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The Ethology of the Solitary Bee Andrena nycthemera Imhoff,1866 (Hymenoptera, Apoidea)

Klaus Schönitzer & Christine Klinksik
Zoologisches Institut der Universität München

Abstract

A large aggregation of nests of the solitary bee *Andrena nycthemera* IMHOFF,1866,was investigated in southern Germany from 1983 to 1988 and in 1990. The nesting site is a sandy slope with several hundreds of nests. Many bees were labelled individually.

The following behavioral patterns of male *Andrena nycthemera* IMHOFF,1866, are described: crawling and inspecting holes, digging, aggressive behavior, patrolling flights, territorial behavior, pouncing and mating. The most important female behaviors described are: searching for a nest site, repulse pouncing males, digging and building nests, emerging from nests, sitting in the entrance, closing the nest entrance, orientation flights, searching the entrance, provisioning, aggressive behavior (not yet described in *Andrena* females) and irregular behavior at the end of the season. The females take care of usually one or two nests, up to four nests. Mating takes place on the surface of the soil at the nesting site.

During one season (1987) the nest aggregation was observed almost every day with suitable weather. For this season the frequency of several behavioral patterns has been compiled (Fig.9a, b) and its correlation with the weather is discussed.

Sphecodes pellucidus SMITH,1845 (Apoidea, Halictidae) and *Leucophora obtusa* (ZETTERSTEDT, 1838) (Diptera, Anthomyiidae) are nest parasites of *Andrena nycthemera* IMHOFF,1866.

Zusammenfassung

Das Verhalten der Sandbiene *Andrena nycthemera* IMHOFF, 1866, wurde von 1983 bis 1988 und 1990 in einer großen Nestaggregation in der Nähe von Dachau (Oberbayern) regelmäßig beobachtet. Der Nistplatz ist ein südexponierter Sandhang mit mehreren hundert Nestern. Viele Tiere wurden individuell markiert.

Folgende Verhaltensweisen der Männchen von *Andrena nycthemera* IMHOFF,1866, wurden beobachtet: Krabbeln am Boden und Inspizieren von Löchern, Graben, agressives Verhalten, Schwarmflüge, Territorialverhalten, Kopulationsversuche, Paarung. Die wichtigsten beschriebenen Verhaltensweisen der Weibchen sind: Suchen nach einem Nistplatz, Abwehren von Männchen, Graben und Nestbau, aus den Nestern kommen, im Eingang sitzen, den Eingang verschließen, Orientierungsflüge, Suchen nach dem Nesteingang, Pollen eintragen, aggressives Verhalten (war bisher für *Andrena* ♀♀ unbekannt) sowie ungewöhnliche Verhaltensweisen am Ende der Saison. Die Weibchen versorgen in der Regel ein oder zwei, maximal vier Nester. Kopulationen finden am Boden am Nestplatz statt.

In einer Saison (1987) wurde die Nestaggregation fast an jedem Tag mit geeignetem Wetter beobachtet, die Häufigkeit der verschiedenen Verhaltensweisen zusammengestellt (Abbildungen 9a, b) und die Abhängigkeit von den Wetterbedingungen diskutiert.

Sphecodes pellucidus SMITH,1845 (Apoidea, Halictidae) und *Leucophora obtusa* (ZETTERSTEDT, 1838) (Diptera, Anthomyiidae) sind Nestparasiten von *Andrena nycthemera* IMHOFF, 1866.

1. Introduction

Due to their great importance for pollination, feral bees are regarded as meaningful for wildlife conservation and are studied increasingly. In the last years, detailed investigations on several species of bees were published (e.g. BELLMANN 1981, HAESELER 1982, HOHMANN 1978, MEYER-HOLZAPFEL 1984, GEBHARD & RÖHR 1987). Furthermore, a comprehensive monograph on the biology of the German species of feral bees has been published (WESTRICH 1989 a, b).

One of the largest genera of bees in Europe is *Andrena* with more than one hundred species in Germany (WESTRICH 1984, WARNCKE 1986). There are several short notes on the biology of different species of *Andrena* and many remarks in the faunistic literature. Nevertheless the behavior of most species is still unknown. The ethology of *A. nycthemera* which is investigated in the present study is virtually unknown. Up to now there were only few remarks in faunistic publications (PEUS 1926, STOECKERT 1954, KOCOUREK 1966, WESTRICH 1989 b). In most cases only the occurence of the species was recorded and its rarity pointed out (e.g. HAMANN & KOLLER 1965, WESTRICH 1985, DYLEWSKA 1987).

Apart from a detailed description of behavioral patterns, this study is focussed on two points: First, by the continuous observation of a nest aggregation throughout a whole season we evaluated the seasonal history in great detail. Secondly, we gained axact data on the life of individual bees with the aid of individual labelling of bees. Part of this material was presented in a preliminary form as an abstract (KLINKSIK & SCHÖNITZER 1988).

2. Methods

2.1 Time and duration of investigation

The nest aggregation was visited in the years 1983 to 1988, and in 1990. Most thoroughly it was observed during the season of 1984 (on 25 days) and 1987 (on 37 days). In the latter year, the colony was visited almost all days with good weather between March 24th and May 14th. On 12 days, the nesting site was not visited, but on most of these days (except three) the weather was so bad, with low temperatures, rain or even snow, that hardly any bees had been active anyway. The observation time on different days depended on the weather. It was usually about 2 to 4 hours in the beginning and at the end of the season and 6 to 8 hours in the middle of the season, sometimes up to 10 hours (altogether more than 200 hours in 1987).

All statements of time mentioned in the text are given in Central European Time (not summer time).

2.2 Observational techniques

For the most part, observations could be carried out with the naked eye. The bees do not seem to be disturbed by the presence of a quiet human observer. Of special help was a monocular field glass (8 x 20) which could be focussed as near as 0.8 m distance. With this field glass it was possible to scrutinize a rather large observation area without moving around.

The behavioral patterns of the bees were recorded with a 16 mm film-camera (24 pictures/s, Kodachrome II) in 1987 and in 1984 with a black and white video camera. The films were analyzed by single frames.

Individual bees were labelled with small dots in five different colors (shellack), according to the code system of v.FRISCH (1923). In 1987, about 150 individuals, 108 of them females, were labelled. 65 (i.e. more than half) of the labelled females were seen again after labelling, 31 of them on 5 or more days. 17 of these females could be observed for two weeks or longer and 3 even for three weeks or longer. If an observation refers to a labelled bee, the individual number is stated throughout the text in brackets with "F" for females and "M" for males, respectively.

The entrance of nests were marked with small rods of aluminum (ca. 15 cm long, 3 mm diameter), labelled with a pen. They were always stuck into sand about 3 cm east of the exact entrance.

2.3 Meteorological data

The elementary meteorological data (temperature of the air and of the soil, cloud formation etc.) were recorded each day we visited the nesting site. In addition we used meteorological data of the weather service (Deutscher Wetterdienst) whose observation station at Dachau and Oberschleissheim is located about 3 or 6 km, respectively, from the nesting site.

3. The nesting site

3.1 Description of the nesting site

The nest aggregation is located near the village of Hebertshausen, close to Dachau, about 25 km north of the center of Munich. It lies in a sandy slope of about 25 x 120 m, about 475 to 485 m above sea level (Fig.1). The slope has an inclination of about 40 to 45 degrees with little steps and edges in some places. It faces the south almost entirely, and at its eastern and western side the ridge is protruding some meters, causing a somewhat amphitheatrical shape. Furthermore at the sides (predominantly at the western side) large trees shelter the area from wind, an important fact for the microclimate.

The vegetation of the slope is Mesobrometum, with *Brachypodium pinnatum* s.str. in the western part and *B. rupestre* and *Bromus erectus* in the eastern part. At the foot of the slope (southward), the vegetation of the ground is Artemisietea. A small beaten path passes through the nesting area.

The soil mainly consists of sand. The mean values of particle size in three probes from the nesting area are (right below the topsoil): 5 % clay, 20.6 % silt, and 74.3 % sand, of which 28 % is very fine sand (0.06 - 0.1 mm), 37 % fine sand (0.1 - 0.2 mm), 8.3 % sand (0.2 - 0.6 mm) and 1 % coarse sand. In the topsoil 8 % clay, 19 % silt and 73 % sand (24 %, 32 %, 16 %, 1 %, respectively) were found. At one place where searching flights of females (paragraph 4.3.1) were quite frequent, but rather few nests were built, the relative amount of clay (14 %) and silt (40 %) was larger (sand 46 %).

Two smaller parts within this area where the nesting density is extremely high were observed with special attention and within these areas the nests were labelled. - An area of about 4 m^2 in the lower third of the slope (a sandy area, Mesobrometum with *Bromus erectus*, *Festuca*

Fig.1: Nesting site of *Andrena nycthemera* near Dachau, southern Germany, facing towards west.

ovina, Arrhenatherum elatius) was mainly scrutinized in in 1984.

- The other area of special attention is a sandy pit with an inclination of about 5 degrees and its rim. It covers a total area of about 7.5 m^2 (Fig.2). About 50 % of the sandy pit is covered by vegetation (*Arrhenatheretum elatioris*). *Arrhenatherum elatius* and *Rubus caesius* are in the majority, further plants found in this area are *Carex hirta*, *Festuca ovina* agg.,*Poa pratensis* s.str., *Anthyllis vulneraria*, *Ononis repens*, *Melilotus albus*,*Vicia cracca*, *Achillea millefolium*, *Hypochoeris radicata*, *Silene vulgaris*, *Taraxacum officinalis*, *Daucus carota*, *Stenactis annua*, *Equisetum arvense*, *Cirsium arvense*,*Origanum vulgare*, *Galium album*, *Plantago lanceolata*, *Cornus sanguinea* juv. This area was mainly scrutinized in 1987.

Willows, the food plant for *A. nycthemera*, are present immediately adjacent to the nesting area (*Salix caprea*) as well as in the near vicinity (50 to some 100 meters distant). Within a distance of about 600 meters there is the narrow lowland forest of the river Amper.

Besides *A. nycthemera* there are many other species of bees to be found at this site. Remarkable is the occurrence of *Rophites canus* (several individuals caught by Dr.K.WARNCKE, July/29/1986), a very rare species that lives exclusively in extremely warm habitats (cf.STOECKHERT 1933, 1954; WARNCKE 1986; WESTRICH 1989). Conspicuous are hundreds of nests of *A. vaga*.

3.2 Preferred nest places and number of nests

The female bees prefer sandy places with scanty vegetation for nesting. They build their nests as well into the flat soil as into small vertical slopes or under little overhangs (cf. Fig.2). Thus some of the entrances of nests may seldom be in the direct sunshine. Often the entrance is partially hidden beneath dry leaves or a tuft of dry grass. The females seem to prefer rugged soil to smooth horizontal places. In two cases it was observed that a female apparently lived in a nest which had been used before by another female. Since we did not observe the bees within the nest itself, we can only state that different bees used the same entrance.We never observed, however, that two or more females used one nest at the same time.

