerell—Johnson 1981). This behavior is presumed to be protective against hot and cold temperatures and likely serves as a camouflage as well (Schönitzer and Klinksik 1990).

Departure from the nest entrance is often followed by orientation flight (Michener and Rettenmeyer 1956; Schönitzer and Klinksik 1990; Miliczky 2008), which helps females learning the position of their nest. Therefore, this behavior occurs most often during the first departure of the day or if the female experience difficulty finding her nest during her last return (Schönitzer and Klinksik 1990; Osgood 1989). When the pollen source is situated in close proximity to the nesting site, orientation flights may be unnecessary, as was discussed by Stephen (1966).

Many *Andrena* species seem to have trouble to finding their nests quickly when returning with provision (Michener and Rettenmeyer 1956; Gebhardt and Röhr 1987; Schönitzer and Klinksik 1990; Miliczky et al. 1990), but this is not true for all species as shown by Linsley and MacSwain (1955). Females probably find their nesting place visually using landmarks, but they find the exact position of the nest through olfactory cues (Steinmann 1990; Weislo 1992).

Bees bask repeatedly before entering of their nests after returning on cold days (Batra 1990; Michener and Rettenmeyer 1956; Davis and LaBerge 1975). The length of basking varies individually, and thus, some female basks more often than others (Michener and Rettenmeyer 1956).

Provisioning flight length differs greatly among various bee species (see Neff 2007, for detailed description of components of provisioning behavior) and varies also among species within the genus *Andrena*. Provisioning flight length ranges from an approximate average of less than one hour [12 min for *A. chalybaea* Cresson (Thorpe 1969); 22 min (60 min for nectar trip) for *A. prunorum* (Miliczky 2008); 26 min for *A. viburnella* Graenicher (Stephen 1966); 33 min for *A. erigeniae* Robertson (Davis and LaBerge 1975); 33.5 min for *A. rudbeckiae* (Neff and Simpson 1997); 38.5 min for *A. nycthemera* (Schönitzer and Klinksik 1990); and 42 min for *A. vicina* Smith (40 min in case of trips where no pollen was brought) (Miliczky and Osgood 1995)] to one hour or more [60 min for *A. fulva* Müller (Paxton 1991); 90 min for *A. cineraria* and 95 min for *A. clarkella* (Gebhardt and Röhr 1987); 87 min for *A. miserabilis* Cresson (as *A. bipunctata* Cresson) (Michener and Rettenmeyer 1956); 60–150 min for *A. vaga* (120–210 min when provisioning nectar) (Bischoff et al. 2003); and 27–235 min for *A. erythronii* Robertson (Michener and Rettenmeyer 1956)].

Similar variability was also described in the length of intranest stay [17–88 min for *A. erythronii* (Michener and Rettenmeyer 1956); 55 min for *A. nycthemera* (Schönitzer and Klinksik 1990); 41 min for *A. vicina* (Miliczky and Osgood 1995); 35 min for *A. nivalis* Smith (Miliczky et al. 1990); 24 min for *A. clarkella* (Gebhardt and Röhr 1987); 16 min for *A. perplexa* Smith (as *A. viburnella* Graenicher) (Stephen 1966); 11 min for *A. rudbeckiae* (Neff and Simpson 1997); and 5–7.5 min for *A. erigeniae* Robertson (Davis and LaBerge 1975)]. *Andrena erigeniae* was observed waiting in the nest entrance after unloading the pollen before the next departure for an average of 2.5 min (Davis and LaBerge 1975).

Female bees provision their nests with pollen and nectar. Bischoff et al. (2003) suggested, based on behavioral observation, that *Andrena vaga* collects all the pollen first and then adds most of the nectar at the end of cell provisioning (although these authors didn't check the crop content on nectar days). Similar behavior was described in *A. vaga* by Friese (1923) and was also described for other bee species (Danforth 1989; Friese 1923; Michener and Rettenmeyer 1956). Although it is likely

that *A. vaga* does not provision with pollen and nectar on the same day, which leads to segregated pollen and nectar days (Bischoff et al. 2003), other species alternate pollen and nectar provisioning trips in 1 day (Westrich 1989). Considering the relatively long provisioning flight lengths and intranest staying times in the genus *Andrena* (the whole provisioning cycle takes often more than 2 h), it is not surprising that females often perform only 1–3 provisioning flights per day, although they can perform up to 9 flights at times (Bischoff et al. 2003; Gebhardt and Röhr 1987; Michener and Rettenmeyer 1956; Miliczky and Osgood 1995; Schönitzer and Klinksik 1990; Neff and Simpson 1997).

With such presumed evolutionary importance, nesting behavior should be well studied in a comparable way across different taxa. We expected a high number of published articles; however, this foundation for all ecological and behavioral studies is largely missing. Here, we present one such elementary study based on individual daily observation, including a detailed ethogram, a time line of basic behavioral components and a behavioral comparison of pollen and nectar days. Our study on the model species *Andrena vaga* includes several unexpected behavioral components or patterns of nesting behavior, which broaden our knowledge concerning the life of solitary bees. Also, our methods of data collection and analysis are widely applicable to other bee or other aculeate species, either solitary, communal or eusocial. We hope that using this approach to the study of other species in the future will help improve our understanding of the complexity of bee life history through the comparison of behavioral patterns in solitary and eusocial species.

Materials and Methods

Nesting Site

Behavioral observations were conducted at Svatý Václav near Čelákovice town, 20 km NE from Prague, Czech Republic (50°11'3.89"N, 14°46'17.46"E). This area is characterized by alluvial sandy soils and belongs to the Elbe river basin. The nesting aggregation was situated on a flat sunny meadow on sandy soil along a pine–oak forest and was approximately 100 m long and a few meters wide.

We chose the part of nesting aggregation with the highest nest density and female activity at the beginning of each season. We chose a rather small area, 5.6 m², to accurately monitor the activities of all marked females, which would have been impossible on a larger scale. This area was divided into 50-cm squares, and each square was identified by a number and letter for accurate orientation on the field site.

Model Species

We chose *Andrena vaga* Panzer, 1799 as a model species for our study. The distribution of this species stretches from Mediterranean Europe to Sweden (44–62° north latitude). *Andrena vaga* is an univoltine early spring species, flying from late March through early May in central Europe (Westrich 1989). This species nests in sandy soil and is strictly oligolectic on willows (*Salix* spp.) (Bischoff et al. 2003; Hallmen and van Leeuwen 1991). These demands make the distribution of *A. vaga*

quite scattered but abundant in suitable habitat (Westrich 1989, Rezkova & Straka, personal observation).

Andrena vaga is a philopatric species (Malyshev 1926), this strategy often leads to the formation of nesting aggregations that range from small (only few females) to very large (up to 10 000 females). The nest density in these large aggregations can be up to 30 females per m² (Westrich 1989; Bischoff 2003).

