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Nesting behaviour of *Anthophora pauperata* (Hymenoptera: Anthophoridae) in the St. Katherine ecosystem, Sinai

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ABSTRACT

Nesting behaviour of the solitary, spring-emerging, univoltine, ground-nesting bee, *Anthophora pauperata* Walker (Anthophoridae), was studied in the semi-arid mountainous environment of Wadi El Arbaein, St. Katherine, S. Sinai, Egypt, during spring and summer 1996 - 1998. Female *A. pauperata* tend to nest on both sides of the wadi bed, on gentle to flat slopes. Nest depth is variable, but digging the nest and constructing new cells occur in the midday hours. One cell is completed per 24 hrs. The females provision the cell with floral nectar and pollen, mainly from *Alkanna* flowers, foraging in a bimodal diel activity of early morning and late afternoon. It takes 11-16 foraging bouts to provision each cell, but the quantity of pollen collected per cell appears to decrease during the season, implying that reproduction may be pollen limited. The female bee may construct up to five different nests during her lifetime. Each nest contains from two to four complete cells arranged vertically or semi-vertically at the bottom of a long tunnel. A high proportion of nests contain a "false" sand-filled cell; this may be a decoy cell to reduce nest parasitism. A probable specialist parasite, a species of *Melecta* (Anthophoridae), is commonly seen prospecting for nests in the wadi.

KEYWORDS: *Anthophora pauperata*, nest, Sinai, Egypt.

INTRODUCTION

In the arid wadis of St. Katherine, South Sinai, *Anthophora pauperata* Walker (Anthophoridae) is an important insect species in the ecosystem. In addition to its valuable role as the main pollinator of *Alkanna orientalis* L. (Boiss.) (Boraginaceae), it has a co-evolutionary importance with the plant (Gilbert *et al.* 1999). Phenologically, the foraging activity period of *A. pauperata* is synchronized with the blooming time of *A. orientalis* (Semida 1994). On the spatial scale, there may be a correlation between the morphology of *A. pauperata* and the floral architecture of *A. orientalis*. (Gilbert *et al.* 1996). The plant floral resources constitute the main source of food for *Anthophora* bees and their offspring.

Anthophora pauperata (Anthophoridae) is a solitary univoltine protandrous species with an activity period during March, April and early May. Male bees have a unimodal diurnal activity pattern with extensive territorial behaviour, feeding only on floral nectar (Semida 1994; Willmer *et al.* 1994; Stone *et al.* 1999), while females exhibit a bimodal pattern of diurnal activity (early morning and late afternoon) and exploit floral nectar and pollen (Semida 1994; Willmer *et al.* 1994; Gilbert *et al.* 1999; Stone *et al.* 1999)

Anthophora pauperata are oligoletic, collecting pollen mainly from *Alkanna*, with a small amount from other flower species. They nest in the ground individually in a widely spaced isolated nests. Each female constructs more than one nest in her lifetime and provisions them with floral pollen and nectar. The current study aims to investigate the female nesting behaviour of *A. pauperata* and to shed light on nest site selection, nest construction and architecture, nesting cycles, floral resources, nest provisioning and female activity.

MATERIALS AND METHODS

Field work was carried out during spring and summer of 1996 -1998 at St. Katherine, South Sinai (34° E, 28.6° N, alt. 1600 m). Most of southern Sinai consists of a mountainous massif of granitic and volcanic rocks, dissected by systems of gorges, each forming a semi-isolated ecosystem. The study site is Wadi El Arbaein, a moderately steep rocky gorge about 2.5 km. long, running in a NNW-SSE direction (see Willmer *et al.* 1994; Semida 1994). The wadi bed contains a community of plants consisting mainly of *Alkanna orientalis* (L.) Boiss., *Stachys aegyptiaca* Pers. and *Fagonia mollis* Delile.

Several females were marked with numbered plastic discs [E.W.Thorne Ltd., Wragby, Lincs, UK.] on the thorax. The marked females were followed throughout the season to estimate the number of nests/ individual female bee during her life. Nests were excavated carefully using a brush and a jet of air (Ordway 1966); their lengths were measured by a fine cotton thread, while Verner calipers were used for cell diameters. The nectar volume in each cell was measured using 1µl Drummond micro-capillary tubes, and the sugar concentration (as weight of sugar per 100gm nectar solution) using a refractometer (Bellingham & Stanley, Tunbridge Wells, Kent, UK). Pollen counts were achieved using a 2µl sample of dispersed pollen placed on a haemocytometer (Dafni 1992).