In the sand pit at its rim we labelled 99 nests of *A. nycthemera* (plus 10 nests of *A. vaga*). It should be noted, however, that at least 13 of these were second or third nests of the same female. The distribution of the nests was far from being homogenous: Some parts of this area were rather free of nests and others were crowded. Several nests were very close to each other (about 5-10 cm), in one case (F44 and F04) the distance between the entrances of the nests was only about 1-2 cm. In 1984 within about 1 m^2 of another place 12 nests of *A. nycthemera* were labelled (plus 40 nests of *A. vaga* and one of *A. fulva*). We estimate from this a total number of about 500 to 1.000 nests in the whole nesting aggregation. We

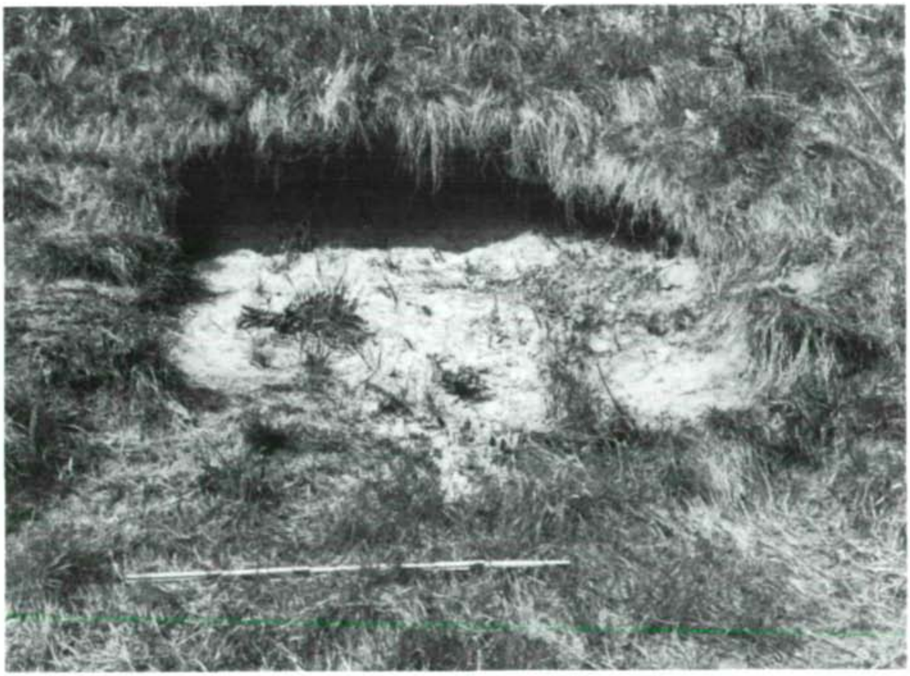


Fig.2: Sand pit in which *Andrena nycthemera* was observed with special attention in 1987. In this area about one hundred nests of *Andrena nycthemera* were recorded. Meterstick in the foreground: 1 m.

could not notice any alternation in population size during the years.

4. Behavioral pattern

4.1 Behavior of males

4.1.1 Crawling and inspecting holes

One of the most common behavioral patterns of males is crawling on the soil, especially when it is cold or cloudy. Frequently the antennae are bent downwards, almost touching the sand, or they are moved up and down. Quite often a male will search again and again at one particular spot. If it is warm and the sun is shining, the crawling is hectic and often interrupted by short flights (typically ca. 25 cm - 1 m). The males inspect every little hole. Either they just poke their head into the entrance for a moment or they enter completely and come out backwards after some seconds. Sometimes they stay in a hole for 5 minutes or even longer.In such cases they emerge from the hole with the head first and almost always clean their antennae immediately after coming out of the hole. It also happens, that a male emerges from a hole, crawls around a little bit (about 10cm) and then reenters the hole.

4.1.2 Digging

While crawling on the soil, the males often dig pits in the sand which are about 1/2 cm in diameter and about 1/4 cm deep. The sand is scraped off with the mandibles and the anterior legs. The anterior legs - and sometimes the middle legs - push the loose sand bachwards.The posterior legs stabilize the bee. Quite often different males dig at exactly the same place one after another or simultaneously side by side.

4.1.3 Aggressive behavior

Males aften compete for females to copulate with (cf. paragraph 4.2) or for a place to dig. Usually one male seems to push the other one away. Sometimes, however, real fights occur in the course of which the bees bite one another with the mandibles, then they (both) roll about. In one case (Apr/4/87) three males were competing for a hole and biting each other several times with the mandibles until one of them, after about 10 minutes, succeeded in chasing the other ones away.

4.1.4 Patrolling flights and sitting in the sun

Usually the males of *A. nycthemera* fly very close to the soil (about 2 to 10 cm) over the nesting area. They do zigzag routes or, less common, large loops. In the first part of the season the males tend to fly in smaller loops than later in the year. Alternating with their flights the males frequently stop to crawl around, dig, or sit down on leaves or stalks. For resting, they prefer sunny places like patches of dry sand or pale leaves, especially in the first part of the season, when it is rather cold but sunny. At low temperatures the males tend to fly close to the soil and mostly perform short flights of only some meters. When it gets warmer they fly higher, faster, and perform longer routes. They may fly up to an altitude of about 1 m.

4.1.5 Territorial behavior

Although the males do not have fixed patrolling routes they are seen again and again in the same area. Very often a male keeps crawling around and digging within a square meter for about half an hour and may be seen at the same place the next day again. In one case, for example, 10 males were labelled within a sandy area of about 5 m^2, some meters away from the main observation area. During the next four days these males were seen again always at their original place or at a maximal distance of 5 m from it. Another male (M10) was for example labelled on March 29th,1987 and seen again at the same place several times on 6 consecutive days. In the contrary to descriptions in *Andrena chrysosceles* (HAAS, 1960) we could not observe any behavior which may be interpreted as scent labelling.

4.1.6 Spending the night

The males spend the night in the soil. In the evening they can be observed to enter holes, the majority of which are probably nest entrances. Some males can be seen to burrow themselves at an existing nest entrance. In the early morning male bees can be found within the holes about 1 to 3 cm below the surface.

4.1.7 Pouncing

A most conspicuous behavior of males is that they pounce on females, trying to mate. They pounce on any female no matter whether it is sitting, crawling or digging. They even pursue females in the flight or follow them into their nests. They also try to copulate with dead females or ones with pollen in their flocculus. Males also often pounce on other males or other dark objects like buds, small leaves or pieces of wood. Usually they realize their error quickly (less than 1 second) and leave.

4.2 Mating

Altogether we could observe nine copulations, three of which were observed in 1983 on one day (Mar/21), shortly after another. All others were seen in 1987, each on different days (Fig.9a). Two copulations were observed from the beginning, these lasted about 2 or 4 minutes, respectively. In two cases the copula obviously had begun within a burrow, since the female emerged from a nest entrance in copula with a male on her back. In one case (Apr/6/1987) the male had entered the hole just five seconds before.

The head of both partners point in the same direction, the male is on top of the female. First the male clasps thorax and abdomen of the female with its legs, then it bends the abdomen downwards to insert its genitals. Some males then raise their body vertically keeping contact to the female only via the genitals. Often the male produces some pulses of a buzzing sound which seems to be evoked by moving the wings and is accompanied by rhythmic contractions of the legs. Sometimes the metasoma is contracted a couple of times in a pumping motion. The female usually does not move during the copula, only in one case its posterior legs were wiping the abdomen. In one case (Mar/27/1987) two males competed on the back of one female, the female first tried to repulse both males but then copulated with one of them, and the other one flew away.

Usually the females terminated the copula by scraping the male down. Afterwards they rested for about a minute before they flew or crawled away. In one case the female was just digging before mating and it continued digging immediately afterwards. In three cases the males were captured after mating to see whether they would survive (cf. MICHENER and RETTENMEIER 1956). They all survived for 48 hours and were then released.

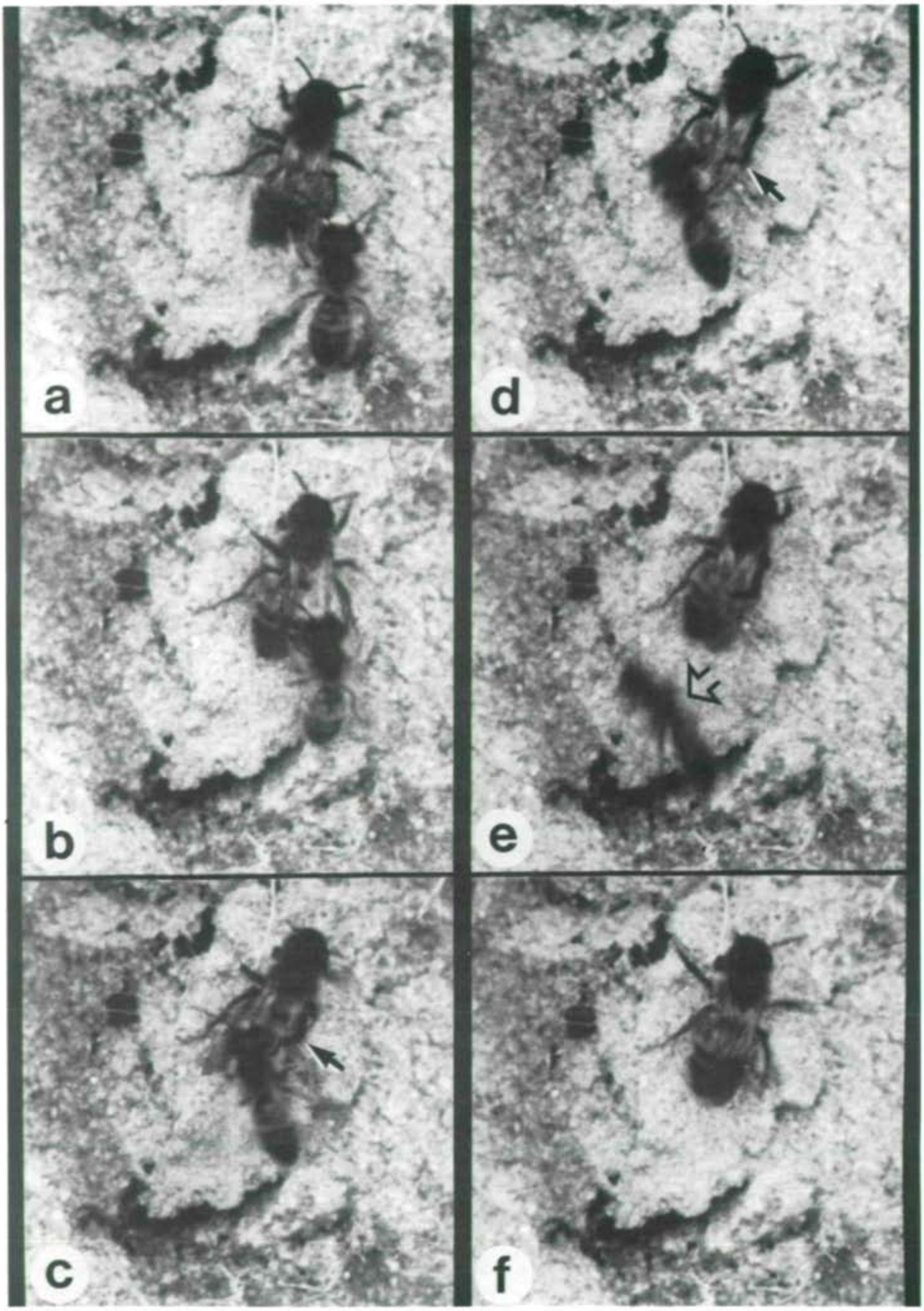
4.3. Behavior of the females

4.3.1 Searching for a nest site, searching flights

Especially in the beginning of the season a great number of females of *A. nycthemera* can be observed to perform a typical kind of flight: They fly in many loops or zigzags over the nesting area, mostly at an altitude of about 1/2 to 1 m over the ground, alternating with flight courses very close to the ground. Certain parts of the area are frequented more than others, but these places are not always identical to those where the nesting density is especially high. In one of these preferred places the soil was analyzed and found to contain a large percentage of clay and silt (cf. paragraph 3.1).