Andrena vaga builds nests up to 60-cm deep (Westrich 1989). The upper 2–7 cm of the nests slant and are filled with loose sand. Females typically cover the nest entrance before departure to protect the nest from parasites and environmental conditions (Malyshev 1926).

Although Westrich (1989) listed only two cleptoparasitic bee species associated with *Andrena vaga*, the specialist *Nomada lathburiana* (Kirby) and *Sphecodes gibbus* (Linnaeus) which also parasitizes a few other bee species, there were two other nonspecialized parasites at nesting aggregation: flies of the genus *Bombylius* (Linnaeus) (Diptera) (Bischoff 2003) and family *Conopidae* (Diptera) (Rezková & Straka, personal observation).

Individual Marking

All the nesting females found on the mapped part of nesting site were individually dye marked by uniPAINT Marker PX–20, Mitsubishi Pencil Co., using three different color spots (two thoracic and one abdominal) for each female. Marking the females allowed for individual recognition during observation. This marking proved to be very wear-resistant, so marked females had to be re-marked only once during the entire flying season.

Nest Marking

We flagged each found nest within the marked part of the nesting site with a stick painted with the same color combination used to mark the female to link the nest to its owner. To distinguish a newly founded nest from an abandoned one, all of the nests belonging to one female were numbered in sequence.

Observation

We individually marked 289 females, of which 164 nested in the marked part of the aggregation. All of the individually marked females were observed for the entire 2008 nesting season (28.3-10.5.2008). Preliminary observations were conducted in April 2007. The nesting site was observed every day from 9AM to 6PM, except on rainy days. We detected and described all of the basic behavioral elements (activities) of the nesting females at the beginning of the season and then used the described behaviors to monitor the marked females for the rest of the season. For each female noticed on the nesting site, we recorded the color mark and exact time of the activity. We also noted information about the location of the female when the activity occurred and about the nest belonging to female at the moment. This method allowed us to monitor all the bee activities and nests during the flying season. These data were analyzed at the end of the season.

Ethogram

All of the recognized behavioral elements were described in an ethogram. We recorded the characteristic features of each activity together with additional information on the activities, such as their length and their relation to subsequent or preceding activities.

Activity Sequence in One Provisioning Cycle

Nesting behavior consists of provisioning cycles. The sequence of activities in one cycle was described during fieldwork and was further specified during data analysis. The final general activity sequence was diagrammatized in an activity scheme, which shows all the detected relations among activities within one provisioning cycle.

Data Cleaning and Processing

The raw data obtained during field observation were stored in a relational database, PostgreSQL Database Server 8.3, and were preprocessed (cleaned from general observational mistakes) using SQL language at the beginning of data processing. We observed that a provisioning cycle consists of a long cycle (L-cycle) (sequence: return with provision → entering the nest → departure) and a facultative repeat cycle (R-cycle) (sequence: return with provision → fast departure without entering the nest → return) that may precede the long cycle. Some of the activities may therefore be present in both parts of the provisioning cycle (e.g., departure or digging). Therefore, we had to distinguish between these two outcomes for further analysis. We first analyzed all sequences that contained activities possibly belonging to both parts of the provisioning cycle. Activities within the sequence return → return without entering the nest were indexed with “r” as they belonged to the R-cycle. Activities within the sequence return → return with the entering the nest were indexed with “l”. Activities belonging specifically to the L-cycle (e.g., covering the nest) and activities without a constant position within the cycle (e.g., waiting or floating) were not indexed. Only data containing activities that were indexed or cycle-specific activities were used for further analyses (using SQL language) described below. Activities (and the activity sequences containing them) that could not be subscribed because of missing data they were omitted from further analysis.

Differences in Provisioning Cycles

We distinguished two types of provisioning cycles: pollen and nectar cycles. Bischoff et al. (2003) suggested, based on behavioral observation, that pollen and nectar provisioning are distinct activities performed on different days. We observed that females bring no pollen on their legs but their crops are full of clear nectar on nectar days, while they bring a lot of pollen on their legs and mixture of pollen and nectar inside their crops on pollen days. (We checked for the crop content repeatedly by the slight pressing of metasoma that leads to the crop volume regurgitation). We found differences in behavior between pollen and nectar days. Thus, we compared

the sequence and length of activities within nectar and pollen provisioning cycles in detail (see below) and analyzed overall daily activity during pollen and nectar days (see below).

Provisioning Cycle Analysis

We computed the duration of long-lasting activities (time from the beginning of one activity to the beginning the following activity) and the length of important intervals between activities in pollen and nectar days. We pooled all of the lengths of activities or intervals from our data, and thus, the analyzed lengths include all activities and interval lengths of all observed females during the entire nesting season. The outliers were removed from these time values [$Q1-1.5 \times (Q3-Q1)$, $Q3+1.5 \times (Q3-Q1)$, where Q = quartile], and the average, median, minimum and maximum time duration for each activity and interval were counted separately for pollen and nectar cycles.

We analyzed the transition probabilities between activities in an activity sequence within pollen and nectar cycles using matrices and Markov chains (Lehner 1998). Two transition frequency matrices (one for pollen and another for nectar days) were constructed for all pairs of consecutive activities consistent with the activity scheme (for details see Caswell 2000). We pooled the data from all the females during the entire season for this computation. The resulting transition probabilities between all activities on pollen and nectar days were organized in Table 3.

Daily Activity

To analyze female daily activity, we used “beedays”, where one beeday is defined as the activity of one female during 1 day (from the definition only the days with any observed activity of each female were included). We pooled all of the beedays from our data (= all female daily observations during the entire season) for this analysis, which should minimize the individual influence or the effect of the weather or the available pollen supplies. Total beedays were divided into pollen and nectar beedays.

We counted the number of returns with provision (= the number of provisioning trips) within each beeday. Pollen and nectar beedays were subclassified into different provisioning categories depending on daily number of returns. The frequency of each of these categories within pollen and nectar beedays was used for analyzing the provisioning frequency in *Andrena vaga*. The number of provisioning trips was also used to estimate the ratio of pollen and nectar provisioning trips which is, along with the total number of provisioning trips per day, important in analyzing the foraging strategy of *A. vaga*.

We counted the medians of all departure and return times in each provisioning category, and these medians were used to construct a diagram of daily activity. The returns provided more reliable information for the analysis of daily routine because the departures were often very fast and were therefore occasionally missed. We also counted the medians of interval lengths between two consecutive returns, between consecutive returns and departures (= time inside the nest) and between departures and returns (= provisioning flight duration). This method allowed us to analyze the daily activity and describe the distribution of provisioning trips within the day according to their type and number per day.

