

Windows of opportunity and the temporal structuring of foraging activity in a desert solitary bee

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Abstract. 1. Females of the desert solitary bee *Anthophora pauperata* collect nectar and pollen almost exclusively from *Alkanna orientalis* (Boraginaceae). The bee and plant are found together in the early spring, living in the bottom of steep-sided wadis (dry river valleys) at an altitude of 1500 m in Egyptian Sinai.

2. Female *A. pauperata* showed clear morning and afternoon peaks in foraging activity, separated by a 2–3 h midday period spent in their underground nests. This study analyses the following in order to identify the factors structuring this daily pattern: thermal aspects of the bee and its environment, temporal patterns of resource provision by the plant, and female nectar and pollen foraging behaviour.

3. Although *A. pauperata* can generate substantial heat endothermically, morning and evening ambient temperatures well below 10 °C defined a thermal window within which foraging occurred. Maximum air temperatures were moderate (25–30 °C), and examination of the physiology and behaviour of *A. pauperata* suggests that the midday reduction in flight activity was not due to thermal constraints.

4. *Alkanna orientalis* produces protandrous hermaphroditic flowers. Female *A. pauperata* collected pollen from male-phase flowers and harvested nectar preferentially from female-phase flowers. Although the nectar standing crop was relatively constant throughout the day, pollen availability peaked strongly in the early afternoon.

5. Female *A. pauperata* visited young male-phase flowers as soon as they opened, generating an early afternoon peak in pollen foraging activity and depleting the pollen standing crop rapidly. A morning peak in pollen foraging occurred when females gleaned remnant pollen from flowers that had opened the previous day. Pollen availability in the morning was far lower than in the early afternoon, and the time taken to collect a full pollen load in the morning was significantly longer. Collection of pollen in the morning despite very low resource availability suggests that pollen may be a limiting resource for *A. pauperata*.

6. In contrast to many existing examples of bimodal activity patterns in highly endothermic bees, the bimodal activity patterns of female *A. pauperata* appear to be driven not by thermal considerations but by daily patterns of pollen release from its principal food source.

Key words. Foraging, nectar, pollination, solitary bees, thermoregulation.

Introduction

Temporal patterns of animal behaviour result from choices between available options whose relative values change through time (Krebs & Kacelnik, 1991). Examination of the factors underlying activity patterns not only provides information on the costs and benefits of particular behaviours, but may also reveal important physiological or economic constraints acting on animals (Mace, 1987; McNamara *et al.*, 1987). For most female solitary bees (Hymenoptera: Apoidea), daily activity patterns involve the construction of a nest cell, provisioning with pollen and nectar, laying an egg on the finished provision, and finally sealing the cell before beginning the construction of another (e.g. Willmer, 1986; Willmer & Stone, 1988). Natural selection should act on female behaviour to structure these activities in time so as to maximize inclusive fitness (Krebs & Kacelnik, 1991). Thus it should be possible to interpret observed temporal patterning of these behaviours in terms of variation in costs of activity and in the quality and quantity of resources collected by a bee (Bertsch, 1983).

Allocation of time to daily activity occurs within constraints imposed by diurnal variation in physical factors; very few bees forage at night, and most species can forage only within a particular range of ambient temperatures during daylight (Chappell, 1982, 1984; Willmer, 1983, 1985; Stone, 1994a). With the exception of very small species, bees warm up endothermically before flight, and the ambient temperatures experienced while foraging have had important evolutionary consequences for this endothermic ability (Stone & Willmer, 1989; Stone, 1994b). Species active at low ambient temperatures typically show high levels of heat generation, but may overheat at high ambient temperatures. In contrast, bees active at high ambient temperatures may tolerate high body temperatures, but typically show lower levels of endothermy and cannot fly at lower ambient temperatures. The conflicting requirements of flight at low and high ambient temperatures mean that the range of temperatures at which a bee can fly is limited. Furthermore, in environments with wide daily fluctuations in ambient temperatures, such as many deserts, activity may be constrained to a given part of the diurnal range, or *thermal window* (Chappell, 1982, 1984; Willmer, 1983, 1986; Gilbert, 1985; Herrera, 1990; Willmer & Stone, 1997). Limits to the thermal window may lie within the absolute physiological limits of the bee, and be determined by the temperatures at which endothermic regulation of flight muscle temperature is uneconomic (e.g. Stone, 1993).