The flights may often be interrupted by crawling around (often with lowered antennae) and a little scraping or digging. In many cases a female will inspect a certain spot (e.g. some 10 x 10 cm) for about 10 minutes or more, alternating with short flights.

Fig.3 (p.389): A female *Andrena nycthemera* repulsing a pouncing male. a and b: the male is approaching in flight. c, d: the female is repulsing the male with the right posterior leg (arrows). e: the male flies away (oppen arrow). f: the female has put its right posterior leg on the ground again. Single frames from a film sequence (0.5 s), with the following numbers in the film: 13.613, 618, 621, 624, 625, 630.


a
b
c
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f

4.3.2 Repulse the pouncing males.

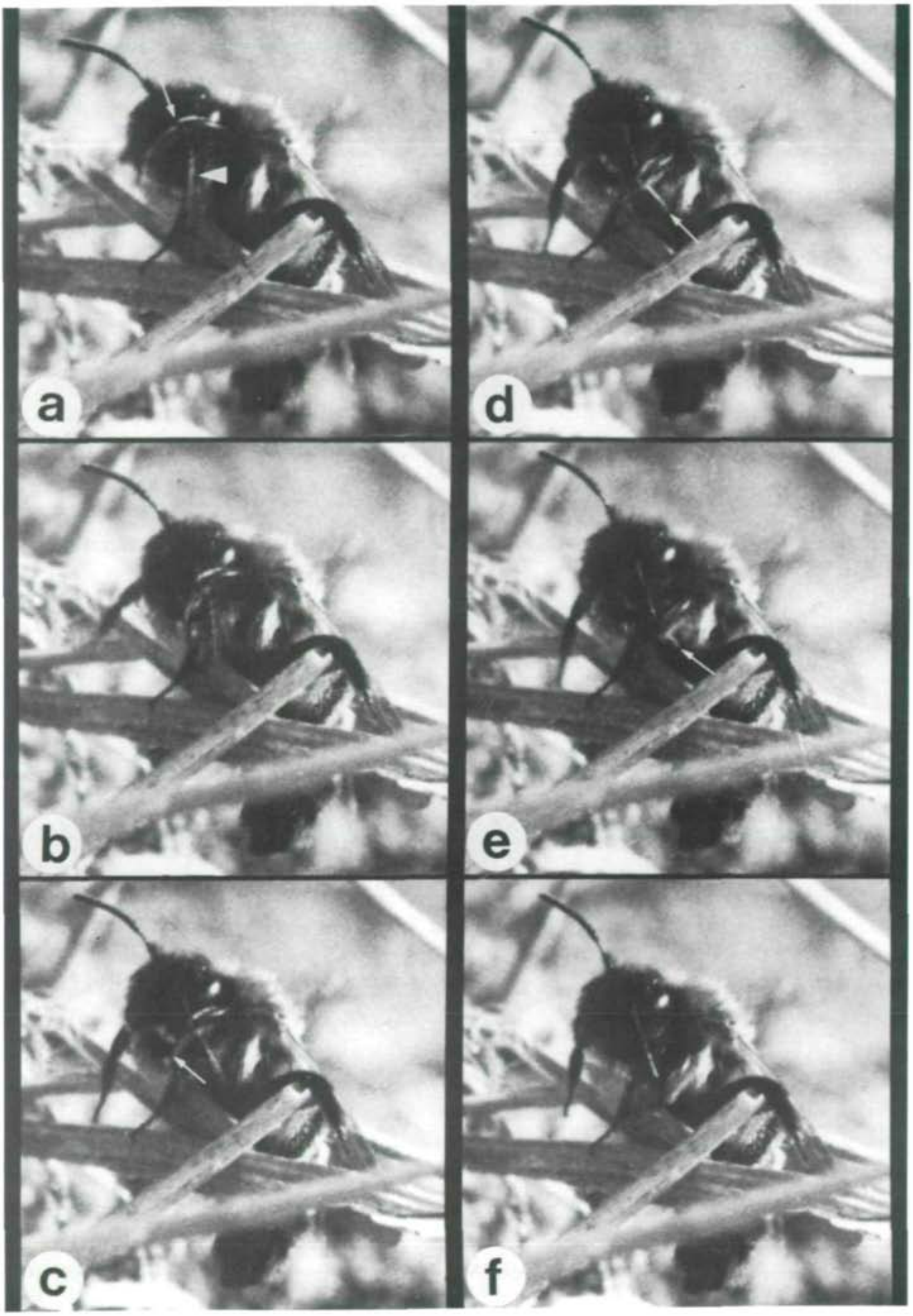
Very often the males pounce onto the females (paragraph 4.1.7), these, however, are usually not receptive and repulse the males in most cases (Fig.3). Any type of female behavior may be interrupted by this. The females crawl away, often beneath grass blades or leaves to strip off the males which try to mount them. Often the females roll over the sand very quickly with the males on top. Sometimes the females use the middle and/or posterior legs to keep the males away (Fig.3). It seems that even during the flight females accelerate or perform sharp turns to escape pursuing males.

Sometimes unsuccessful mating attempts are initiated within the nests. For example, it was observed (Apr/6/1987, 11:30) that a male entered a hole and some seconds later a female came out with the male on its back. The female tried to scrape it off with the posterior and middle legs, but the male clinged to the back with all legs. It took almost two minutes untill the female got rid of the obtrusive male.

4.3.3 Spending the night

Before the females have constructed their own nests they, like the males, spend the night in holes which probably are mostly old nests. Sometimes, however, in the eveneing they burrow themselves into the sand at a

Fig.4 (p.391): Female *Andrena nycthemera* scraping the left antenna. a: the right foreleg is lifted over the antenna; arrow: tibio-tarsal joint,with the antenna cleaner beneath; arrowhead: lowered left antenna. b: the flagellum is inserted into the antenna cleaner. c: beginning of the stroke, arrow points to the praetarsus of the left (cleaning) leg, beneath it is the left middle leg. d and e: the flagellum is cleaned, the part of the flagellum which is not yet cleaned is indicated by an arrow. Note that it is bent upwards. f: end of the cleaning stroke. Single frames from a film sequence (0.6 s), with the following numbers in the film: 12.541, 545, 546, 548, 550, 555.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place which is quite obviously not suitable for a nest, like i.e. a lump of earth.

4.3.4 Grooming

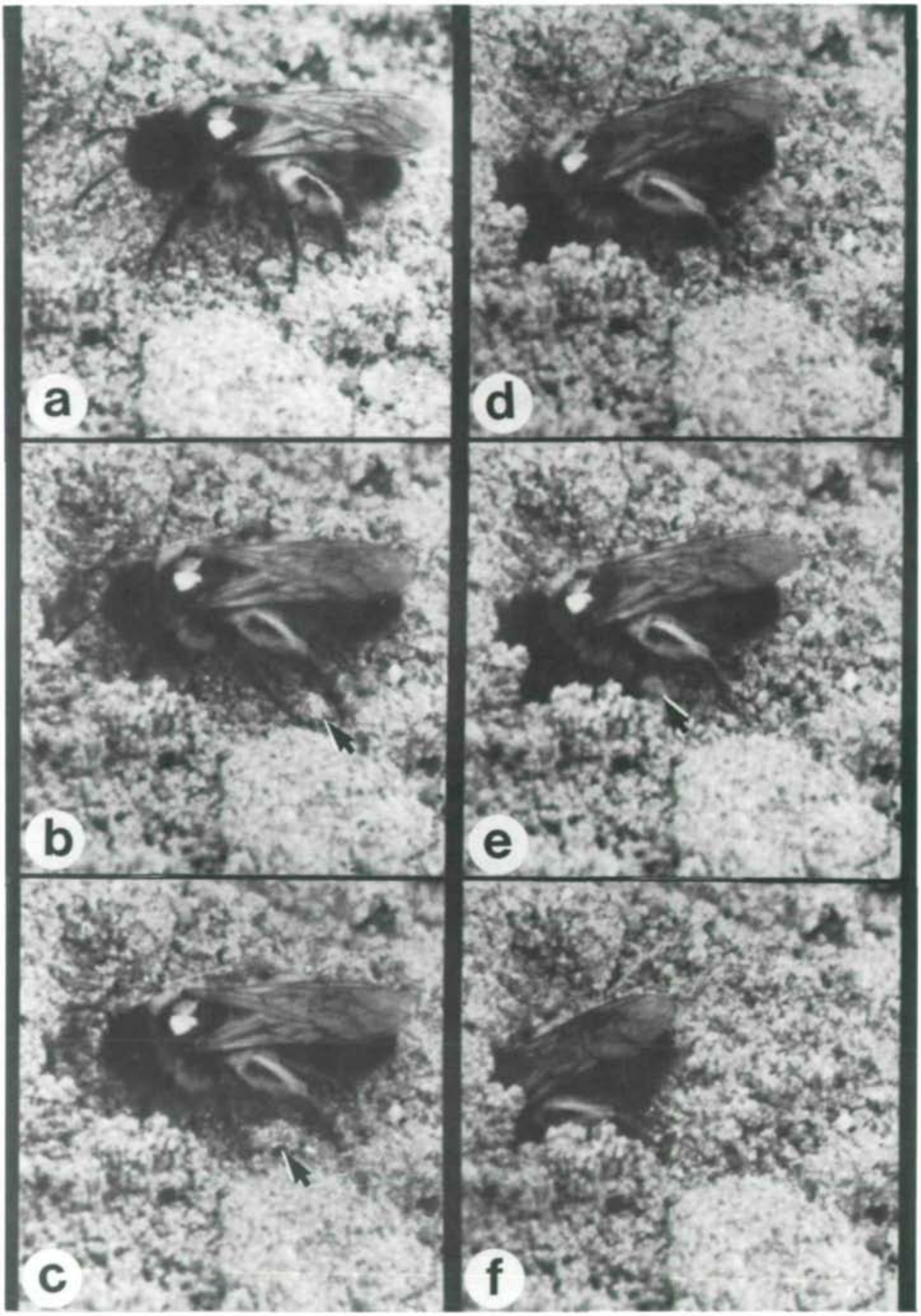
Any other behavior can be interrupted by self-cleaning behavior. Since single cleaning procedures are quite fast, they were usually not recorded. We did not find any difference to the grooming behavior previously described for other species of *Andrena* (JANDER 1976).

By analyzing film sequences of the cleaning of the antenna it is seen that the first part of the cleaning stroke (when the basal part of the antenna is cleaned) is clearly faster than the second half of the stroke, cleaning the distal part of the flagellum (cf. Fig.4: the time elapsed between frame d and e is 2/24 s, the time between e and f is 5/24 s). Similar to the situation in the honeybee the distal part of the flagellum is bent upwards, and the tibio-tarsal joint is bent strongly (SCHÖNITZER and RENNER 1984).

4.3.5 Digging and building the nests

Digging is accomplished by biting the sand with the mandibles to loosen it (Fig.5). With the anterior legs the bees scrape the sand out of the depression and shove it under the body. Then the middle legs push the sand further backwards. The anterior legs scrape in a much faster rhythm than the middle legs. The posterior legs stay remarkably immobile, they are sometimes stretched out perpendicularly from the body. When the animal is already partly dug in, it turns the whole body, usually performing one or two complete turns counterclockwise. In few cases they do half a turn to the right, then to the left etc. The loose sand is pushed out of the burrow

Fig.5 (p.393): Female digging into its nest with pollen on its posterior legs. The two patches on the thorax are labels. Note the lowered antennae in a and b. a is somewhat differently trimmed than the following fotos.Arrows point to grains of sand just being pushed out. Single frames from a film sequence (4.8 s), with the following numbers in the fim: 15.063, 071, 074, 110, 113, 178.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with the abdomen and/or legs (Fig.5).