Results

Ethogram

We can divide the behavioral elements (activities) observed on the nesting site in two ways (a and b):

- a) According to their position in the provisioning cycle:
 - i) Activities linked to departure—e.g., covering the nest or imprinting flight.
 - ii) Activities linked to return with provision—e.g., digging.
 - iii) Activities not linked to the position in provisioning cycle, which can occur at any time during the cycle—e.g., basking or mating.
- b) According to their length:
 - i) One-off activities—return, departure, entering the nest. These activities occur in one moment and we therefore cannot estimate their length.
 - ii) Long—lasting activities—waiting, basking, digging into the nest, servicing of the nest, sitting in the nest entrance, covering the nest entrance, fake entrance digging and imprinting flight. We can estimate the length of these longer lasting activities.

Behavior Linked to Return With Provision

Return With (Rp) or Without (R) Pollen

Return with pollen and nectar are behaviorally similar. The returning female lands on the surface in close proximity to her nest but not on the tumulus itself. She then walks toward the tumulus. When cold, the female typically crawls to the top of the tumulus and basks for a few seconds or minutes before the digging into the nest. The female often flies away from the tumulus without any digging attempt resulting in the Repeat—cycle (see below).

Females return approximately 1.5–2 h after the departure on pollen days but return closer to 2.5 h after departure on nectar days (see Table 2). The interval between these two activities equals the provisioning flight length.

Digging into the Nest (G)

Andrena vaga females cover their nest entrances before departure (see Covering the nest), and thus, the returning female must dig into the nest. She begins to dig on the tumulus by placing her forelegs on the spot that she suspects to be the nest entrance. On nectar days when she is not returning with pollen, she also uses her hindlegs. The female digs persistently until she successfully pokes head first into the nest entrance. Once half of her body is inside the nest, her hind legs freeze in a position stretched behind her body until she pokes into the nest completely. This behavior was

observed only in pollen—carrying bees; therefore, it likely protects the pollen provisions on the hind legs.

Digging typically lasts for less than a minute (see Table 1) but can extend to several hours under specific conditions. Bees are persistent diggers and do not give up before entering the nest. If a female does not manage to enter her nest that day, then the next day she will often float over the nesting site searching for a new nest or will be found in a newly built or usurped nest.

Repeat Cycle

Unlike other behavioral elements described here, the R—cycle is not a single activity but rather a sequence of activities. We describe it separately because it represents a self-standing and important behavioral pattern.

The R—cycle is characterized by the activity sequence return → departure → return without entering the nest. The female does not enter the nest after returning with the provision but flies away almost immediately, often trying to dig into the nest for approximately a minute before leaving. However, she returns to the nest quickly, after approximately 1 min, and this behavioral sequence may repeat several times until the female finally manages to dig into the entrance successfully. A single R—cycle usually takes only few minutes, but the entire repetition of R-cycles may take more than half an hour until the female manages to enter the nest (see Table 2).

Table 1 Lengths of long-lasting activities within the provisioning cycle

Length		Avg.	Median	Min	Max	N
B/W	PD	0:00:54	0:01:00	0:00:00	0:05:00	85
	ND	0:00:42	0:01:00	0:00:00	0:03:00	26
F	PD	0:01:23	0:00:00	0:00:00	0:08:00	28
	ND	0:03:13	0:02:00	0:00:00	0:09:00	13
G _l	PD	0:00:32	0:00:00	0:00:00	0:19:00	661
	ND	0:00:29	0:00:00	0:00:00	0:10:00	235
G _r	PD	0:00:29	0:00:00	0:00:00	0:09:00	413
	ND	0:00:19	0:00:00	0:00:00	0:05:00	123
S	PD	0:03:20	0:03:00	0:00:00	0:04:00	3
	ND	0:03:00	0:03:00	0:03:00	0:03:00	1
SE	PD	0:05:04	0:02:00	0:00:00	0:24:00	14
	ND	0:04:30	0:02:00	0:00:00	0:14:00	7
C	PD	0:00:35	0:00:00	0:00:00	0:14:00	392
	ND	0:00:41	0:00:00	0:00:00	0:11:00	159

Averages, medians, minima and maxima of long-lasting activity lengths within the provisioning cycle. N indicates the number of activities (excluding outliers) used for calculation. B/W—basking/waiting, C—covering of the nest entrance, F—fake entrance digging, G—digging into the nest, S—nest servicing, SE—sitting in the nest entrance. Indexes r and l show the incidence of the activity to the repeat (R)- or long (L)-cycle. We computed two different statistics for each activity, one for pollen day (PD) and one for nectar day (ND).

Table 2 Lengths of key intervals within the provisioning cycle

Length		Avg.	Median	Min	Max	N
Provisioning cycle	PD	2:49:04	2:32:00	1:17:00	5:58:00	207
$R(p)_l-R(p)_l$	ND	2:01:55	2:13:30	0:23:00	4:54:00	26
L-cycle	PD	2:31:37	2:26:00	0:59:00	4:28:00	230
$(Rp_l-Rp_{r/l})$	ND	–	–	–	–	–
R-cycle	PD	0:05:26	0:04:00	0:01:00	0:15:00	183
$R(p)_r-R(p)_{r/l}$	ND	0:07:58	0:06:30	0:01:00	0:23:00	62
All R-cycles	PD	0:16:37	0:09:00	0:01:00	1:05:00	117
$R(p)_r-D$	ND	0:36:31	0:11:00	0:01:00	2:32:00	25
Provisioning flight	PD	1:56:49	1:39:00	0:27:00	4:35:00	286
$D_l-R(p)_{r/l}$	ND	2:16:19	2:34:00	0:18:00	3:16:00	21
Intranest stay	PD	0:55:41	0:50:30	0:12:00	2:06:00	217
E-C/D _l	ND	1:14:25	1:05:30	0:15:00	2:36:00	21
$R(p)_r-D_r$	PD	0:00:00	0:00:00	0:00:00	0:00:00	421
	PD + out	0:00:29	0:00:00	0:00:00	0:15:00	495
	ND	0:00:00	0:00:00	0:00:00	0:00:00	149
	ND + out	0:00:14	0:00:00	0:00:00	0:05:00	170
$R(p)_l-E$	PD	0:00:00	0:00:00	0:00:00	0:00:00	549
	PD + out	0:00:46	0:00:00	0:00:00	0:33:00	650
	ND	0:00:00	0:00:00	0:00:00	0:00:00	185
	ND + out	0:00:31	0:00:00	0:00:00	0:10:00	220
$R(p)_l-D_l$	PD	0:51:21	0:49:00	0:15:00	1:25:00	157
	ND	1:40:00	1:41:00	1:33:00	1:47:00	2

Averages, medians, minima and maxima of most important interval lengths within one provisioning cycle. N indicates the number of intervals used for calculation. Outliers were excluded prior computing. If their exclusion caused zero variance, then the statistics were computed again including outliers (+out). C – covering of the nest entrance, D – departure, E – entering the nest, R – return with nectar, Rp – return with pollen. Indexes r and l show the incidence of the activity to the repeat (R)- or long (L)-cycle. We computed two different statistics for each interval – one for pollen day (PD) and one for nectar day (ND).

