

Territoriality and foraging behaviour of some solitary wasps in Egypt

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ABSTRACT

The daily and seasonal abundance including the foraging behaviour of some solitary wasps were observed in two different ecosystems (agricultural & natural desert areas) in the Governorate of Port Said, Egypt. The results showed that numbers varied considerably in the different seasons of the year. All species of wasp show peaks of abundance in spring or summer, rarely in autumn, and they disappear in winter. Daily abundance peaked between 9 - 11 am, disappearing completely by 12 am. All species normally have a unimodal activity peak, but this becomes bimodal on hot days. The frequency of flower visits is higher in males than females, perhaps because males may carry smaller volumes of nectar than females. Males became increasingly scarce relative to females as the season progressed.

KEYWORDS: solitary wasps, territoriality, foraging, Port Said, Egypt

INTRODUCTION

In Egypt, the aggressive black and yellow wasp (*Polistes dominulus*) and the brown-yellow hornet (*Vespa orientalis*) are the most common social insects: female workers co-operate with their sisters and their mothers in the maintenance of a colony that may contain hundreds of individuals. Solitary wasps, on the other hand, do not collaborate in this way. Each female makes a nest of some sort for her own young (Corbet & Yeo 1983). The mother wasp has no contact with her offspring after laying her eggs, and hence she provides them with a complete food supply (Eickwort 1981). Most adult wasps feed exclusively on carbohydrates derived mainly from the nectaries of flowers and the honeydew of aphids, and the larvae of these species are generally carnivorous. Solitary wasps have complex behaviour patterns; their daily activities can be specified as foraging, flying (Abraham 1982), digging (Brockmann 1979), and provisioning (Evans *et al.* 1980).

The nesting and foraging behaviour of solitary wasps is well studied. Digger wasps (Sphecidae) generally prefer sandy habitats, exposed to the sun: they can nest

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gregariously in dense aggregations (Larsson 1986), and in some species, such as *Sphex*, two or more females share the same nest (Brockmann & Dawkins 1979). Female *Rubrica surinamensis* nests in a wide variety of habitats, in bare areas cleared of rocks and vegetation, or in scrubby woodland, or even in much harder and coarser soil (Evans et al. 1974). Many solitary ground-nesting wasps in the families Pompilidae and Sphecidae only excavate nests after capturing prey for provisions (Rosenheim 1990).

Solitary wasps are very sensitive to changes in weather. Just before rain, some species return from foraging to the nest without prey (Nachtigall 1983). Two major factors determining foraging behaviour and activity patterns in nectar foraging insects are quality and quantity of floral resources (including sugars, amino acids & water) and microclimate (Corbet et al. 1993). For example, the maximum activity of the beewolf, *Philanthus triangulum*, was in August, but then the abundance decreased sharply in November as the dominant weather factors (relative humidity, maximum and mean temperature) affected greatly the number of foraging beewolves (Eshbah et al. 1995). The activity of *Anoplius viaticus* (Pompilidae) began when the air temperature reached approximately 17°C: at high temperatures, females moved very rapidly in the manner typical for the group, running interspersed with short flights, while at lower temperatures, they could only walk (Field 1992). Overwintered females of *Larra argentata* began nesting during the first warm spring days (O'Brien & Kurczewski 1982).

In their predatory behaviour, solitary aculeates are mainly predatory wasps which paralyse their prey before carrying it into the nest to feed their larvae (Fabre 1855). Sphecid wasps have a wide range of hosts including Orthoptera (Malyshev 1968), Araneidae (Eberhard 1970), Acrididae (Roth 1928), Homoptera (Bohart and Menke 1976), Diptera (Elliott et al. 1979) and Hymenoptera (Iwata 1972).

In the paper, we study the seasonal and diurnal patterns of abundance, and the foraging behaviour of solitary wasps common on the Mediterranean coast in the Port Said area.