Once the bees have completely disappeared in the soil their digging activity can be seen by the movement of the soil and the periodical discharge of sand. The digging is alternating with intervals of no visible activity. The sand is piled up and forms little tumuli at the entrances, these may be up to about 3 cm high and have a maximum diameter of about 10 cm. Usually they are washed away by the next rain.

During that time the females rarely leave their nests but dig for about 2 to 4 days. Afterwards they supply the nest with pollen. It seems that the females prefer days with bad weather to work in the nests. It happened that bees dug for one day only before bringing pollen into the new nest (F56, Apr/14/87; F84, Apr/10/87), on the other hand, a bee (F93) had been living in a nest for 5 days before it brought the first load of pollen in. Sometimes a female continues digging within its nest into which it has already brought pollen, and it supplies the same nest with pollen later (e.g. F23, F17). Or a bee digs at a new site for one day, but then takes care of the former nest again (F01, 24.4.87).

4.3.6 Duration of living in a nest

Usually the females spend about 5 to 10 days in the same nest, i.e. were seen to emerge from it or enter it (with or without pollen loads). This is recorded in 23 cases, but lack of observations possibly biases these results, thus the real times may be longer in some cases.

Some bees have been observed to live in a certain nest for a remarkably longer time. For example the bee F03 was altogether seen on 11 days out of a total of 26 days. The first and the last time it was seen (Apr/6, May/1/87), it could not be related to a nest, but at 9 days (between Apr/9 and Apr/28) it was seen to enter and/or emerge from the same nest. Thus it may be concluded that it used this nest throughout the whole period of three weeks. Other bees were recorded to live in one nest for 11, 12, 13, 14, 15 (two cases), 17, and 18 days respectively.

On the other hand, it should be noted that some bees spend only few days in the same nest. For example, the female F44 lived in three of its nests for only one or two days (possibly 3 days, due to lack of observation).

4.3.7 Number of nests per bee

Of those 17 bees, which could be observed over a period of more than two weeks, 10 were noticed to bring pollen into one nest only; one bee (F03, cf.above) was observed to inhabit one nest for about three weeks. Four bees provisioned two nests, two bees three nests and one (F 44) even four nests.

The bee F44 inhabited 6 nests, the maximum number in our investigation, and it brought pollen into four of them. All those nests were within the above described sandy pit.

4.3.8 Emerging from the nest

When females emerge from the nest, they come out with the head first and usually remain in the entrance for some time (about 5 seconds or longer, cf. next paragraph). Typically they walk some centimeters southwards (downhill) and then take off. The bees which nest under an overhang (thus the entrance ia always in the shadow) usually crawl to a sunny place and stay there before they take off. Sometimes females fly directly from the entrance to a blade of grass or a pale leaf and stay there for about 1/2 to 2 minutes before leaving the area. Predominantly at the end of the season, when the vegetation has grown, bees frequently climb the top of a stalk or blade of grass and start from there.

4.3.9 Sitting in the entrance

Especially if the weather is too cold or too cloudy to fly (cf. paragraph 5.4), the females often sit in their nest entrances for quite some time. They often remain quite immobile for several minutes with the head in the nest entrance and only the antennae projecting outside. At times the majority of females in the nest aggregation may be seen sitting and waiting in the entrance. When the temperature is rising the animals leave their nests; if it stays cloudy and cool they return into the burrows after some time. This behavior, however,is not seen during the first part of the season (i.e. before the females have adopted their own nests).

4.3.10 Closing the nest entrance

Before the females take off from their nests (e.g. for collecting food) they usually close the entrance of their nests. With the posterior part of their abdomen still in the entrance, the females shove loose sand under their body with their anterior legs and push it into the hole with the middle legs. Sometimes females turn around afterwards and brush some sand over the entrance with the anterior legs. In some cases a small depression is still visible indicating that the bee has left the nest and closed it from the outside. At times, however, females do not close their nest entrance after emerging. This is especially frequent for bees nesting in a vertical slope. If the closing procedure is interrupted, for example when the bee is falling and rolling down the slope, the bee does not continue to close the entrance, but take off.

Usually the bees also close their nest entrance when they return into the nest. They first dig themselves into the loose sand and then push the sand backwards with the abdomen. Sometimes, however, in about 5-10% of the cases, females enter their nests and leave the entrance unsealed.

4.3.11 Orientation flights

After take off the females frequently perform some loops which obviously are orientation flights. Immediately after take off they turn around in the air to face the entrance of the nest. In this position they have the same view as at the landing approach. For a moment they stay in the air (about 5 to 10 cm high), then they fly some turns which are about semicircular, first narrow and then larger, until the bees leave the nesting site with a large loop. Similar orientation loops are seen before landing.

Especially during the first days in a new nest, the females perform long and exhaustive orientation flights.

After some days they only do few loops. If, however, the immediate surroundings of the nest have been altered (by external events, e.g. someone stepping on the nest entrance) the bees once again perform extensive orientation flights.

4.3.12 Returning into the nest

Especially in the beginning of the season the females do not always succeed in finding their nests at once. When they come back from collecting pollen or from feeding they usually fly in loops or zigzags for some minutes at an altitude of about 1 meter. Then they go deeper (some 5 to 10 cm) and scan a small area (about 30 x 30 cm). Sometimes they stay in the air for a moment before they land and crawl to the entrance of the nest. After some days the bees find their nest entrances usually within a few seconds after a rudimentary orientation loop. They land close to the entrance (within a few centimeters) and dig in very fast.

The females nesting in a vertical slope or under an overhang usually do not fly directly to the entrance, but land further down on the flat ground. From there they crawl up the slope clumsily with buzzing wings. Often, this is followed by tumbling and rolling downwards over the loose sand then again crawling up and so on. Generally we had the impression that the females on the vertical slope had more problems finding the entrances of their nests than those on the flat ground. Sometimes, however, they fly directly to the entrance hole and enter it very quickly.

The returning to the nest by the females seems to be somehow synchronized. Quite often there is not a single bee to be seen at the nesting site for several minutes and then suddenly several bees return to their nests at the same time. This is especially frequent at the late afternoon in the beginning of the season.

4.3.13 Searching the entrance

The female bees find the appropriate site of their nests right away, but often they have problems in finding its entrance. So they crawl around and search all over the sand. Lowering the head they bend the antennae downwards, touching the sand with them. For a time they will dig, sometimes burrowing themselves in the soil and staying there for up to about 10 minutes. Occasionally they take off again, leave the nesting area, stay away up to half an hour and return again with a new orientation flight.

One female (F07, Apr/17/1987) was observed twice to search its nest entrance digging at a wrong place although the entrance of its nest was open and undisturbed. Such a search may even take some hours. One bee (F18, Apr/18/1987) was seen to search again and again at the same place almost for a whole day (about 6 hours) and for about another two hours on the following day. Then it began to rain and the bee was not seen again any more.

Nevertheless it should be noted that the great majority of females find their nest within only a few seconds.

4.3.14 Provisioning

The number of pollen loads per day which the females bring into their nests obviously depends very much on the weather. There are many days, especially at the beginning of the season, when no more than one load of pollen is brought in by the females. In the afternoon of such days, several females can be seen within a short time (about 15 minutes) to return into the nests with pollen. Early in the season, even if the weather is good, most females bring only one or two loads of pollen.Later at the peak of the season, the standard is three pollen loads a day, ranging from one to as many as six loads. Towards the end of the season the number of pollen loads goes back to one or two again (Fig.6).

The average duration of pollen collecting flights is about 30 minutes, but it may be as long as 100 minutes ($\bar{x}$ = 38.45 min; σ = 17.7; n = 60; Fig.7). After returning with pollen, the bees usually stay in the nest for about 20 to 75 minutes, sometimes up to 145 minutes ($\bar{x}$ = 54.9; σ = 77.0; n = 72; Fig.8).

In many cases the females also leave the nesting area for some time and return to their nest without any pollen. These flights are interpreted as self-provisioning flights and usually last for 10 to 65 minutes with a mean value of about 30 minutes ($\bar{x}$ = 29.25; σ = 17.25; n = 12). Towards the end of the season the duration of these flights increases (95, 105, and twice 150 min respectively, Apr/23 and Apr/24/1987).

4.3.15 Aggressive behavior

In seven cases agressive behavior of females has been

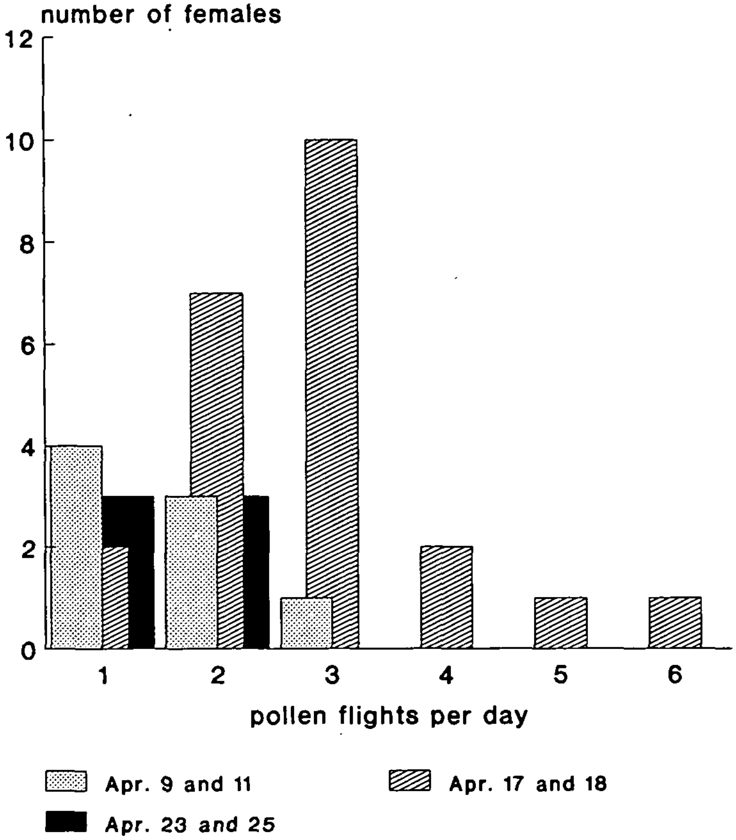


Fig.6: Number of pollen flights per day: at the beginning, in the middle and at the end of the season. Each set of columns counted at two days with good weather and an observation of at least 8 hours.

observed. In all except one case (see below) the reason was clearly competition for a nest caused by a female which occupied - or tried to occupy - the nest of another female.