The quantity and quality of available floral nectar and pollen also often change throughout the day. Daily cycles in relative humidity determine when anthers dehisce, and also influence the volume and concentration of nectar available in flowers (Corbet, 1978; Corbet *et al.*, 1979; Bertsch, 1983; Stone *et al.*, in press). Longer-term responses of nectar to environmental humidity and active secretion/resorption processes in the plant mean that flowers of different ages on a plant also often differ in the quality and quantity of resources presented to foragers (Corbet & Delfosse, 1984; Nicolson, 1993; Gonzalez *et al.*, 1995). Female bees are thus faced with a range of floral resources that change in quality and quantity with time

(Harder, 1986; Kacelnik *et al.*, 1986; Kadmon *et al.*, 1991; Kadmon & Shmida, 1992). Bees can assess the quality and quantity of pollen and nectar available in flowers, and use a variety of cues to distinguish among flower age groups (Harder, 1988; Buchmann & Cane, 1989; Gonzalez *et al.*, 1995).

To understand the influence of resource availability on foraging behaviour, it is therefore necessary to assess (1) temporal variation in floral rewards as a result of daily rhythms of release or of flower ageing, and (2) forager preferences for a particular subset of the available resources. Understanding activity patterns thus requires teasing apart the underlying interactions between these factors, and in natural systems the interactions involved can be extremely complex (e.g. Frankie *et al.*, 1983; Herrera, 1987, 1988, 1990; Stone *et al.*, 1996, in press). The system studied here is unusual in that it effectively comprises only one plant species and one bee species (Willmer *et al.*, 1994; Gilbert *et al.*, 1996), allowing detailed examination of the interactions among microclimate, pollen and nectar provision by the plant, and pollinator physiology and foraging behaviour. *Alkanna orientalis* (L.) Boiss. (Boraginaceae) is a desert herb that provides almost the entire pollen and nectar requirements of a solitary bee species, *Anthophora pauperata* Walker 1871 (Hymenoptera: Anthophoridae), during spring in Sinai, Egypt. *Alkanna orientalis* grows at altitudes above approximately 1500 m in the bottom of extremely arid, steep-sided dry valleys (wadis), subject to wide daily fluctuations in temperature and humidity. Previous work has shown that foraging by *A. pauperata* shows a daily bimodal pattern (Willmer *et al.*, 1994), prompting the question of what structures their behaviour. Here the following questions are addressed: (1) Do daily fluctuations in ambient temperature define a thermal window within which bee activity is possible? Can avoidance of thermal stress explain the observed midday drop in foraging activity? (2) Is the observed bimodality a response to temporal variation in floral resources? Analysis of floral resources requires consideration of two components. First, patterns of resource provision by the plant are described, including timing of pollen and nectar release, and changes in the characteristics of these resources (particularly nectar) as flowers age. Second, the foraging preferences of female bees for flowers of particular ages and resource qualities are quantified. Combining these components allows identification of underlying patterns in availability of preferred resources that might structure female activity patterns.

Materials and methods

Study sites

This study was carried out principally in March and April 1994, with additional data from the same months in 1992 and 1996, at the St Katherine Field Station of Suez Canal University, southern Sinai, Egypt (latitude 34°E, longitude 28.6°N; Willmer *et al.*, 1994; Gilbert *et al.*, 1996). *Anthophora pauperata* is a strongly protandrous species, and because sexual interactions may have complex effects on female

foraging behaviour (Willmer *et al.*, 1994; Stone, 1995), the study period chosen represents the latter part of the *A. pauperata* season, during which females are far more abundant than males.