MATERIALS AND METHODS

Two different sites were chosen to conduct these observations. The first site, located 5 km south of Port Said (El-Raswa) represents an agricultural ecosystem with vegetation cover dominated by *Medicago* sp., and few patches of *Lathyrus odoratus*, *Ficus nitida*, *Lantana camara*, *Dunata* sp., *Calendula* sp. and *Rosmarianus officinalis*. The second site situated about 8 km south-east of Port Said, near Port Foad, represents a natural sandy area with sparse vegetation of wild plants, such as *Senecio* sp. and *Casuarina* sp. Each site was visited four times per month (Oct 1997 - Sept 1998). Daily temperature and relative humidity were recorded half a metre above the ground using a digital thermohygrometer. To determine the daily abundance of wasps, an ordinary sweep net was used. In each visit, sampling occurred from 7am to 6pm. Five sweeps were done each hour within each site, and the collected wasps identified and counted. Selected areas were observed from sunrise to dusk, recording all the major activities of solitary wasp species, including flying, feeding, basking in the sun, resting in the shade, chasing, mating and nesting.

Data gathered during the study period were tabulated. Temperature, relative humidity, seasonal abundance and daily abundance were expressed as means \pm standard error. The data were analysed using one way Analysis of Variance (Anova).

RESULTS

The average temperature and relative humidity in both agriculture and desert sites are presented in Table 1. The pattern of temperature and humidity variation was similar in the two sites, reaching a maximum of 32-33 °C in summer, and a minimum of 16-17 °C in winter.

Table (1): Average temperature and relative humidity in the two studied areas during the period of investigation (1997-1998).

| Month | Site I (Agriculture) | Site II (Desert) | Site I (Agriculture) | Site II (Desert) |
|-----------|-------------------------|---------------------|-------------------------|---------------------|
| | Temp. (°C) | RH (%) | Temp. (°C) | RH (%) |
| January | 17 ± 1.0 | 62 ± 0.8 | 18 ± 0.5 | 56 ± 0.9 |
| February | 16 ± 1.0 | 61 ± 0.9 | 17 ± 0.5 | 55 ± 0.8 |
| March | 19 ± 0.9 | 58 ± 0.9 | 20 ± 0.5 | 54 ± 0.7 |
| April | 21 ± 1.9 | 57 ± 0.8 | 22 ± 2.1 | 52 ± 0.9 |
| May | 23 ± 0.8 | 59 ± 0.7 | 25 ± 0.3 | 54 ± 0.8 |
| June | 27 ± 0.7 | 65 ± 0.9 | 28 ± 1.0 | 59 ± 0.8 |
| July | 31 ± 0.8 | 67 ± 1.0 | 31 ± 0.8 | 61 ± 0.9 |
| August | 32 ± 0.5 | 64 ± 0.9 | 33 ± 0.5 | 56 ± 0.9 |
| September | 30 ± 0.5 | 59 ± 0.8 | 30 ± 0.8 | 53 ± 1.0 |
| October | 24 ± 0.9 | 57 ± 1.0 | 23 ± 0.9 | 52 ± 0.9 |
| November | 20 ± 0.9 | 56 ± 0.9 | 20 ± 0.8 | 50 ± 0.8 |
| December | 18 ± 1.0 | 55 ± 0.8 | 19 ± 1.0 | 50 ± 0.9 |

In the agricultural ecosystem, only one species was observed (*Larra anathema*: (Sphecidae). The species was common from April to August, and abundant during June, disappearing between September and March (Figure 1). In April/May, female activity began at 8 am, reaching a maximum around 11am, and then activity decreased to a minimum by 1 pm. In the summer (June to August), females had a bimodal activity pattern, i.e. one peak was in the morning between 9 - 11 am, and another was between 2 - 4 pm. Males were unimodal, starting activity at about 9 am, and reaching a maximum at 11 am.

Females spent their time feeding, flying, resting and basking. They began their period of activity by flying from their nests, but with no visits to flowers. In the morning, a substantial proportion of females were seen basking (20-50%), and the rest were mainly seen flying and visiting the flowers. In the afternoon (12 pm), more than 80% of females were found resting in the shade, with the remaining females flying about without visiting flowers: few were basking. By late afternoon (2 pm), about 90% were flying, with only a few resting in the shade and no visiting or basking activity.

Females of *Larra anathema* tend to search in a moist muddy area for a suitable nesting place. One female was observed digging a nest in August at 3 pm; it tested the ground several times with its antennae, dug with its mandibles, using its front legs to remove the mud. The whole process lasted about fifteen minutes for digging one cell, about 7 cm in length.