In two cases the confrontation was rather short (about 1 to 2 minutes): A female returned to her nest with pollen, found the nest occupied by another female, nevertheless entered the nest and pushed the intruder out. After the fight the winner stayed in the entrance of the

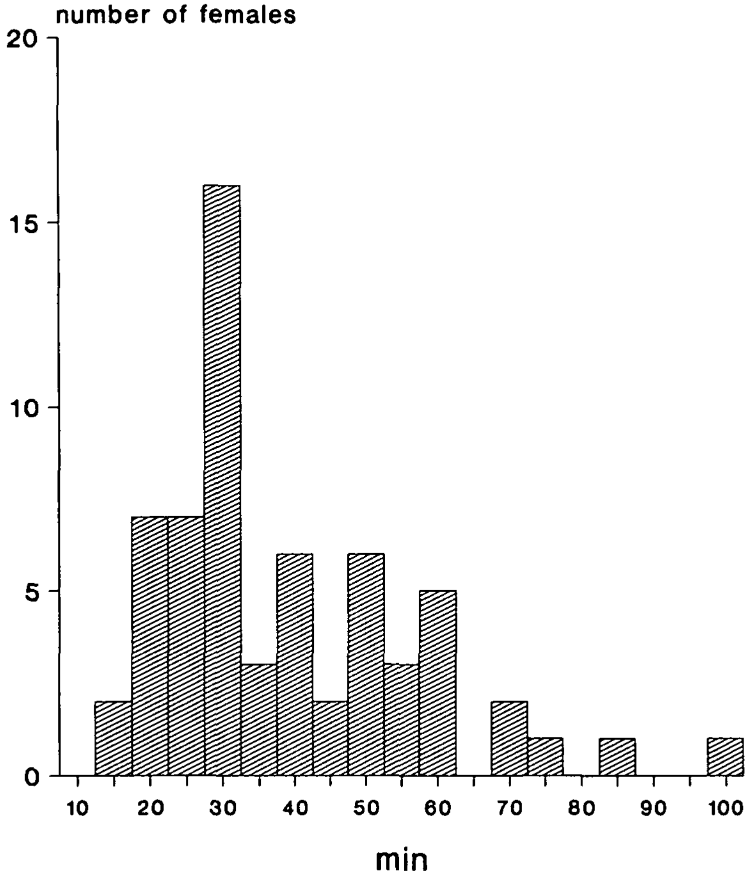


Fig.7: Duration of pollen collecting flights of *Andrena nycthemera*.

nest, sticking the head out of it for at least 20 minutes as if now guarding the nest.

In another case the bee who returned to its nest (F94, Apr/8/87) tried to enter it several times for about 10 minutes but was pushed out again and again. Finally it succeeded to enter the nest and about 4 minutes later the entruder (F50) came out. Then this bee (F50) was repeatedly hindered from entering the nest again. Some minutes later it began to dig somewhere else, first at a

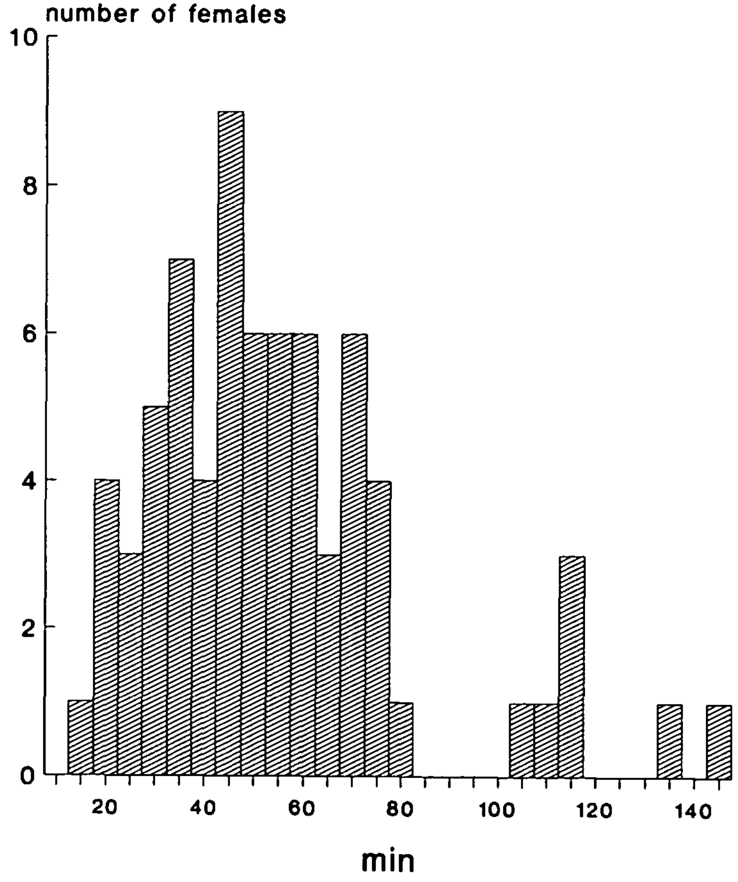


Fig.8: Length of time spent in the nest by females of *Andrena nycthemera* after having brought pollen into it.

place which was obviously unsuitable for a nest, later at a possible nesting site. Two days later this bee (F 50) was seen to take care of a nest at yet another place. The other female (F94), however, was not seen any more. In a similar case, in which the whole conflict took about 20 minutes, the intruder was the winner.

In two cases a female of *A. vaga* occupied a nest of an *A. nycthemera* female. The larger *A. vaga* was the winner in one, and the smaller *A. nycthemera* was the winner in the other short struggle.

In one case, which took part at the very end of the season (Apr/27/87), two females (one with, the other without pollen load) were searching and digging around at a short distance of one another for about 45 minutes. They did not dig at a certain place like they usually do when searching a nest entrance but within a larger area (about 15 x 15 cm). They faced one another with open mandibles and raised forelegs.They thretened and bit each other with the mandibles, while rolling down the slope. After this they separated and again searched and dug around until, 30 minutes later, a similar confrontation took place.

The fights in which a female occupied the nest of another bee took place between 8th and 11th of April which is in the middle of the season, shortly after the provisioning of the nests had begun. In one case (Apr/9/87) the invading bee (F44) had already had another nest before. Only in one confrontation (at the end of the season: Apr/27/1987) both bees were outside the nest.

4.3.16 Irregular behavior at the end of the season

At the end of the season, the last days in April and the first ones in May, the females more and more show

Fig.9 (p.403-404): Frequency of different behaviors of *Andrena nycthemera* during the season of 1987 in relation to important meteorological data. a: behavior of males, b: behavior of females. Dots below the data scale indicate days without observation. Only on those days marked with large dots the weather was good and the bees were very active. Refer to text for further explanation.

Fig.9a (text p.402).

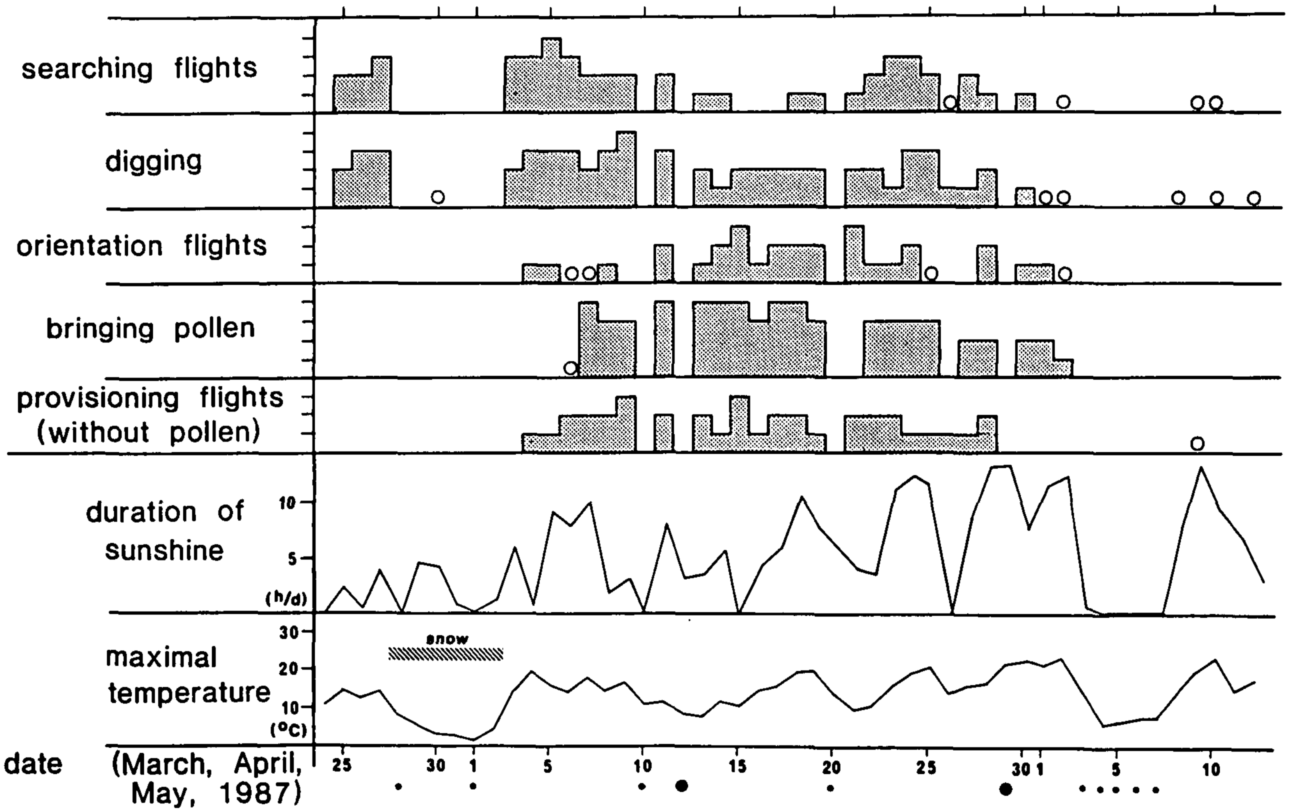
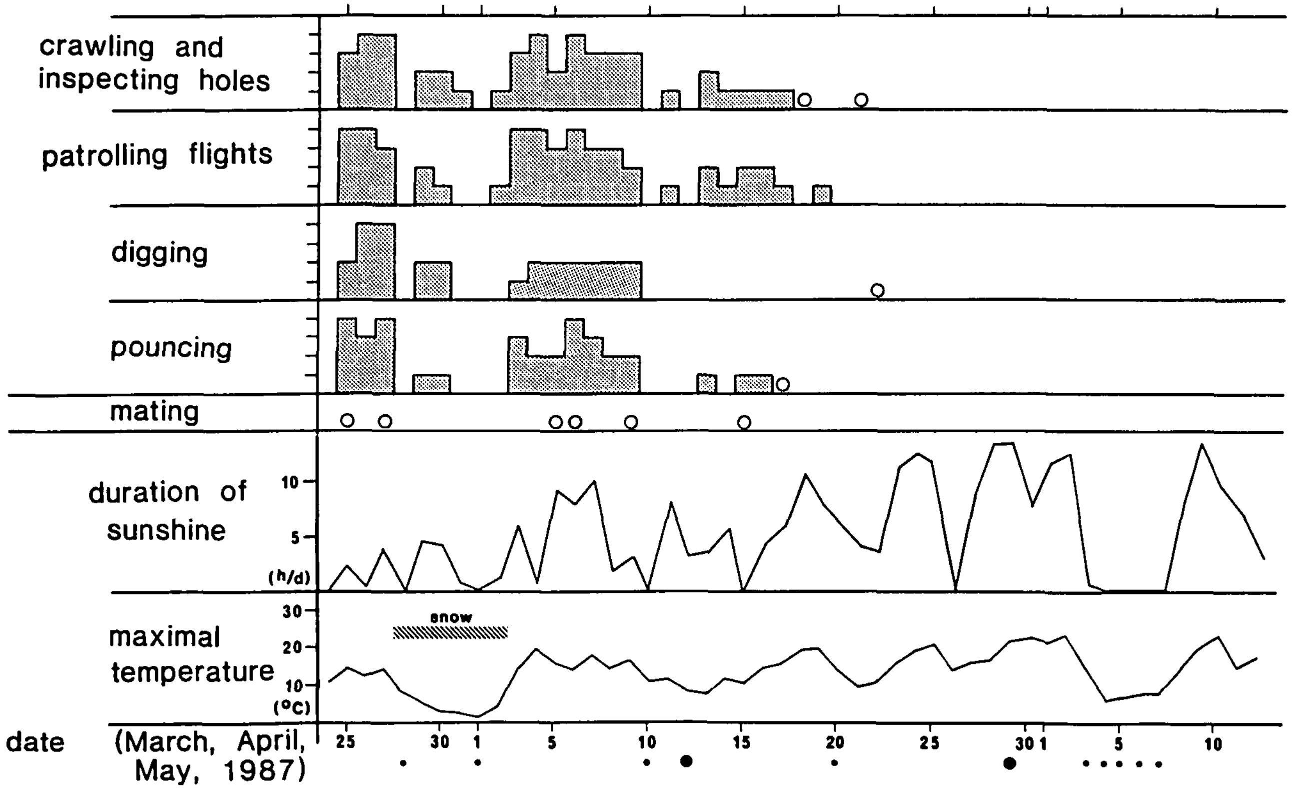


Fig.9b (text p.402).



some unusual behavior. It resembles the search for a nesting place and the digging at the beginning of the season, but is performed less consequently and efficiently. Any occupation is interrupted after a short while, nothing seems to be performed completely.