Entering the Nest (E)

This activity is defined as the moment when a female pokes completely into the nest, and it separates provisioning flight (outer activities) from intranest behavior.

Behavior Linked to Departure

Nest Servicing (S)

All the pre-departure behaviors may start with nest servicing. The servicing female crawls backward from the nest entrance and pushes the soil out of the nest (up to 1–2 cm distance from the nest entrance) using her hindlegs. She then enters the nest again and repeats the process. She finishes by trimming the edge of tumulus and

entering the nest for the last time before the departure. This behavior takes approximately 3 min (Table 1) but can be shorter or absent entirely. Nest servicing might be followed by short periods of sitting in the nest entrance or by nest covering and departure.

Sitting in the Nest Entrance (SE)

This behavior can be observed before departure, when the female sits in the nest entrance with her head and antennae outside the entrance. Sitting in the nest entrance is typical during poor weather conditions when females can spend several hours, possibly waiting for an improvement in the weather. The length of this behavior is therefore extremely variable: it often takes only 2–3 min before departure (see Table 1) but can take many hours during unpleasant weather.

Covering the Nest (C)

Andrena vaga females usually cover the nest entrance with the sand before departure. This behavior is characterized by a backward skating movement of the female over the tumulus, during which the female rakes sand underneath with her forelegs while pushing sand aside with her hind legs. This behavior usually takes less than 1 min (see Table 1), but it can take up to 14 min when digging a fake entrance (see below). Nests covered from the outside or the inside look very similar.

Fake Entrance Digging (F)

This behavior often follows, or rather is connected to, covering the nest. After covering the nest, the female turns backwards on tumulus and begins to dig a new hole 0.5–2 cm away from the nest entrance. The depth of the hole is a function of the time invested. It is usually quite shallow and digging takes only a few seconds (Table 1). However, on a few occasions, we observed a female digging a fake entrance with a huge tumulus and a depth so great that the entire female was hidden. Such behavior can take up to 10 min.

Fake entrance digging may be followed by a short simulation of its covering, but more often, the female flies away immediately after digging.

Departure (D)

Departure finishes all the pre-flight activities. Its exact form depends on the weather condition and on its order per day. Bees only depart when weather conditions are satisfactory for a provisioning flight. If conditions are not acceptable, then they stay in the nest, often sitting in the nest entrance.

The first departure of the day is usually followed by an imprinting flight (see below), whereas the others are fast either without an imprinting flight or with a greatly shortened one. On cold days, the first departure is more complex because females are not able to fly away before heating up to flying temperature. Therefore, they usually walk away from the nest, bask in the sunshine and then perform the imprinting flight or depart without it.

Imprinting Flight (I)

This behavior is usually performed on the first departure of the day. The imprinting female flies above the nest entrance, first in small circles a few centimeters above the nesting site and later expanding the range. The size and height of the flight slowly rise until the female flies away at the height of about 70–200 cm. This behavior is usually completed in less than 30 s. Imprinting flight is very indistinctive or absent during the other departures of the day, but females perform the imprinting flight again during the day if they had trouble finding their nest during their last return.

Activities Non-Linked to the Position in Provisioning Cycle

Basking (B)

Basking can occur in any part of the day when the temperature is not sufficiently high for flying. Basking is often part of the pre-departure behavior, but on cold days, females use it after returning and prior to digging. They usually remain still on a sunny place, not necessarily close to the nest, during basking.

Basking takes less than 1 min on average, but it can take up to 5 min (see Table 1). The values in Table 1 also include waiting because of its similarity to basking (see below).

Waiting (W)

This activity is behaviorally similar to basking but was distinguished from it in situations when warming up could not have a function, typically on very hot and sunny days. This behavior usually occurred after a return, when females often landed and sat in different parts of the nesting site. Because of its similarity to basking, we did not estimate its time separately; thus, the length of this activity is also less than 1 minute with 5 min the maximum (Table 1). It likely represents a short rest after the long provisioning flight. Other functions and its relation to basking remain unclear.

Floating (Fl)

Floating may occur whenever female cannot find her nest or does not manage to enter the nest for a long period of time. Such a lost female then flies around the entire nesting site, lands, tries to dig on various places for a few seconds and then flies away to try it elsewhere. This behavior may consequently lead to visiting conspecific's nests (see below).

The duration of such behavior depends on the nest state. If the female has lost her nest because of usurpation or disturbance, then it takes several hours or days for her to find or build a new one. However, floating is often merely caused by orientation mistakes. In this case, the female flies away after a few minutes, and when she returns, she is usually able to find her nest without incident.

Visiting of Conspecifics Nest (V)

This behavior is usually connected with floating and is not very common. We suppose that it represents mistakes in searching while floating. The female usually enters some uncovered nest during searching and sometimes digs incidentally into the alien nest. The visit is usually very short, less than 1 min, and the female starts to search again when she leaves.

There is one other type of visiting of conspecific nests that is not linked to floating. A female may occasionally dig into her neighbor's nest by mistake, but when she realizes the mistake, she will usually leave the alien nest immediately and will begin to dig into her own nest.

Mating (M)

Mating, or rather mating attempts, occur only at the beginning of the season when the males are present on the nesting site and are very numerous. In this study, we present this behavior in the sense of influence on female nesting behavior and its possible costs. Males are often extremely obstinate, and it is not unusual to see several males attempting to copulate with one female at the same time. They also often wait for a female around the tumuli and attack her immediately when she leaves the nest entrance.

Females must often fly away from the nesting site during covering of the nest or digging to avoid males, which cost a lot of time and energy.

Provisioning Cycle Analysis

a) The activity sequence in the provisioning cycle:

A provisioning cycle is defined as a sequence of activities from one return with provision $[R(p)]$ to another. All of the activities included within the provisioning cycle are organized in a specific order. The return with provision (pollen or nectar) must generally be followed by entering the nest, covering the nest entrance and departure. The relationship between these and other activities are diagrammed in an activity scheme (Fig. 1), which is generally similar for pollen and nectar provisioning cycles. The particular differences between them are described below.