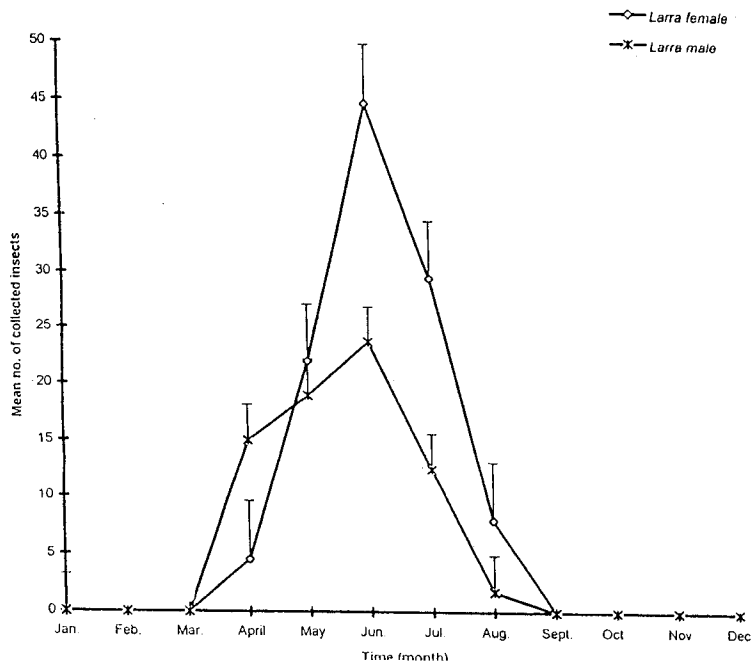


Figure 1: Seasonal abundance of *Larra anathema* collected from agriculture area (site 1) during the period from Oct 1997 to Sept 1998.

In the natural desert site, three species were observed: *Dielis collaris*, *Scolia erythrocephala* (both Scoliidae) & *Bembix oculata* (Sphecidae).

Dielis collaris (Figure 2) appeared first in April. Fewer were seen in May, but numbers gradually increased again in June, reaching a maximum in August. No wasps were collected between September and March. In April/May, female activity began at 8 am, but earlier at 7 am in June-July. Females had a bimodal activity pattern, peaking at 10 am and 3 pm. Males began activity at about 9 am, and reached a maximum at 11 am. Females began their activity in the early morning by flying (80%), with only a few individuals seen basking. Later on in the day about 80% of females were seen basking in the sun. At 1 pm, no individuals were recorded visiting flowers, while the majority (about 90%) were seen flying. Males were seen visiting the flowers at high frequency, and spent more time on the flowers than females.

Scolia erythrocephala (Figure 2) first appeared in late May, reaching a maximum in July; numbers then gradually decreased, disappearing in September. No wasps were collected between September and April. Female daily activity began at 8 am in April/May, and at 7 am in summer. Female had a bimodal activity pattern, reaching maxima at 10 am and at 3 pm. Males began their activity at 9 am, reaching a maximum at 11 am, and then gradually decreasing. In the morning about 50% of females were seen beginning to visit the flowers for nectar, with only a few basking in the sun. By 10 am, females divided their activity equally among basking, feeding, flying and resting. By late afternoon (3 pm), more than 50% of females were seen resting in the shade.

Bembix oculata (Figure 2) was common by late April, reaching a maximum in June, and then decreasing gradually between July and August. No individuals were observed between September and early April. Females began their activities at 8 am, reaching a maximum at 10 am, and then gradually decreased, reaching minimum activity around 1 pm. It was obvious that in spring (April-May) female activity had one peak, but in the heat of June-August there were two peaks of activity, the first one at 10 am and the second one in the late afternoon, around 3 pm. Males began to be active at 9

am, reaching maximum activity at 11 am. All females started their activities by flying, with no visits to flowers. The maximum period of basking was around 9 am, at which time more than 30% of females were seen visiting flowers. By late morning (11 am), more than 60% of females spent their time resting with a few females being seen visiting flowers or flying. Females stopped basking in the afternoon. By late afternoon (2 pm), more than 90% of females were seen flying, with few visiting flowers.