Frequently the females can be observed to move sand backwards with the anterior and middle legs, but they do not keep to one spot as when digging or closing the nest entrance. Rather they move about (mainly backwards) and scrape over the sand, but without any visible purpose. It seems to be an uncoordinated rudimentary diggiung behavior.

5. Seasonal history and dependence on weather

As the nest aggregation was observed in 1987 most consequently throughout the whole season we describe the seasonal history of this year in detail with some supplementary notes from the other years. If not stated else this chapter refers to the season from 1987. The occurence and frequency of significant behavioral patterns is compiled in Figure 9a and b. The frequency of observed behavioral patterns is indicated in five levels:

- Circles are given if a behavior was seen only once a day.
- One square: the corresponding behavior was seen 2 to 3 times per day.
- Two squares: the corresponding behavior was seen about once an hour.
- Three squares: the corresponding behavior was seen several times per hour.
- Four squares: the corresponding behavior was seen several times within a quarter of an hour.

Despite these definitions it could not be avoided that in some cases the presentation of the data in Figure 9 is ambiguous. For example, if the bees were observed for about three hours only and a behavior was recorded three times, we could either make the column one or two squares high.

5.1 Beginning of the season

After hibernation in the soil the *A. nycthemera* emerge between the middle and end of March. The first bees of the season were seen on March 21st 1983, March 16th 1984, March 24th 1985, March 25th 1986, March 24th 1987, March 19th 1988, February 23rd 1990, respectively. In some years the observation started on days mentioned above (1983, 1984, 1986); since the weather conditions on the previous days were bad, i.e. cold and rainy, it can be assumed that the bees were hardly active on those previous days.

The earliest date of emergence ever observed was in 1990, a year with very warm winter, extremely little snow, and unusually warm days in February. In 1987 the winter was unusually long and cold with temperatures below 0°C until March 20th. Until this day the soil was still covered with snow. From March 21st the soil was frozen only in the mornings. March 24th was the first day without ground frost, and it was the first day when the bees were seen.

In 1984 on 16th and 18th of March only males were seen, and the first females were observed on March 19th. In the other years both males and females were seen during the first days.

5.2 Activity of males

During the first three days of the season (Mar/25 to Mar/27, 1987; Fig.9a) there are about 3 or 4 times more males than females to be seen. The males are very active during this time, their main behavioral patterns are searching, digging and pouncing. After the relatively warm days it became cold again and snow fell (Mar/28 to Apr/2). During these days the males were less numerous and less active, especially flying was rather rare. But they could be seen searching on the soil as soon as the sun was out for a short while.

The males were numerous and very active again throughout the next week (Apr/3 to Apr/9) when the weather was warm again. This period of time may be regarded as the peak of male activity and number of individuals at this season (for Apr/5/87 see paragraph 5.4).All male behavioral patterns could frequently be observed during this time.

After two more cool days (Apr/10 and 11) the number of males decreased clearly. During this last period of male activity (Mar/11 to Mar/17) no more digging was observed. Most males observed within this period were active on flat ground in about 10 m distance of the main observation area. It was at this place where at the beginning of the season the snow had melted later than at the slope where most nests were found.

The very last active male was seen on April 22nd, 1987 and April 12th, 1984. Thus the whole duration of male activity is only about 30 days.

Remarkably, however, the matings observed in 1987 were distributed over almost the whole period of male activity. In 1983, however, three copulations were observed which all took place on the first day of the season (Mar/21/1983).

5.3 Activity of females

During the first three days of the season (Mar/25 to (Mar/27; Fig.9b) the females concentrated on the search for a nesting site, digging and repulsing pouncing males. The latter behavior is not included in Figure 9b, but its frequency is the same as "pouncing" of the males (Fig.9a).

During the next cold week (Mar/28 to Apr/2) the females were practically inactive and hardly came out of their holes. On April 3rd, the first warm and sunny day after the cold period, the females were active again with the same behavioral pattern as described above. New patterns of behavior could be observed during the next two days (Apr/4, Apr/5): orientation flights, and provisioning flights. Both these indicate that some females now have acquired own nests in which they live. The number of orientation flights is, however, rather low until April 10th.

On April 4th the blooming of the willows, the food plants (HAMANN and KOLLER 1956, STOECKHERT 1954, WE-

STRICH 1989b) which are abundant near the nesting site, began. On April 6th a first female was seen with pollen, and already on the next day several, at least 20, females brought pollen to their nests. On the next day (Apr/8/87, with only little sunshine) less females brought in pollen. The peak of pollen flights was in the week between April 13th and 19th: on April 15th, 17th, and 18th the number of pollen flights recorded was 51, 63 and 82, respectively, in the sand pit. These large numbers are also due to the fact that many bees perform several pollen flights a day. Later in the season, after April 25th there are only few pollen flights.

During the time of maximal pollen collection also the number of orientation flights increases while searching for nesting sites was rare. At the end of the season (Apr/23 to Apr/25) the females remarkably often performed searching flights as they did at the beginning of the season. Digging activity was observed during the whole season, but it seemed to be especially frequent at the beginning of the season (Apr/4 to Apr/11/87). The number of provisioning flights (i.e. flights where the females return to their nests without pollen) varies considerably from day to day and does not seem to depend on the weather.

At the end of the season (after Apr/25) the bees show some unusual behavior. On these days digging and flight actions (included in Fig.9b) are only rudimentary or ineffective (cf. paragraph 4.3.16). At those days a great number of dead or dying bees may be found in the grass. They are often eaten by ants. On April 30th only about 10 bees were still living within the observation area. The last *A. nycthemera* female with a pollen load was seen on May 2nd, and the very last living female on May 12th, 1987. The total period in which females were active thus lasted 49 days of which only 21 days were for provisioning the nests with pollen.

5.4 Daily activity and dependence on the weather

On sunny mornings the first bees leave their burrows at about 8:00 to 8:15. At this time the temperatures are usually about 8° to 10°C. Usually the males are acrive earlier in the morning than the females.

At air temperatures between about 8° and 14°C the bees generally fly only if the sun is shining. When the sun is out there is a lot of activity in the colony with many bees flying at sunshine, a few minutes later, however, when a cloud has come, only very few or even no bees will be flying, although the air temperature has not altered significantly. These activity changes may happen several times per day due to the unsettled weather conditions typical for March and April. At such temperatures the females tend to sit in the entrances of their nests waiting for sunshine, the males just sit anywhere in the grass or in any holes. It is important to keep in mind that in the first days of the season (until Apr/4/87; Fig.9) the activity of the bees depends very much on the sunshine since during those days the temperature hardly exceeds 15°C. If the air temperature is about 15°C or more the bees also fly on cloudy days (e.g. Apr/4, Apr/15/87; Fig.9).

Usually there is very little activity on rainy days. The bees hide in their holes as soon as the clouds become very dark or it starts raining. In some cases, however, females came back from a provisioning flight after it had begun to rain already. One day with an air temperature of 19°C quite a few flying bees where observed although is was slightly raining (Apr/8/87). Sometimes male bees are found to sit around in the grass during rain.

The male period of daily activity exceeds the female one both in the morning and in the evening. On sunny days the females tend to come back to their nests at about 17:30, some females, however, return later and may return to their nest as late as 18:15 when there is no more sunshine at the nesting site.

On a day with unusually warm, sunny weather (Apr/5/87; Fig.9a) it was observed that the males disappeared around midday. They emerged from the nests at about 8 o'clock, with sunshine (about 10°C air temperature). In the morning they were abundant and active around the nesting site, later their number decreased and the last male was seen at 11:45 when the temperature had risen to 22°C. They were seen again after 17:30 when the temperature had fallen again to 16°C. Then they disappeared at about 18:15 in the evening at an air temperature of 12°C.

On very warm days at the end of the season (May/1/1987 and May/2/1987) it seemed that females avoided to dig in the hot sand as if it was too hot. Very often they landed close to their nests, did not dig in as usual but flew away after some moving back and forth. The temperature of the sand surface was 41°C. The bees which had their nests under the overhang (i.e. in the sand), however, were active as usual.

6. Parasites

The cuckoo bee *Sphecodes pellucidus* has been observed frequently close to the nest entrances of *A. nycthemera* from the middle of April until about middle of May. First they predominantly crawl over the sand at the nesting area or fly around. About a week after their first appearance they begin to enter the nests of *A. nycthemera*. Usually they stay about 5 to 7 minutes in the nest and after leaving they close the entrance of the nest in most cases.

The cuckoo bee *Nomada leucophthalma*, which is a putative parasite of *A. nycthemera* (PITTIONI & SCHMIDT 1943), has not been observed by us. *Nomada lathburiana* was frequently seen at the nesting site, it was, however, never observed to invade nests of *A. nycthemera* but nests of *A. vaga*.

Furthermore,the fly *Leucophora obtusa* ZETTERSTEDT (Anthomyiidae) was often observed at the nesting site. In four cases it was observed to follow a *A. nycthemera* female returning to the nest with pollen. When the bee landed the fly sat down on a blade of grass or on the sand at a distance of ca. 10 to 20 cm and remained there quietly, obviously watching the bee. After the bee had disappeared in the nest, the fly came to the nest entrance and stuck its abdomen into the sand. It remained about 30 seconds in this position and then took off.

7. Discussion

7.1. Nesting site

The aggregation of *A. nycthemera* which is described in this communication is located in an anthropogenous habitat. This place used to be a shooting range until the end of World War II, the slope being the backstop. Since then, however, this area has been left undisturbed and only served as a memorial site. To preserve this aggregation it is necessary to protect it from succession, i.e. to cut back bushes and trees. Fortunately a project for protection had been initiated four years ago.