Ambient temperature and humidity were recorded one metre above the ground using a thermocouple thermo-hygrometer (Vaisala HMI 31 probe). A soil thermometer was used to measure nest temperature, placing the probe down into the nest a distance of approximately 2 cms. These measurements were made for three full days in early, mid and late season. The number of female foraging bouts was recorded by continuous nest observation, starting before sunrise and extending to sunset. A stopwatch was used to record the duration of each foraging bout.

RESULTS

Female bees of *Anthophora pauperata* tend to nest quite near their foraging area where the *Alkanna* patches grow. They avoid hard rocky areas, restricting their nesting sites to the bottom of mountain slopes and both sides of the semi-flat wadi bed (where the soil is usually hard-packed, sandy or silty loam with few stones). Sometimes their nests were located close to one or more patches of *Fagonia* in the loose fine soil (Table 1), where the vegetation and the presence of small rocks give some shelter and support to the nest. Figs. (1a-c) illustrate the pattern of ambient and nest temperatures at the study area throughout the season.

Table 1: Mechanical analysis of soil collected from different nest sites of *Anthophora pauperata* at the study area. (s.e = standard error) (n = 9)

Soil size	Gravel	Coarse	Medium	Fine	Silt & clay
Mean % ± se	24.9 ± 2.6	33.3 ± 1.5	27.8 ± 0.7	29.7 ± 1.5	9.4 ± 0.3

Most matings took place with females with very clean and undamaged wings, which I interpret as newly emerged. Thus, newly emerged females probably seek mating before starting to construct the nest. Digging was preceded by a characteristic slow flight near the ground, frequently interrupted by stops near small stones or rocks and depressions. Once a suitable site was found a female would begin to dig the nest.

The nest of *A. pauperata* consists of a vertical, or near vertical, shaft with one cluster of cells at the bottom of a long tunnel. The nest entrance usually opens to the surface at an angle when on flat ground or into the side of a small depression in otherwise flat surfaces. Observations indicate that the direction that the nest entrance faces appears to be random in relation to the prevailing wind or sun. Nest dimensions are given in Table 2, while nest structure and architecture are shown in Fig. 2.

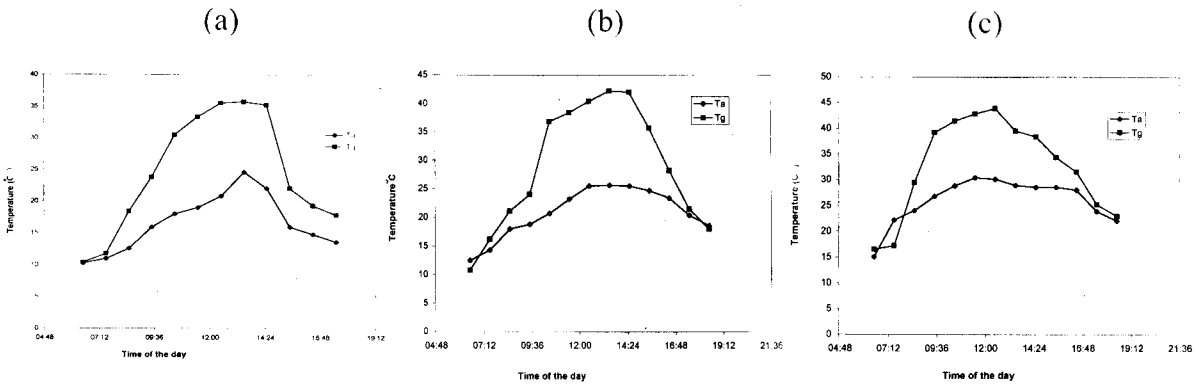

Figure 1: The daily ambient and ground temperature at Wadi El Arbaein, South Sinai. (Ta= ambient temperature, Tg= ground temperature). a) early season (26th of March); b) mid season (6th of April); c) late season (28th of April)

Table 2: Dimensions of the *Anthophora pauperata* nests at the study sites. (All measurements in mm.)