One female was seen digging her nest at the end of May. While searching for a place to dig, she moved in a zigzag manner and hovered, and after landing she knocked the sand with both antennae, probably trying to test the desired site for its suitability. After a while (3-5 min), she began to excavate a burrow using her mandibles to loosen the substrate, and her forelegs to remove the accumulated sand. It took her about 15-20 minutes to dig a one-celled nest 21-22 cm long and 0.5 cm wide. The nest was shallow and oriented obliquely. The female then spent some time in the nest, perhaps for egg laying. After a while she left the nest. At the end of the day, she closed the nest entrance, using the accumulated sand to hide it from being seen.

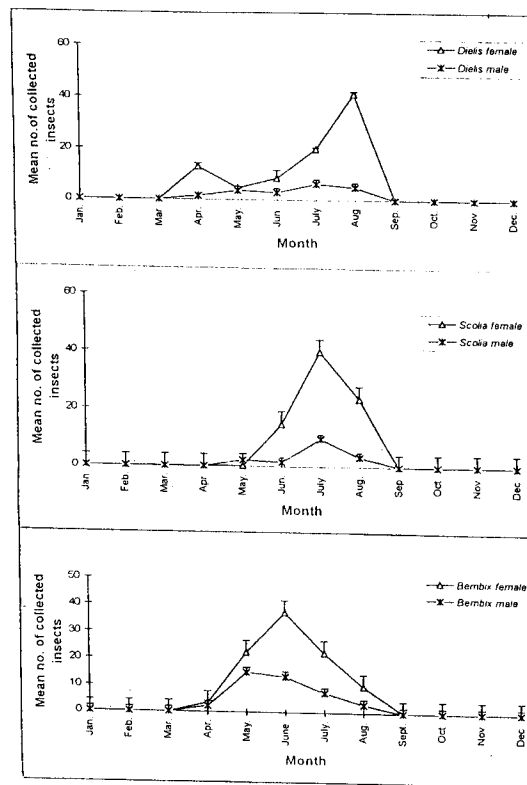


Figure 2: Seasonal abundance of the three species (*Dielis collaris*, *Scolia erythrocephala* & *Bembix oculata*) collected from desert ecosystem (site 2) during the period from Oct 1997 to Sept 1998

DISCUSSION

Most of the species of solitary wasp began their activities in April, and disappeared in cold weather from September until March, except *Scolia erythrocephala* which started in May. These results lead to the suggestion that the weather plays an important role in

determining the activities and the frequency of insect visits to flowers, as high activity and visitation rates are associated with warm conditions. *Dielis collaris* was abundant during summer (August) on *Senecio* sp., while the maximum activity of *Scolia erythrocephala* was in July: this may be because by July, the soil is very dry and many plants have died, and these conditions suit the activities of Scoliidae (Day et al. 1981). The first appearance of *Bembix oculata* was in the second half of April, presumably when the temperature was first suitable for their activities; the cost of flight activity and endothermic heat generation at low temperature may be too high earlier in the season (Ghazoul & Willmer 1994), or may be due to the absence of their prey. *Bembix* was abundant in June. *Larra anathema* began its activity in April with maximum activity in June, as in *Bembix oculata*. We can conclude that all wasps are mostly found in spring and summer in this area, and only rarely in autumn.

In all species, males became active a few days before females; this is a very common pattern in many species of insect, and may give an opportunity to mate with unmated, recently emerged females (Bulmer 1984). The foraging activity of all species found in the studied areas took place earlier (7 am) in June than in April (8 am), probably due to reaching a temperature threshold for activity earlier. The spring diurnal activity of these wasps indicated that the first foraging activity took place early in the morning with peak at midday with minimum activity at late afternoon (cf. Maingay et al. 1991). The activity of all species was unimodal on temperate days and bimodal on hot days. This is probably due to the very high temperature in the afternoon, during which females cannot continue being active, but must avoid the danger of overheating during the hottest period of the day (Pivnick & Neill 1987). Alternatively, this may be the time females spend egg laying.