Apart from the characteristics of the nesting site also the presence of nearby willows, the food plants, is an important prerequisite for the aggregation of *A. nycthemera*. This species seems to require sandy places close to a lowland forest with willows (PEUS 1926, PITTIONI & SCHMIDT 1943, WESTRICH 1985, 1989b, GRÜNWALDT pers. comm.). These special demands for its nesting site are probably an important reason for the rarity of *A. nycthemera*.

Another smaller aggregation of *A. nycthemera*, which existed for years in close vicinity ("Leitenberg", ca. 2 km distant), has been abandoned (WARNCKE pers. comm.).

There are several species of *Andrena* which preferably live in anthropogenous habitats (HAESELER 1972, WESTRICH 1989a, b). Some species, like *A.fulva* (KLAUSNITZER 1976, GUSENLEITNER 1983), *A. cineraria* (PITTIONI and SCHMIDT 1943) and *A. tibialis* (in the city of Munich, unpublished) are even found in small grass-plots at the side of roads with a great deal of traffic. Nevertheless the occurrence of quite a lot of species of bees is severely endangered, and it is very important to protect the respective biotopes (see WESTRICH 1989a, b for review and further references).

A. nycthemera builds its nests in aggregations. Up to now only considerably smaller aggregations have been reported (up to about 50 females: PEUS 1926, STOECKHERT 1954, DYLEWSKA 1987). The nesting site described in this communication seems to be unusually large. Remarkably *A. nycthemera* was also previously found to be associated with *A. vaga* (PEUS 1926, ULRICH 1933).

There are many species of the genus *Andrena* which nest in aggregations. In some species these aggregations may be very large, with thousands of females (*A. fulva*: WESTRICH 1989b, *A.thoracica:* EMEIS 1955, *A. vaga*: MALYSHEV 1926, VLEUGEL 1947). REICHHOLF (1976) counted 50.000 tumuli of *Andrena* in several aggregations along a dam of 12 km length. WARNCKE (pers. comm.) determined them as *A. vaga*.

The nesting sites of many gregarious species of *Andrena* are stable thoughout the years like in *A. nycthemera*. The nesting site described in the present paper has been known for about ten years (WARNCKE unpublished). ULRICH (1956) reports nest aggregations of *A. vaga* which were known for more than 30 years. RAU (1935) observed an aggregation of *A. erythrogaster* at the same place for 6 years. Generally it is assumed that at least some females use the old nests again, and only some dig entirely new nests (MALYSHEV 1926, RAU 1935, STEPHEN 1966, GUSENLEITNER 1983). Thus always the same place is used for generations. Probably the females digging for a rather long period of time (paragraph 4.3.5; F93) will dig entirely new nests. The males of *A. flavipes* also prefer to keep to their old nests: they are attracted by the scent of the soil at the nesting place, not by the scent of the females (BUTLER 1965). On the other hand,in Egypt *A. ovatula* nest in aggregations which are not stable: every year the females found a new aggregation which is about 200 m to 1 km distant from the previous one (WAFA et al. 1972, RASHAD & MOUSTAFA 1973).

7.2 Behavioral pattern

7.2.1 Behavior of males

In *A. nycthemera* the males are found to be swarming at the nesting site. Their behavioral pattern is remarkably similar to that of *A. erythronii* (MICHENER & RETTENMEYER 1956). Also in other species of *Andrena* the males swarm predominantly above the ground of the nesting site (e.g. *A.vaga*: VLEUGEL 1947, *A.chrysoceles* : HAAS 1960, *A. perplexa*: STEPHEN 1966, *A. potentillae* and *A. ovatula*: WESTRICH 1989b). In other species the males patrol on bushes or trees (e.g. *A. praecox*: STOECKHERT 1933, *A. ovatula*: RASHAD & MOUSTAFA 1973) or on flowers (e.g. *A.chalybaea*: THORP 1969, *A. erigeniae*: BARROWS 1978, *A. pandellei*: WESTRICH 1989b).

In addition to visual orientation the males probably use chemical clues like the scent produced by mandibular and/or Dufour glands to find the females (BUTLER 1965, WESTRICH 1989a). Furthermore, as in *Colletes succinctus* (LARSEN et al 1986) a buzzing sound emitted by females may help to locate the females underground.

7.2.3 Mating

In spite of rather intensive observation we saw only few copulations,corresponding to previous investigations of other species of *Andrena* (VLEUGEL 1947, MICHENER and RETTENMEYER 1956, MATSUMURA 1970, GEBHARD & RÖHR 1987). The prevailing opinion therefore is that females copulate only once, and this seems to be the rule for most bees (ALCOCK et al. 1978). Monandric behavior could be proved for the females of *A. clarkella* and of *A.sublevigata* with bees in captivity (MATSUMURA 1970, GEBHARD and RÖHR 1987). Multiple matings in *Andrena* are only reported for *A. flavipes* (BUTLER 1965) and in other genera of Andrenidae (*Calliopsis andreniformis*: SHINN 1967, *Perdita texana*: BARROWS et al. 1976).

In many species copulations take place on the ground of the nesting site as in *A. nycthemera* (*A. lapponica*: DYLEWSKA 1987, *A.vaga*: VLEUGEL 1947, *A.foxii*: THORP 1969, *A. erythronii*: MICHENER & RETTENMEYER 1956, *A.erigeniae*: BARROWS 1978, *A. argentata*: DONISTHORPE 1930, *A. dunningi*: JOHNSON 1981). In *A.nycthemera* mating may also begin underground, previously only seen in two other species (*A. dunningi*: JOHNSON 1981, *A. cineraria*: GEBHARD & RÖHR 1987), although it may occur in many species where the males search and dig at the nesting site. Copulations may occur underground, which might be another explanation why only few copulations were observed (see above).

Other species of *Andrena*, however, mate on flowers (*A. curvungula*, *A.pandellei*, and *A. humilis*: WESTRICH 1989a, *A. ventralis*: DYLEWSKA 1987, *A. polita*: MÜLLER 1944, *A. crataegi*: OSGOOD 1989, *A.carlini*: JOHNSON 1981). Matings in flight are hardly known from bees except in Xylocopini (ANZENBERGER 1977, OSTEN 1989) and have only been reported once for andrenide bees (*A. lapponica*: HÖPPNER 1899).

Copulations described for *A. erythronii*, *A. erigeniae*, and *A. cineraria* (MICHENER and RETTENMEYER 1956, BARROWS 1978, GEHARD and RÖHR 1987) are similar to those in *A. nycthemera*. In *A.vaga* the males are supposed to bite the wings of the females (VLEUGEL 1947) which in turn embrace the males with their posterior legs (MÜLLER 1944). These descriptions correspond neither to our observations on *A. nycthemera* nor to those of *A. vaga* (SCHÖNITZER & KLINKSIK, unpublished).

The duration of copulations in most species of *Andrena* is about 20 to 60 seconds (*A. scita*: KOCOUREK 1966, *A. erigeniae*: BARROWS 1978, *A. dunningi*: JOHNSON 1981, *A. cineraria*: GEBHARD and RÖHR 1987). Only in *A. erythronii* (MICHENER and RETTENMEYER 1956) and *A. nycthemera* a longer duration (2 to 4 min) has been recorded.

7.2.4 Behavior of females

The behavior of sitting in the entrance of the nest was previously pointed out to be frequent in *A.vaga* (MALYSHEV 1926), *A. erythronii* (MICHENER and RETTENMEYER 1956) and in some species of the subgenus *Melandrena* (LINSLEY et al. 1955). In all these cases as well as in our observations on *A. nycthemera* the weather is remarkably variable during the season. This behavior may be interpreted as waiting for sufficient temperature or sunshine, and it seems to represent an adaptation of those species which are active early in the springtime.

The digging behavior in *A. nycthemera* is very similar to that in other species of *Andrena* (MALYSHEV 1926, GEBHARD and RÖHR 1987). In *A. erigeniae* (DAVIS and LABERGE 1975), however, the posterior (not the anterior and middle) legs push the sand backwards, and in *A. erythronii* the movement of legs differs depending on whether the female carries pollen or not (MICHENER and RETTENMEYER 1956). *A. labiata* is remarkable because of its low digging speed compared to the other species of *Andrena*: it needs eight days of digging to build a nest (JANVIER

1977).

In *A.nycthemera* the females usually close the entrance of their nests, so that normally a nest can only be recognized by watching the bee emerging from it or returning to it. This also applies to *A. vaga* (MALYSHEV 1926, VLEUGEL 1947), *A. fulvago* (GRÜNWALDT and GRÜNWALDT 1939), and *A. clarkella* (GEBHARD and RÖHR 1987). Many species leave their nests open during the day and close them overnight (*A. cineraria*, *A. fuscipes*: GEBHARD and RÖHR 1987, *A. chalybaea* and related species: THORP 1969, *A. erigeniae*: DAVIS and LABERGE 1975, *A. dunningi*: JOHNSON 1981). In *A. accepta* (ROZEN 1973), where several females have a communal nest, the entrance is left open permanently. *A.florea*, being active during the summer months, closes the entrance of the nest during the hot hours around noon (WESTRICH 1989b). Thus, closing the entrance may be as well a protection against low temperatures at night as against the heat of midday, and in species like *A. nycthemera* it possibly serves as a camouflage, too.

In most cases the females of *A.nycthemera* find the entrance of their nest very quickly, but sometimes their search for it takes rather a long time. This is similar to other species of *Andrena* (VLEUGEL 1947, GEBHARD and RÖHR 1987). *A. erythronii* (MICHENER & RETTENMEYER 1956), however, has more problems in finding the entrance than *A. nycthemera* . It is evident that the females find the place by visual information, orientating themselves with the aid of landmarks and find the exact entrance by olfactory clues. The scent may originate from the cell lining which is produced by the Dufour gland (shown in the halictide bee *Evylaeus* spec.: HEFETZ 1987). The importance of chemical clues is also demonstated by the observation that the bees frequently touch the sand with the tips of their antennae.

The length of the time that females of *A. nycthemera* spend on their pollen collecting flights is about the same as in *A. knuthi* (mean time $\bar{x}$ = 30 min, HIRASHIMA 1962), *A. perplexa* ($\bar{x}$ = 26 min, STEPHEN 1966),and *A.erigeniae* ($\bar{x}$ = 33 min, DAVIS and LABERGE 1975). Other species take considerably longer (*A. cineraria*, $\bar{x}$ = 90 min, *A. clarkella*, $\bar{x}$ = 95 min: GEBHARD and RÖHR 1987, *A. ery-*

thronii, $\bar{x}$ = 98 min, calculated from the histogram Fig. 10 in: MICHENER and RETTENMEYER 1956). Even more time is needed by the females of *A. crataegi* ($\bar{x}$ = 170 min, OSGOOD 1989). Remarkably short times for collecting pollen are reported for *A. chalybaea* ($\bar{x}$ = 12 min, THORP 1969), *A. haynesi* ($\bar{x}$ = 12 min, PARKER and GRISWOLD 1982), *A.mojavensis*, *A. oenotherae*, and *A. deserticola* (x = 1 to 8 min, LINSLEY et al. 1955). Of course the time needed for collecting pollen depends on the proximity of food sources and may possibly vary between populations of a given species, but up to now there are no such data.

The length of time that females spend in the nest after bringing in pollen is remarkably long in *A. nycthemera* as compared to any other species of *Andrena*. A relatively long time, though clearly shorter than in *A. nycthemera*, is reported for *A. erythronii* ($\bar{x}$ = 35 min, computed from the histogram Fig.11 in MICHENER and RETTENMEYER 1956), *A. clarkella* ($\bar{x}$ = 24 min, GEBHARD and RÖHR 1987), and *A. perplexa* ($\bar{x}$ = 16 min, STEPHEN 1966). Other species of *Andrena* usually stay in the nest for less than 10 minutes, *A. chalybaea* even less than one minute ($\bar{x}$ = 35 sec!, THORP 1969).