	Nest Entrance n = 11	Tunnel Diameter n = 11	Nest Depth n = 11	# cells /nest n = 9	Cell Width n = 9	Cell Length n = 9	Egg Width n = 5	Egg Length n = 5
Mean ± se	8.3±0.3	9.8±0.8	73.3±9.2	3±1	9.1±0.8	16.6±1	0.97±0.02	3.38±0.09
Range	7- 9.5	8- 12	40- 170	2- 4	7.2- 12	13.6-20	0.9- 1	3.1- 3.5

The nest tunnel angles gradually deeper into the soil and ends in an expanded cell-like chamber (Fig. 2). Cells radiate in a cluster from this chamber at an angle or vertically downward. The number of cells varies from one nest to another, ranging from 2 to 4 cells/nest. The depth differed among nests and seemed to depend on soil conditions at the time of construction.

Completed cells are joined together forming a cluster, with a wall formed of clay cemented by some sort of fluid. The cell has a cap which has a slightly concave exterior surface. Cells are arranged with their caps towards the top, opening onto the chamber at the bottom of the tunnel. Although the maximum number of cells in a completed nest was four, there was sometimes a curious false cell filled with fine sand and clay, positioned either before or with the other cells. The minimum number was two cells in a completed nest that had no false cells.

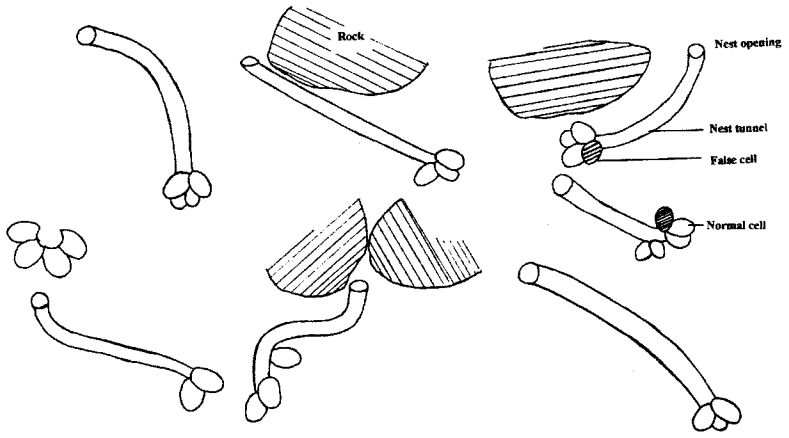

Figure 2: Nest structure and architecture of the female *Anthophora pauperata* at Wadi El Arbaein, South Sinai.

Nesting cycle: In the study area, the female bees emerge in mid-March, 10-15 days later than males. The newly emerged female starts to feed on the floral nectar of *Alkanna* and probably gets mated by one of the territorial males, although non-territorial "floater" males and sedentary site-and-wait males also seem to obtain some mating. It was quite hard to detect a

true mating. The longest time spent in mating was 15 seconds, between a territorial male and a newly emerged female at 10.30 a.m. on a flowering patch of *Alkanna*. After mating, the female probably starts immediately to select a place to nest (one marked female was mated, and on release, immediately started the searching flight behaviour). The maximum duration of nest occupation by marked females was five days, during which time she formed four complete cells in the nest. When the female had finished nest formation and the provisioning of all cells sequentially, she closed its entrance with small stones, coarse sand and debris. After that, she shifted to another place to dig a new nest. The female constructs up to four different nests during her lifetime, distributing them within a single foraging area of about 50 x 50 m. There was no record of the re-use of old nests by females.

Provisioning takes place once the female finishes each cell. She provides the cell with a considerable amount of pollen and nectar as food resources for the offspring. Nectar volumes in completed cells were 189 ± 17.3 (160-200: n = 11) µl at a mean concentration of 69 ± 4.5 %. When the female completes the provisioning of the cell, she lays her egg on top of the food material inside the cell. The egg has an oval-shape and floats on the nectar surface. Lastly, the female closes the cell and starts to construct a new one. She constructs and provisions one cell each day, spending the midday hours digging and constructing the new cells, while the morning and late afternoon periods are mainly for cell provisioning. During resource gathering, the female has several foraging bouts through the day. The number of bouts and their duration varies on a diel cycle (Figs. 3 & 4). Moreover, the quality of food differs throughout the season (Table 3). It appears to be striking that the amount of pollen per cell decreases during the season (due to the laborious nature of collecting these data, I have only one nest for each part of the season). As this happens, females switch from just *Alkanna* to collecting significant quantities of *Fagonia* and *Stachys* pollen. *A. pauperata* is clearly a mass-provisioning bee. Each cell needs 11-16 different pollen and nectar bouts for full provisioning; each trip lasts about 19.3 ± 3.8 min. during the morning hours and 19.9 ± 2.7 min. at the afternoon hours.