These daily patterns of activity in wasps may have evolved in response to ecological factors. Females may use the first flight to provide their own food supply (nectar). During early morning, wasps pressed their bodies to the sun-warmed ground to elevate body temperature above ambient by basking. At the start of the day, they lack the initial energy necessary to warm up endothermically, an extremely costly process. During the heat of midday, females fly up off the hot soil surface and rest in the shade in grass clumps or near vegetation, and basking activity declined rapidly in the late afternoon. This is further evidence that temperature is the most important factor influencing wasp activity. Males also bask like females in early morning and maintain high thoracic temperature, but when the air temperature increased the basking activity decreased abruptly (cf. Stone et al. 1995). The frequency of flower visits is higher in males than females, perhaps because males carry much smaller volumes of nectar than females (Stone 1995).

Males became increasingly scarce relative to females as the season progressed and they did not participate in any aspect of the nest activities. *Bembix* nest gregariously, and females tend to build successive nests in the same area. Nests are built in sandy soil, and females did not close their entrance when going foraging, as in *Tachysphex acutus* (Kurczewski 1989). Female *Dielis* and *Scolia* were not seen building nests, but were observed to walk between grasses on the ground, probably searching for subterranean beetle larvae (Piek et al. 1983; Day et al. 1981).

REFERENCES

- Abraham R (1982) Zur Biologie von *Trypoxylon attenuatum* smith, 1851 und *T. figulus* (Linnaeus, 1758) (Hymenoptera: Sphecidae) Entomol. Mitt. Zool. Mus. Hamb. 114: 137-147.

- Bohart RM & Menke AS (1976) Sphecoid wasps of the world: a generic revision. Univ. of California Press, Berkeley.
- Brockmann HJ (1979) Nest site selection in the great golden digger wasp, *Sphex ichneumoneus* L. (Sphecidae). *Ecol. Entomol.* 4: 211-224.
- Brockmann HJ & Dawkins R (1979) Joint nesting in a digger wasp as an evolutionarily stable preadaptation to social life. *Behaviour* 17: 203-245.
- Bulmer MG (1984) Risk avoidance and nesting strategies. *J. Theor. Biol.* 106: 529-535.
- Corbet SA, Fussell M, Akre R, Fraser A, Gunson C, Savage A & Smith K (1993) Temperature and the pollinating activity of social bees. *Ecol. Entomol.* 18: 17-30.
- Day MC, George ER & Morgan D (1981) The most primitive Scoliidae (Hymenoptera) *Journal of Nat. history* 15: 671-684.
- Eberhard WG (1970) The predatory behaviour of two wasps, *Agenoideus humilis* and *Sceliphron caementarium* on the orb weaving spider, *Araneus cornutus*. *Psyche* 77: 243-251.
- Eickwort GC (1981) Presocial insects. In: *Social Insects*. Hermann HR (ed.). 11: 199-280. Academic Press, New York.
- Elliott N, Kurczewski FE, Claflin S & Salbert P (1979) Preliminary annotated list of the wasps of San Salvador Islands, the Bahamas, with a new species of *Cerceris* (Hym.: Tiphidae, Scoliidae, Vespidae, Pompilidae, Sphecidae) *Proc. Entomol. Soc. Wash.* 81: 352-365.
- Eshbah HM, Attalla MA, Shoriet MN, Mohmoud AA & Omar MS (1995) Ecological studies on the bee wolf *Philanthus triangulum* (Fabricius) in Dakhla Oasis, new valley, Egypt. *6th Nat. Conf. of Pest. Diseases of Vegetables & Fruits in Egypt*. 101-117.
- Evans HE, Matthews RW & Callan E (1974) Observations of the nesting behaviour of *Rubrica surinamensis* (De Geer). *Psyche* 81: 334-352.
- Evans HE & Kurczewski FE & Alcock J (1980) Observations on the nesting behaviour of seven species of *Crabro* (Hymenoptera: Sphecidae). *J. Nat. Hist.* 14: 865-882.
- Fabre JH (1855) Observations sur les moeurs de *Cerceris* et sur la cause de la longue conservation des coleopteres *dontils* approuvisiement leurs larves. *Annl. Nat.* 4: 129-150.
- Field J (1992) Guild structure in solitary spider-hunting wasps (Hym: Pompilidae) compared with null model predictions. *Ecol. Entomol.* 17: 198-208.
- Ghazoul J & Willmer PG (1994) Endothermic warm-up species of sphecoid wasp: a relation to behaviour. *Physiol. Entomol.* 19(2): 103-105.
- Iwata K (1972) Evolution of Insects. Comparative studies of Hymenoptera behaviour. Amerind Publ., New Delhi.
- Kurczewski FE (1989) Ecology, mating and nesting of *Tachypompilus ferrugineus nigrescenc* (Hym: Pompilidae). *Great Lakes Entomologist.* 22: 75-78.
- Larsson FK (1986) Increased nest density of the digger wasp *Bembix rostrata* as a response to parasites and predators (Hymenoptera: Sphecidae). *Entomol. General.* 12(1): 71-75.
- Malyshev SI (1968) Genesis of the Hymenoptera and phases of their Evolution (Transl. from Russian by Richards OW and Uvarov B, eds.). Methuen, London.
- Nachtigall W (1983) Zum Einflug verhalten der sandknoten Wespe, *Cerceris quadrifasciata*, bei schon Wetter und Witterung zum Schwung. *Entomol. Gener.* 8: 283-285.
- O'Brien MG & Kurczewski FE (1982) Ethology and overwintering of *Podalonia luctuosa* (Hym.: Sphecidae). *Great Lakes Entomologist.* 15: 261-275.
- Piek T, Buitenhuis A, Simonthomas RT, Ufkes JGR & Mantel P (1983) Smooth muscle contacting Factors in the venom *Megascolia flavifrons*. *Comp. Biochem. Physiol.* 75(C): 145-152.
- Pivnick KA & Neill MC (1987) Diel patterns of activity of *Thymelicus lineola* adults (Lepidoptera: Hesperidae) in relation to weather. *Ecol. Entomol.* 12: 197-207.
- Rosenheim JA (1990) Aerial prey catching by solitary ground-nesting wasp: A test of the predator defence hypothesis *J. Insect Behaviour.* 3: 241-250.
- Roth P (1928) Les ammophiles de l'afrique du nord (Hym.: Sphecidae). *Ann. Soc. Entomol. Fr.* 97: 153-240.
- Stone GN (1995) Female foraging responses to sexual harassment in the solitary bee *Anthophora plumipes*. *Anim. Behav.* 50: 405-412.
- Stone GN, Loder PMJ & Blackburn TM (1995) Foraging and courtship behaviour in males of the solitary bee *Anthophora plumipes* (Hym.: Anthophoridae), thermal physiology and the roles of body size. *Ecological Entomology* 20: 169-183.