Those species needing very little time for pollen collecting and for depositing it in the nest (*A.mojavensis*, *A. oenotherae*, and *A. deserticola*: LINSLEY et al. 1955, *A. chalybaea*: THORP 1969) can manage as many as 6 to 8 collection trips per day, whereas for most other species of *Andrena* only 1 to 3 trips per day are reported. The fact that we could observe more trips (up to 6) in *A. nycthemera* may be due rather to the lack of sufficiently extensive observations in other species than to differences between the species. We also recorded that an individual female may live in as many as 6 nests, a fact that was never observed before.

Most of the females of *A. nycthemera* take care of one or two nests, only few have 3 or more nests. Assuming that in some cases we might have overlooked the second nest of a bee, we estimate that about half the population of females has two or more nests. But the fact that one bee (F03) was observed to inhabit one nest for as long as three weeks demonstrates clearly that some bees have only one nest. Other species of *Andrena*, too, usually have one or two nests (*A. vaga*: MALYSHEV 1926, *A. erythronii*: MICHENER and RETTENMEYER 1956). One nest only has been reported for *A. clarkella* (GEBHARD and RÖHR 1987); *A. cineraria* has generally two nests (GEBHARD and RÖHR 1987).

Aggressive behavior in females has not been recorded previously in any species of *Andrena*. Only in the andrenid bee *Perdita octomaculata* "agonistic behavior" has been reported (EICKWORT 1977). Since we could also observe fights between females of *A. nycthemera* and *A. vaga*, it may be that this behavior is more common in other species of *Andrena* than it appears from the lack of data. The occurence of the fights clearly demonstrates the shortage of suitable sites for nesting. Aggressive behavior in males, i.e. competition for females, however, is well known and common in *Andrena*.

7.3 Seasonal history

The following problems appear when comparing data on seasonal history: 1. Usually the data on the phenology of different species of *Andrena* are compiled from the dates of catching (e.g. KOCOUREK 1966, SAKAGAMI and MATSUMURA 1967, WARNCKE 1981, WESTRICH 1989b). 2. Many notes in the literature describe occasional observations and do not contain too many exact data on the seasonal history. 3. Frequently in the literature there is no clear difference between actual "descriptive" and "concluded" data. RIDLEY (1989) even claims, "It is a noisy literature".

There are only few species of *Andrena* of which the seasonal history is documented in greater detail, most of all: *A. erythronii* (MICHENER and RETTENMEYER 1956), *A. vaga* (MALYSHEV 1926, 1935, VLEUGEL 1947), *A. sublaevigata* (MATSUMURA 1970), *A. clarkella*, and *A. cineraria* (GEBHARD and RÖHR 1987). But even in these reports the data are not always as comprehensive as in the present investigation. Thus it is difficult to compare the different species and to draw conclusions. Although we tried to document the frequency of the behaviors as completely and exactly as possible we have to admit, that some of the data compiled in Figure 9 are unavoidably tentative (see remark in chapter 5). Furthermore it is obvious that an observer never can watch and record everything.

In some descriptions of the seasonal history of other species of *Andrena* one gets the impression that the behavioral patterns change much more distinctly over the season than in *A. nycthemera* (MALYSHEV 1926, 1933, VLEUGEL 1947). Due to our (unpublished) observations on *A. vaga* we suggest that sometimes the literature contains tentative interpretations which give the impression of a clearer sequence of behavioral patterns than in our investigation. But it may well be that the life history of some species of *Andrena* is more synchronized than in *A. nycthemera*. This seems to be the case in *A.clarkella* and *A. cineraria* (GEBHARD and RÖHR 1987).

The season of *A. nycthemera* (♂♂: 4 weeks, ♀♀: 7 weeks) is about as long as that of *A. vaga* and *A. erythronii* (MALYSHEV 1926, VLEUGEL 1947, MICHENER and RETTENMEYER 1956); It is shorter than in *A. cineraria* (♂♂: 5 weeks, ♀♀: 11 weeks) and *A. fuscipes* (♂♂:7 weeks, ♀♀:10 weeks). A very short season is described for *A. clarkella* (♂♂: 2 1/2 weeks, ♀♀: 5 to 6 weeks; GEBHARD and RÖHR 1987) and for *A. erythrogaster* (♂♂ and ♀♀: 3 to 4 weeks; RAU 1935). In *A. clarkella* there are only 6 to 7 days during which pollen is collected by the females (GEBHARD and RÖHR 1987) which is clearly less than in *A. nycthemera* (21 days) and also less than in the other investigated species. In all species of *Andrena* the males have a shorter adult life than the females.

Most species of bees are considered as proterandrous, i.e. the males emerge from their nests earlier in the season than the females. This is also considered to be a general rule in the genus *Andrena* (PERKINS 1919, ROBERTSON 1918, 1930, FRIESE 1923). Unequivocally proterandrous are for example *A. clarkella* and *A.cineraria* (GEBHARD and RÖHR 1987), *A. crataegi* (OSGOOD 1989), and *A. vaga* (MALYSHEV 1926, ULRICH 1933, VLEUGEL 1947). This, however, does not apply to *A. nycthemera*, since in most seasons observed both males and females were seen on the first day of the season. But at the beginning of the season,the number of males exceeds the number of females by far. Thus we conclude that a majority of females emerge later than the males.

It should be noted, that any observer certainly would have concluded that *A. nycthemera* is clearly proterandrous had he visited the colony for example on those days with cold weather at the beginning of the season 1987 on which only males were active (Mar/29 to Apr/2/87). Our observation from 1984 may be explained in this way. A similar situation was described for *A.erythronii*, which was considered to be proterandrous until the species was thoroughly investigated (MICHENER and RETTENMEYER 1956). This demonstrates the need for continuous observation. Another species of *Andrena* in which the emergence of males and females is fairly synchronized is *A. perplexa* (STEPHEN,1966).

A. nycthemera is one of those species of *Andrena* which are known to emerge very early in the spring. Also PEUS (1926) found them as early as March 17th. The unusually early emergence in 1990 indicates that temperature is the important factor for emergence. In Central Europe there are some species of *Andrena*, for example *A. ruficrus* and *A. clarkella*, tending to emerge even earlier than *A. nycthemera* (FRIESE 1923, STOECKHERT 1933, KOCOUREK 1966, GEBHARD and RÖHR 1987). These species, like *A. nycthemera*,are specialized to *Salix* spec. as food plants, probably because this is nearly the only source of pollen which is available that early in the year.

It is not clear what the bees feed upon during the very first part of the season before the willows bloom (i. e. for 1987:Mar/25 to Apr/4). There are no blossoms at all to be found in the vicinity of the nesting site during this time. Especially the males are affected as this condition is prevailing for about one third of their lifespan. It seems that they have enough fat-body for these first days but this should be investigated histologically.

In the beginning of the season females seem to emerge from their nests over a relatively long period of time (cf. above). This explains why the behavior of digging a new nest is not only seen for a definite period but almost throughout the season. Also, the surprising observation of copulations as late as April 9th and 15th may be explained by females emerging that late from their nests. Notably these late copulations took place at a site where the snow had melted very late in the year and where the very last males had been observed (cf. paragraph 5.2).

We suggest that the different time of emergence reflects two different females strategies: The females emerging early have the advantage of a free choice of unoccupied nesting places (e.g. their own old burrows) but the drawback of a great risk of bad weather and scarcity of food. On the other hand, the females which emerge later generally have better weather conditions, but more problems in finding a suitable nesting place which is not yet occupied by another female. The importance of the competition for nesting places is shown by the occurrence of fights (cf.paragraphs 4.3.15, 7.2.4).

7.4 Dependence on the weather

The behavior of *A.nycthemera* shows several adaptations to the unstable weather conditions typical for the early springtime, for example, the behavior of the females to sit in the entrance of the nest (paragraph 4.3.9). Both males and females take advantage of the direct sunshine to get a sufficient body temperature for flying. Once they are flying they probably warm up the body by movements of the wing musculature (STONE and WILLMER 1989). Other species of *Andrena*, too, may be active at very low temperatures already; *A. clarkella*, *A. cineraria*, and *A. erythronii* may be active at an air temperature of about 10°C (MICHENER and RETTENMEYER 1956, GEBHARD and RÖHR 1987). According to GRÜNWALDT (pers. comm.) *A. clarkella* may even be active at 4°C in case the sun is shining. In *A. labiata*, however, the temperature must exceed 18°C for flight (JANVIER 1977). On the other hand, high temperatures can also impede the activity of *A. nycthemera*, a possible drawback of their adaptation to activity at rather low temperatures.

8. List of species

To avoid confusion in citation and to indicate synonyms which help to understand the literature cited in this paper, the mentioned species of bees are listed in full below.

Andrena carlini COCKERELL, 1901
A.chalybaea (CRESSON,1878)
A.chrysosceles (KIRBY,1802)
A.cineraria (LINNAEUS,1758) (= *A.danuvia* E.STEOCKHERT,1950)
A.clarkella (KIRBY,1802)
A.crataegi ROBERTSON,1893
A.curvungula THOMSON,1870
A.deserticola TIMBERLAKE, 1937
A.dunningi COCKERELL,1898
A.erigeniae ROBERTSON,1891
A.erythrogaster ASHMEAD, 1890 (= *A.rythrogaster*)
A.erythronii ROBERTSON,1891
A.flavipes PANZER,1799
A.florea FABRICIUS,1793
A.foxii COCKERELL,1898
A.fulva (MÜLLER,1766)
A.fuscipes (KIRBY,1802)
A.haynesi VIERECK and COCKERELL,1914
A.humilis IMHOFF,1832
A.knuthi ALFKEN,1900
A.labiata FABRICIUS,1781 (= *A.cingulata* FABRICIUS,1775)
A.lapponica ZETTERSTEDT, 1838
A.mojavensis LINSLEY and MACSWAIN,1955
A.nycthemera IMHOFF,1866
A.oenotherae TIMBERLAKE, 1937
A.ovatula (KIRBY,1802)
A.pandellei PÉREZ,1895
A.perplexa SMITH,1853 (= *A.viburnella* GRAENICHER,1903)
A.polita SMITH,1847
A.potentillae PANZER,1809
A.praecox (SCOPOLI,1763)
A.scita EVERSMANN,1852
A.sublaevigata HIRASHIMA, 1966
A.thoracica (FABRICIUS,1775)
A.tibialis (KIRBY,1802)
A.vaga PANZER,1799 (= *A.ovina* KLUG,1810; = *A.pratensis* NYLANDER,1848)
A.ventralis IMHOFF,1832
Calliopsis andreniformis SMITH,1853
Colletes succinctus (LINNAEUS,1758)
Nomada lathburiana (KIRBY, 1802)
N.leucophthalma (KIRBY,1802)
Perdita texana CRESSON,1878
P.octomaculata (SAY,1824)
Rophites canus EVERSMANN, 1852 (= *Rhophitoides canus* (EVERSMANN,1852))
Sphecodes pellucidus SMITH, 1845

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Anschriften der Verfasser:

Dr. Klaus SCHÖNITZER
Zoologisches Institut
der Universität München
Luisenstraße 14
D-8000 München 2

Christine KLINKSIK
Zoologisches Institut
der Universität München
Luisenstraße 14
D-8000 München 2