Table 3: Floral constancy represented by the number of pollen grains found in different cells of different nests constructed by *Anthophora pauperata* at different times of the season in the study area.

Time of the Season	Cell No.	No. of pollen grains (millions)	*Alkanna orientalis* %	*Stachys aegyptiaca* %	*Fagonia mollis* %
Early season (29th of March)	1	44.3	100	0	0
	2	42.1	100	0	0
	3	38.7	100	0	0
Mid season (10th of April)	1	28.4	68	11	21
	2	32.6	62	17	21
	3	36.1	99.4	0.6	0
Late season (3rd of May)	1	11.5	63	12	20
	2	9.5	100	0	0
	3	12.3	83.3	7.6	9.1

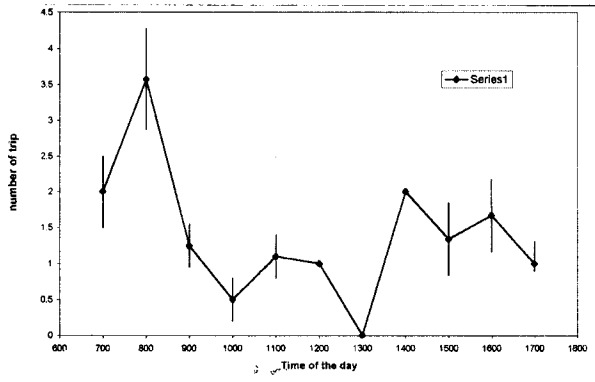

Figure 3: Number of trips done by *A. pauperata* throughout the day at the study area

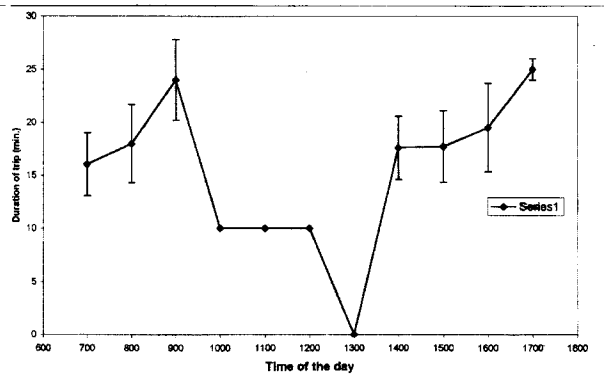

Figure 4: Duration of foraging trips done by the female of *A. pauperata* throughout the day

DISCUSSION

The burrowing members of the family Anthophoridae show a wide range of variation in their nesting sites and nesting strategies. While some members nest in woody plants (*Xylocopa* sp., Stephen *et al.* 1969)], some others are ground-nesting. Some of the ground-nesting bees are gregarious in their nesting strategies (e.g. *Anthophora abrupta*, Norden 1984; *A. plumipes*, Stone 1995; *Diadasia opuntiae* Ckll., Ordway 1984), but other species are true solitary bees, nesting individually well apart from each other. Moreover, some species reuse the old nests (e.g. *A. atriceps*, Kamel 1981), but others do not adopt this strategy. *Anthophora pauperata* is clearly a ground-nesting solitary species that always digs a new nest every time.

Nest site selection may depend on several intrinsic and extrinsic factors. The morphology, mechanical structure and moisture of the substrate, presence of food resources and shelter, in addition to the physical ability of the nesting bee may determine the best site for nesting. Sometimes, the climatic conditions, such as wind direction, exposure to sun, and flooding pathway may play a role in nest site selection. The females of *A. pauperata* tend to nest where the soil structure enables them to dig the nest using the stones as a shelter and support. They seem to have no particular orientation in their site selection, but they avoid nesting on the wadi bed, presumably to escape the danger of the flooding that often occurs in these wadis in spring and autumn.

Nest construction usually starts directly as the females emerge and mate (Alcock 1991). The nest architecture is characteristic of the species with some individual variations (Stephen *et al.* 1969). Some females of *A. pauperata* dig their nests deep in the ground (up to 17cm. depth), while others nest quite near the ground surface (4 cm.) this variation may be related to soil conditions. They select the nest entrance either between small stones or under plants (particularly *Fagonia*). Burrow construction in soil nesting species involves the excavation of considerable amount of soil which is usually deposited at or near the entrance (Stephen *et al.* 1969). Burrow diameter is generally determined by the diameter of the adult bee. The nest entrance and tunnel diameter of the studied bee corresponds to the female body width.