الملخص العربي

النشاط اليومي والموسمي وسلوك البحث عن الغذاء لبعض أنواع الزنابير
الإنفرادية في مصر

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تم دراسة النشاط اليومي والموسمي شاملاً سلوك البحث عن الغذاء لبعض أنواع الزنابير الإنفرادية في نوعين من النظم البيئية (نظام بيئي زراعي ونظام بيئي صحراوي) في محافظة بورسعيد. ولقد أوضحت النتائج تباين تواجد أنواع الزنابير الإنفرادية خلال المواسم المختلفة حيث أنتشرت الأنواع ووصلت إلى أعلى معدلات للتواجد خلال فصل الربيع والصيف، وندرت خلال الخريف، وأختفت تماماً خلال فصل الشتاء. أيضاً أوضحت دراسات النشاط اليومي أن الزنابير الإنفرادية تبدأ نشاطها في حوالي الساعة التاسعة صباحاً لتصل إلى أعلى معدلات التواجد خلال الفترة من ٩ حتى ١١ صباحاً وتختفي في فترة الظهيرة. وضح أيضاً أن الزنابير الإنفرادية تنشط في فترة واحدة صباحاً في الأيام ذات الجو المعتدل، وتصبح ثنائية النشاط (فترة صباحية وأخرى مسائية) في الأيام شديدة الحرارة. أوضحت النتائج أن تواجد زيارات ذكور الزنابير للإزهار أعلى من الإناث وربما يعود هذا إلى أن الذكور تقوم بجمع كميات قليلة من الرحيق مقارنة بالإناث. وأخيراً وجد أن أعداد الذكور تتناقص في نهاية الموسم مقارنة بأعداد الإناث وربما يرجع هذا إلى ميل الإناث إلى بناء الأعشاش ووضع البيض في نهاية الموسم حتى تكتمل دورة حياة الأنواع.