One provisioning cycle may consist of two different parts: the repeat cycle (R-cycle) and the long cycle (L-cycle). The L-cycle represents the key part of the provisioning cycle, and it is the entire interval between two following returns with provisions $[R(p)_l-R(p)_{r/l}]$. The R-cycle $[R(p)_r-R(p)_{r/l}]$ is a subsection of the provisioning cycle, which may precede the long cycle. It is characterized by a fast departure shortly after the return with provision on the nesting site without entering the nest (see ethogram, R-cycle). There may be a variable number of R-cycles before the long cycle. All of the parts of the provisioning cycle are separated by single key activities (pointed bold in activity scheme) that are present on both pollen and nectar days.

b) Time parameters in pollen and nectar days depending on the R- and L-cycles:

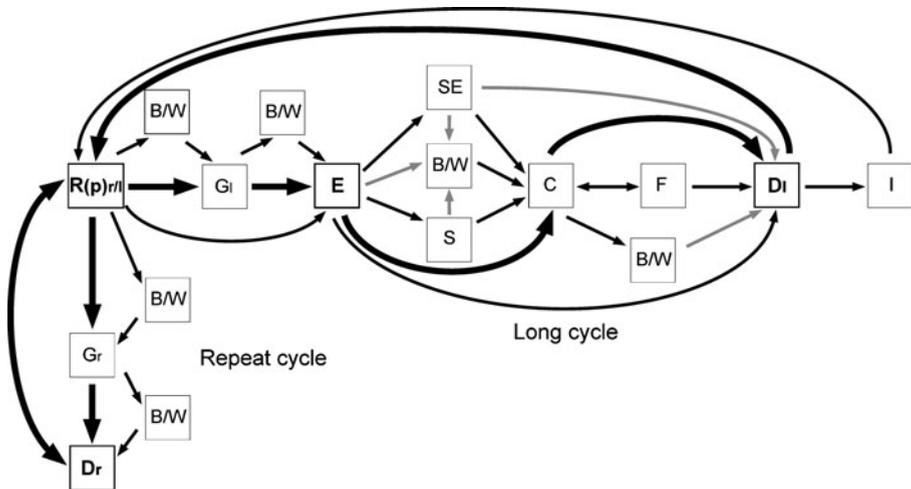


Fig. 1 Activity scheme. Behavioral elements of *Andrena vaga* in sequential scheme; activities connected by arrows show the known direction of transitions between elements and show that behavioral patterns are context dependent. *R(p)* return with nectar (pollen), *G* digging into the nest, *B/W* basking/waiting, *E* entering the nest, *SE* sitting in the nest entrance, *S* nest servicing, *C* covering of the nest entrance, *D* departure, *F* fake entrance digging, *I* imprinting flight. Indexes *r* and *l* show the incidence to the repeat (R)- or long (L)-cycle. The key activities of the provisioning cycle are in black frames; the bold arrows show the most important transitions between activities. Gray arrows represent the transitions not found in real data, but expected. Sequence *R(p)l*-*R(p)l* represents the long cycle, *R(p)r*-*R(p)r/l* represents R cycle

The median length of the long cycle is 2 h 26 min (N=230) for pollen returns, which nearly equals the length of the entire provisioning cycle (2 h 32 min, N=207). We were not able to distinguish between long cycle length and complete provisioning cycle length in the nectar cycle because of insufficient data (the entire nectar provisioning cycle was quite a rare event; females usually performed only one half of it: the provisioning flight, see part daily activity). The median length of the nectar provisioning cycle is 2 h 14 min (N=26).

The key parts of the long cycle are the provisioning flight (*Di*-*R(p)r/l*), with a median of 1 h 39 min (N=286) for the pollen cycle and 2 h 34 min (N=21) for the nectar cycle (finished or unfinished), and the intranest stay (*E*-*C/Di*), with a median of 50 min (N=217) for the pollen cycle and 1 h 5 min (N=21) for the nectar cycle.

The R-cycle is typically much shorter than the L-cycle (median for pollen cycle is 4 min, N=183; median for nectar cycle is 6.5 min, N=62). There may be several R-cycles within one provisioning cycle, or there may be none. The summary interval length statistics are shown in Table 2.

We did not find any major difference between pollen and nectar cycles in the length of single long-lasting activities. The length statistics of single, long-lasting activities are listed in Table 1.

c) Transition probabilities between activities:

We estimated the transition probabilities between all activities diagrammatized in the activity schemes for pollen and nectar cycles separately using transition matrices. Transition probabilities between key activities were quite similar in pollen and nectar cycles (see Table 3), but nectar cycles (and therefore, pairs of activities within nectar

Table 3 Transition probabilities between activities within the provisioning cycle

Activity1	Activity2	PD		ND	
		N	Probability	N	Probability
B/W	E	3	—	3	—
B/W	G _l	42	—	5	—
B/W	G _r	16	—	1	—
B/W	D _r	13	—	3	—
B/W	C	5	—	0	—
E	S	4	1.9%	0	0%
E	SE	7	3.2%	2	25%
E	D _l	13	6%	0	0%
E	C	192	88.9%	6	75%
F	D _l	20	95.2%	3	75%
F	C	1	4.8%	1	25%
G _l	E	614	99.7%	188	98.9%
G _l	B/W	2	0.3%	2	1.1%
G _r	D _r	402	99.3%	113	100%
G _r	B/W	3	0.7%	0	0%
S	C	3	100%	0	0%
R(p) _l	E	3	0.5%	6	2.9%
R(p) _l	G _l	575	92.9%	185	88.9%
R(p) _l	B/W	41	6.6%	17	8.2%
R(p) _r	G _r	387	80.3%	112	69.1%
R(p) _r	D _r	69	14.3%	46	28.4%
R(p) _r	B/W	26	5.4%	4	2.5%
R(p)	R-cycle	619	56.2%	208	56.2%
R(p)	L-cycle	482	43.8%	162	43.8%
SE	C	10	100%	5	100%
D _l	R(p) _l	130	72.2%	15	68.2%
D _l	R(p) _r	50	27.8%	7	31.8%
D _r	R(p) _l	135	45.8%	21	28.0%
D _r	R(p) _r	160	54.2%	54	72.0%
C	F	30	12.6%	12	25.5%
C	D _l	202	84.9%	33	70.2%
C	B/W	6	2.5%	2	4.3%
R(p)	E	3	0.3%	17	4.6%
R(p)	G _l	575	52.2%	185	50%
R(p)	B/W	41	3.7%	6	1.6%
R(p)	G _r	387	35.1%	112	30.3%
R(p)	D _r	69	6.3%	46	12.4%
R(p)	B/W	26	2.4%	4	1.1%

Transition probability between pairs of consecutive activities within one provisioning cycle. The most common transition for each activity is in bold. N stands for the number of activity pairs used for calculation. B/W—basking/waiting, C—covering of the nest entrance, D—departure, E—entering the nest, F—fake entrance digging, G—digging into the nest, R—return with nectar, Rp—return with pollen, S—nest servicing, SE—sitting in the nest entrance. Indexes r and l show the incidence of the activity to the repeat (R)- or long (L)-cycle. The transition probabilities were computed separately for pollen day (PD) and for nectar day (ND).

cycle used for analysis) were rarer than pollen cycles, so the less common transitions within nectar cycles could be underestimated or even missed.