Under adequate conditions, female *Anthophora* typically constructs only one cell each day (Batra 1994). Nest completion not only requires collection of floral resources, but also the construction of the cell chamber before provisioning and sealing the complete cell (Stone *et al.* 1999). Both the construction and sealing of cells are complex processes in *Anthophora* (Norden 1984), that take considerable time and must be fitted into daily scheduling. Some anthophorids dig new cells predominantly in the evening and collect nectar throughout the day (Stone 1994). In the current study, females *A. pauperata* dig their nests and construct the new cells during the midday hours; possibly because only this time is warm enough for digging to be energetically feasible (Stone *et al.* 1999).

The number of cells per nest in ground-nesting bees ranges from one to many. Most soil-burrowing species make only one nest, which contains as many cells as foraging conditions and the reproductive potential of the bees allow. A few soil-burrowing species characteristically limit the number of cells per nest and make several nests (Stephen *et al.* 1969; Kamel 1981; Coville *et al. 1983;* Norden 1984; Neff & Simpson 1992). In *A. pauperata*, the female usually constructs only 2-4 complete cells per nest and 3-5 nests over her lifetime. Why should she do this, rather than dig one nest with more cells? Sometimes the female bee fills the first cell with soil, perhaps as a decoy cell to reduce the impact of natural enemies. This may be a clue that nest predation and/or parasitism rates are high, and in fact a specific parasite, a species of *Melecta*, is very commonly seen prospecting for nests in Wadi El Arbaein..

The cell building materials belong to three categories: secreted, substrate and foraging. In Anthophorinae, the secreted material is a waxy-like material used to line the cells. This wax is apparently secreted from the accessory gland of the reproductive tract and is applied with the pygium (Stephen *et al.* 1969; Michener 2000). Soil particles obtained from the substrate are cemented together with water gathered from sources outside of the nest.

It has been generally considered that two methods of provisioning exist among bees, progressive and mass (Stephen *et al.* 1969). In progressive provisioning, the food is supplied to the larvae at intervals, the amount and interval of feeding corresponding to the needs of the individual larvae. In mass provisioning, a full complement of food is provided each cell before the egg is laid (Stephen *et al.* 1969). Food stored by bees ranges from liquid honey to nearly dry, friable masses of pollen. Mass-provisioned food is always a mixture of pollen and nectar, but it may include a glandular additive (Michener 2000). The decrease in the amount of pollen provisioned in the cell during the season, if correct, is interesting. It may indicate intense competition for pollen among females, and in fact females fight each other for pollen when large amount is available (Gilbert *et al.* 1999). Alternatively, it may indicate scarcity of their favorite *Alkanna* pollen as the season progresses.

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الملخص العربى

سلوك بناء العش لنحلة *أنثوفورا بيوبوراتا* (رتبة غشائية الأجنحة – فصيلة أنثوفوريدى) في النظام البيئي لسانت كاترين – سيناء

فايز محمد محمد صميدة

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تم دراسة سلوك بناء العش للنحل الانفرادي المعيشة "*انثوفورا بيوبوراتا*" والذى يبني أعشاشه فى التربة . وذلك بوادى الاربعين – سانت كاترين خلال فصلى الربيع والصيف من ١٩٩٦ الي ١٩٩٨. ومن خلال الدراسة أتضح أن ذلك النحل يميل لبناء أعشاشه فى المنحدرات الخفيفة على جانبي بطن الوادى حيث التربة الملائمة لبناء العش. وتحفر بعض اناث ذلك النحل أعشاشها فى التربة بعمق يصل الى ١٧ سم بينما يعشش البعض الآخر قريبا من السطح (٤سم). ويتم حفر العش وتكوين الخلايا فى وقت الظهيرة بينما تخصص فترتي الصباح وما بعد الظهيرة لامداد الخلايا بحبوب اللقاح والرحيق الذى تجمعه من أزهار نبات اللبيد. وتستطيع النحلة بناء حوالي خمسة أعشاش متفرقة خلال فترة حياتها، ويحوي كل عش من خليتين الى أربعة خلايا مرتبة على شكل عنقودي ومثبتة فى نهاية نفق يربطها بفتحة العش. وتتناسب أبعاد العش مع أبعاد جسم النحلة البالغة. كما تم وصف تركيب وشكل العش تفصيليا.