The return with provision was in both pollen and nectar cycles, followed by the R-cycle in 56% cases and immediately by the L-cycle in 44% of cases. The transition probability between the R-cycle and L-cycle differed in nectar and pollen cycles. The first R-cycle was followed by another R-cycle in 54% of cases within pollen cycles (the L-cycle followed the first R-cycle in 46% of cases) but only in 30% of cases in nectar cycle (the L-cycle was entered after the first R-cycle in 70% of cases) (see Table 3).

The return with provision within the L-cycle ($R(p)_l$) was most often followed by digging into the nest (G_l) (93% of cases in pollen cycles and 89% in nectar cycles). Entering the nest without digging was a rare event (0.5% cases in pollen cycles and 2.9% cases in nectar cycles). Digging was a consequence of covering the nest entrance before departure, which occurred in the majority of departure behavior regardless of the cycle type. Departing without the covering the nest was observed in only 6% of cases in pollen cycles and none in nectar cycles (which is possibly the consequence of insufficient data). The departure was preceded by sitting in the nest entrance in 25% of cases on nectar days, while such behavior was observed in only 3% of cases on pollen days.

Daily Foraging Activity

The daily activity of bees depends on weather conditions and on nest provisioning state. First females started to activate between 8 and 9 a.m., and their activity generally ceased around 6 p.m. on days with adequate weather conditions (the times of medians of first departures and last returns in Figure 2 are slightly shifted compared to the values indicated above because there was large variability within departure times). The females remained active throughout the entire day with slightly lower activity around noon during sunny and warm weather. However, their activity was much lower and shorter during unpleasant weather conditions (cloudy, windy), and no activity occurred on rainy days or even the following day if the ground was not sufficiently dry. We also noticed that females did not activate each day of their life regardless of the weather conditions.

We analyzed the daily provisioning activity in detail. We registered 695 provisioning beedays: 35.5% of them represented nectar days and 64.5% represented pollen days. The pollen–nectar day ratio was approximately two pollen days to one nectar day.

Only one nectar load (= one half of provisioning cycle—provisioning trip) was brought in 89.5% of nectar beedays, and the whole provisioning cycle was finished in only 10.5% of nectar beedays (see Table 4).

On 54% of pollen beedays females provisioned their nets by only one pollen load per day; on 34% by two pollen loads; on 10% by three pollen loads; and on 2.2% by four pollen loads (see Table 4). The average number of pollen loads per pollen beeday was 1.6.

There is a negative relationship between the length of the provisioning flights and their numbers per day. We also observed that the length of the provisioning

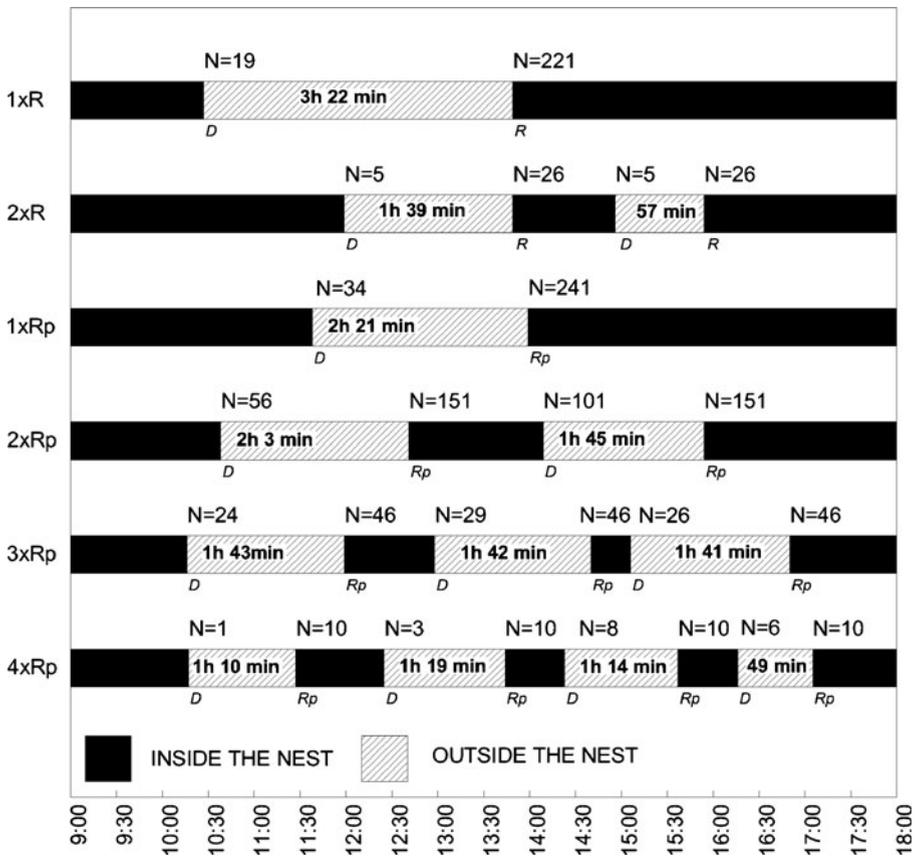


Fig. 2 Daily foraging activity. The graph shows the median lengths of provisioning flights and intranest stays depending on the number of provisioning flights per day and the type of day (pollen/nectar day). N stands for the number of intervals and activities used for calculation of diagrammatized values. R—return with nectar (nectar day), Rp—return with pollen (pollen day)

cycle shortened gradually during the day. The pollen provisioning cycle took 3 h 13 min (median, N=151) on beedays with only one provisioning cycle per day, but the first cycle on beedays with three pollen cycles took 2 h 17 min and the third one only 1 h 28 min (medians, N=10). The parts of provisioning cycle (provisioning trip, D–R(p) and intranest stay, Rp–D) shortened accordingly, which is recognizable even in pollen beedays with one and two nectar returns per day. The compilation of daily schedules for all pollen and nectar days is diagrammatized in Figure 2.

We further observed that the bees departed earlier in the morning on the days when the daily provisioning trip number was high. The first departure on beedays with three pollen returns occurred nearly half an hour earlier (median 10:16) than the first departure on beedays with two pollen trips (median 10:38, N=56). However, the times of first departure on beedays with three and four pollen trips per day were nearly the same (medians 10:16 (3P) and 10:17 (4P)) (see Figure 2) as the provisioning females probably reached their limits.

Table 4 Pollen and nectar beeday numbers

		Number of beedays	%
Nectar days	1 × R	221	89.5%
	2 × R	26	10.5%
Total (nectar days) days)		247 (35.5%)	100%
Pollen days	1 × Rp	241	53.8%
	2 × Rp	151	33.7%
	3 × Rp	46	10.3%
	4 × Rp	10	2.2%
Total (pollen days)		448 (64.5%)	100%
Total		695 (100%)	

Number of beedays (one beeday = activity of one female on one day) with the given number of daily returns with provision on pollen and nectar days respectively during the whole season. R—return with nectar, Rp—return with pollen, 1 × R = one return with nectar per day.

Discussion

Ethogram

Many behavioral elements described here are common for numerous bee species, but the composition, exact sequence and length of behavioral elements are likely species specific. Here, we discuss the behavioral elements that are characteristic of *Andrena vaga* or are interesting from an evolutionary perspective.

Sitting in the nest entrance (SE) is an activity likely used to control for weather conditions outside the nest because it usually precedes departure and was often observed during poor weather conditions. In such cases, SE behavior could take several minutes or even hours. It is possible that bees assess weather conditions and then wait for an improvement prior to departure. Schönitzer and Klinksik (1990) described similar behavior in *Andrena nycthemera*, and their interpretation is consistent with ours.

Covering the nest entrance before the departure (and related digging into the nest after return) is an ecologically dependent behavior. It is typical of many psammophilous species of the genus *Andrena* (e.g., Malyshev 1926; Gebhardt and Röhr 1987; Schönitzer and Klinksik 1990; Bischoff et al. 2003) and may be used to maintain a constant thermal condition inside the nest (Westrich 1989) or more probably to defend the nest from parasites and predators (Wcislo and Cane 1996).

The close relation of nest covering and nest defense is supported by the existence of fake entrance digging. Some other authors described similar behavior (Malyshev 1926; Schönitzer and Klinksik 1990; Osgood 1989) but did not usually consider its function. We therefore assume that fake entrance digging, along with nest covering, may be a widespread behavioral pattern in species nesting in sandy soil. We observed that fake entrance digging may be quite an effective defense against parasites (especially the cleptoparasite *Nomada lath-*

buriana), which attempt to dig into the nests of *A. vaga* when bees are absent from their nests (Rezkova & Straka, personal observation). We often observed that *Nomada* spent considerable time digging in the fake entrance rather than digging in the correct entrance position. Such behaviour is costly in terms of time and energy and, thus, sometimes leads to abandoning the digging attempt. However, further research targeted on this problem would be needed to properly understand the potential evolutionary importance of this behaviour. The negative consequence of fake entrance digging is that returning females often confused themselves. We observed *Andrena* female trying to dig in the fake entrance after the return with provision many times. Such a female may spend several minutes trying to get into the nest in a fake entrance position before beginning to dig at the correct place of entrance. Fake entrance digging also increases the danger of predator attack because it prolongs the time spent uncovered on the nesting site, and it also increases the danger of overheating during very hot and sunny days. We observed that this behavior, along with covering the nest, depends on the surface temperature. Females only performed short nest covering and usually did not perform fake entrance digging at all on very hot and sunny days.

Considering the time and energy investment and potential risk connected with predators and overheating, we suppose that this behavior must have great evolutionary significance. It probably represents one of few nest defense possibilities available to *Andrena vaga*, a species with a small sting and which displays low levels of aggression when confronted with a parasite. The low level of aggression on the intraspecific or interspecific level is probably typical of the entire genus *Andrena* (Osgood 1989; Michener and Rettenmeyer 1956; Davis and LaBerge 1975) because aggression has only been described rarely (e.g., Eickwort 1977; Schönitzer and Klinksik 1990).

Floating behavior represents another interesting behavioral element and has been reported in many aculeate species that nest in aggregations (Miller and Kurczewski 1973; Eickwort et al. 1977; Jang et al. 1996). This behavior is characteristic of individuals searching for a suitable place for new nest founding (Schönitzer and Klinksik 1990; Jang et al. 1996). It was described in detail for *Crawfordapis luctuosa* (Smith), where females regularly leave their provisioned nests and found new ones. Therefore, they switch between floating (when searching for a new nest) and nest provisioning several times per life cycle (Jang et al. 1996). However, we observed that floating is rather closely connected to nest loss (involuntary) or orientation problems in *Andrena vaga*. Females typically became lost when flushed out on departure without carrying out an imprinting flight. In such cases, floating took only few minutes, and the female found her nest within a short period of time. Bees that lost their nest due to usurpation or disturbance floated over the nesting site until they found a new nest, which could take several hours or even days. Some females disappeared after nest loss, while some females that floated over the nesting site the day before were found in a new nest at the same nesting site on the next day.

Visiting of conspecific nests is a behavior closely connected to floating. Visitors are searching females trying to dig in various places during floating behavior. Likely by mistake, they dig into conspecific's nest at times. Such visits took only few seconds, which is too short time for visiting a conspecific's nest cells. We therefore

do not consider these visits as example of brood parasitism in *Andrena vaga* as it was interpreted in Jang et al. (1996) in *Crawfordapis*.

Basking and waiting are two behaviorally similar activities and, thus, are difficult to distinguish in the field. The only difference between them was the temperature at which they occurred. Basking is considered behavior necessary for heating to flying temperature before departure if the outside temperature is too low (Stone and Willmer 1989). This behavior is typical on mornings or cold days and has been described in other species as well (Michener and Rettenmeyer 1956; Batra 1999; Schönitzer and Klinskik 1990; Davis and LaBerge 1975). Waiting was typical for situations when activity of an *Andrena* female was unexpectedly interrupted, for example by another *Andrena*, by a parasitic *Nomada* Scopoli or by falling leaves, as well as a post-flight resting behavior. Recognition of the reason for waiting is difficult on most occasions, and we therefore included all stationary behavior in waiting activities. Waiting and basking increase the time costs of bee nesting. Also, waiting increases the probability of overheating, and basking increases the probability of predation and parasitization.

Repeat Cycle

We described the existence of R-cycle, a special behavioral pattern connected with covering the nest and returning with provisions. We were only able to find short notes about similar behavior in scientific publications. Schönitzer and Klinskik (1990) mentioned that *Andrena nycthemera* departed from the nest probably due to overheating; Davis and LaBerge (1975) described that *A. erigeniae* females often land close to the nest and wait for a while upon return and that females are very easy to chase away during this waiting, sometimes performing a series of fast escapes and returns. It is therefore probable that behavior similar to R-cycling in *A. vaga* may be common in other bee species as well. However, no attention was paid to this behavior in previous studies.

The R-cycle (similarly to digging into the nest) in *Andrena vaga* is most probably a consequence of covering the nest entrance. If a digging female is disturbed by other female or *Nomada* or if she fails to dig into the nest within a suitable amount of time, then she then flies away (we are sure that the existence of R-cycles was not a mere artifact of our presence because we observed it also often in the remote parts of the nesting sites where we did not manipulate with the females at all). The R-cycle is commonly observed during hot and sunny days, and we therefore ascribe it to the negative influence of high temperature. We assume that females break from digging because they suffer from overheating. They are forced to fly away for a few minutes to cool themselves before returning. The R-cycle may repeat several times during one provisioning cycle, which prolongs the overall time accordingly.

R-cycles are evidently very disadvantageous for the females because they increase the time and energy costs of the provisioning cycle. Considering that R-cycles are consequence of covering the nest, it points out again (similarly as fake entrance digging) to the high evolutionary significance of the nest covering. The increase of female fitness connected to nest covering must be higher than the energetic and time costs connected to R-cycles and fake entrance digging.

Differences Between Pollen and Nectar Days

We confirmed the existence of strictly separate pollen and nectar days described by Bischoff et al. (2003). We analyzed nesting behavior within pollen and nectar cycles and days in detail to detect and define the differences between these two different daily patterns. We found no important differences in the length of key intervals and long-lasting activities between both cycles. We also failed to find any important difference in the majority of transition probabilities between activities, except the higher probability of sitting in the nest entrance before the departure and a faster switch from the R-cycle to the L-cycle during nectar cycles than during pollen cycles (see Table 3). The higher probability of transition from R-cycle to L-cycle on nectar days may be caused by better female mobility without pollen on the hind legs, thus enabling more efficient digging using all legs.

Although we did not find any important differences between pollen and nectar days in behavioral patterns within provisioning cycles, we found and described differences in overall daily activity during pollen and nectar days, especially in the number, length and timing of provisioning trips. Most frequently, we observed only one return with provision during nectar days but up to four provisioning trips per day during pollen days (on average 1.6 pollen trips). Our results agree with data in Bischoff et al. (2003), who observed one nectar trip on nectar days and three pollen trips on average per pollen day. We suppose that a single provisioning trip represents the standard behavior during nectar days and the occasional second trip may represent a feeding trip, which is typical of some species at the end of the day (Danforth 1989; Danforth 1990). Nectar provisioning of the nest is the last activity before final cell adjustment, egg laying and cell closure in many species (Danforth 1989; Danforth 1991; Bischoff et al. 2003) and highly probably also in *A. vaga*. When we experimentally dug several nests of this species, we found small precisely shaped firm balls of pollen within all nonclosed (and therefore probably just being provisioned) cells while the closed cells always contained big amount of nectar and the content of such cell was very fluid. Female brings pollen on her legs and mixture of pollen and nectar within her crop on pollen day. We assume that the mixture is used to shape the pollen load into the ball between the provisioning flights, while on nectar days the female brings only clear nectar in her crop that is probably used at the end of provisioning to moisture the cell content prior egg laying. This behaviour may explain why the ratio of nectar-pollen trip is skewed in favor of pollen trips in many species and also in *Andrena vaga*. Bischoff et al. (2003) described the ratio as 1:2–1:9 (nectar : pollen trip) in *A. vaga*, but we only observed the average ratio 1:2. It is possible that this ratio differs between populations depending on food source distance, or between different seasons depending on various disturbance factors such as weather or population density.

The number of provisioning trips per day seems to be closely related to their length. The shorter the length of the trip, the greater the number of trips a female is typically able to perform per day (Neff and Simpson 1997; Bohart and Youssef 1976; Neff and Danforth 1991; Danforth 1991; Danforth 1990). We observed a similar relationship on an intraspecific level in *A. vaga*. When females performed more provisioning cycles per day, their length was shorter, the shortest provisioning trip was usually the last one each day. In contrast, Neff and Simpson (1997) described

the opposite situation in *Andrena rudbeckiae*, where provisioning trip duration was extending during the day. This relationship was ascribed to the decrease of pollen source availability during the day in *A. rudbeckiae*, in contrast to *A. vaga* with unlimited pollen sources, but variable in distance from the nesting site.

The length of provisioning flight is thus determined by the distance from the food source (Goodell 2003) and on the pollen amount collected and carried. *Andrena vaga* is a species with a long provisioning flight—1.5–2.5 h. A similar length of provisioning flight was observed in other *Andrena* species such as *A. cineraria*, *A. clarkella* (Gebhardt and Röhr 1987) and *A. erythronii* (Michener and Rettenmeyer 1956).

The length of intranest stay is also quite variable among different species and is probably connected with the handling of provision inside the nest. The species with a very short intranest stay only take the pollen off the scopas quickly and immediately fly for a new load (Danforth 1991; Bohart and Youssef 1976; Alcock 1999). The species with longer intranest stays usually adjust the cell and handle the pollen inside the nest before every subsequent departure (Miliczky et al. 1990; Schönitzer and Klinksik 1990). The intranest stay of *A. vaga* was long (nearly 1 hr in average), which indicates that this species probably handles the pollen inside the nest cell after each pollen trip. This is further supported by the presence of pollen balls inside the nonclosed cells discovered repeatedly during experimental nest excavation.

Different *Andrena* species usually bring 1–8 pollen loads per day (for summary see Giovanetti and Lasso 2005). The daily transferred amount of pollen is usually not sufficient for provisioning one cell, which results in a low rate of reproduction (<1 provisioned cell per day) described for many species of *Andrena* (Giovanetti and Lasso 2005; Schönitzer and Klinksik 1990; Neff and Simpson 1997; Gebhardt and Röhr 1987). The slow rate of oocyte maturation described for many *Andrena* species (Neff and Simpson 1997; Bischoff et al. 2003) is another factor closely connected to or even may be the reason for the low rate of reproduction.

Giovanetti and Lasso (2005) proposed that this low provisioning efficiency may be caused by phylogenetic constraints related to typical early spring emergence in the genus *Andrena*. Provisioning behavior of these species depends on the unstable weather conditions typical of this season, which probably makes higher provisioning efficiency nonadaptive. However, knowledge that summer *Andrena* species (that should not be limited by weather conditions) have similarly low provisioning efficiency to their spring relatives (e.g., Neff and Simpson 1997) suggests that there may be another reason for this low efficiency.

The pollen provisioning trip took approximately 2 h in *A. vaga*, while the intranest stay took less than 1 h. If the female provisions her nest with pollen, then she can depart every 3 h and perform up to four pollen trips per day. We observed large differences in provisioning activity among *A. vaga* females bringing pollen on different pollen days. Females managed to perform up to four pollen provisioning trips per day, but on average, they performed only 1.6 flights per day. This finding indicates that bees in the studied population need up to three active days (two pollen days and one nectar day) to provision one cell, if we calculate upon the estimate of Bischoff et al. (2003) of three provisioning trips to complete one cell. *Andrena vaga* is therefore another species of the genus *Andrena* with a low rate of reproduction.

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