The plain of St Katherine lies at approximately 1600 m, and steep-sided wadis radiate between mountain ridges rising to approximately 2400 m. The environment is extremely arid, with 60 mm of rain per year, concentrated in the winter months. In the spring, clear skies and intense solar radiation during the day result in a rapid heat gain from the sun, followed by a rapid cooling in the subsequent shade. The orientation of a wadi to the sun determines the period that it receives direct sunlight during the day, and hence the diurnal patterns of temperature fluctuation.

Alkanna orientalis grows most abundantly in wadi bottoms (Gilbert *et al.*, 1996). Each plant forms a discrete clump, reaching 1 m in diameter and bearing up to 700 bright yellow flowers, although the majority of the plants bear 100–300 flowers. *Alkanna* flowers were far more abundant than those of any other species during the study period, and were effectively the only food source for *A. pauperata*. Similarly, more than 99% of bee visitation to *A. orientalis* during the study period involved *A. pauperata*. *Anthophora pauperata* and *A. orientalis* (henceforth referred to as *Anthophora* and *Alkanna*) were studied at three locations selected because they experience differing microclimates: the central Plain, a flat expanse of sandy soil and rock exposed to the sun for most of the day; Wadi Arbaein, a steep rocky gorge running for 2 km southeast from the plain; and Wadi Tofaha, an even steeper and rather narrower gorge running for 1 km south from the plain.

Microclimate

Three measures of ambient temperature were used to describe the different thermal environments experienced by *Anthophora*: shade air temperature 1 m above the ground, and two measures of standard operative temperature (Bakken, 1976; Chappell & Bartholomew, 1981; Chappell, 1982). Standard operative temperatures were obtained using a copper-constantan thermocouple 0.5 mm in diameter inserted into the body of a dried *A. pauperata* and connected to a P.I.8013 meter (Portec, U.K.). Such a measure estimates more accurately the combined effects of air temperature, air movement and solar radiation for a living individual than does an unspecialized thermometer. The two standard operative temperature measures used were the standard operative temperature in the sun, with the dried *A. pauperata* held 15 cm above the ground, and the standard operative temperature on the ground, with the bee-covered thermocouple placed in contact with the ground surface in a lifelike attitude.

Humidity was measured using a Vaisala HMI 31 humidity and temperature probe (Vaisala U.K., Newmarket, U.K.). When studying nectar standing crop, humidity and temperature were recorded with the sensor next to flowers on the plant

being examined. Light levels were measured using a dome light meter (LX-101, Lutron, Micropulse Technology, Fenstanton, U.K.) held horizontally at the same height as the flowers.

Anthophora activity

Female activity patterns were quantified at forage plants and at nest sites. At each recording interval, the numbers of *Anthophora* females visiting a given plant, or part of a larger foraging area, were counted over a 30-min observation period. To control for variation in the attractiveness of *Alkanna* plants to foragers, plants with similar numbers of flowers were observed at each site. Patterns of ambient temperature and bee activity over time are presented for representative days in the 1994 field season; very similar patterns were recorded at the same study sites in 1992 and 1996.

Activity patterns observed at flowers were corroborated by watching known nest entrances throughout the day at Wadi Arbaein in 1994. Trips were identified as pollen-collecting (with or without nectar) if the scopae were loaded with pollen, and as nectar-only if the scopae were clean. Periods of digging and nest construction were identified whenever a bee ejected loose material from the nest entrance or made the buzzing noises characteristic of excavating *Anthophora* (Norden, 1984; Stone, 1994a). The duration of periods within and away from the nest was timed with a stopwatch.

Bee body temperatures and thermoregulatory ability

Anthophora species regulate thoracic temperatures during flight and will not fly if these fall below or rise above a narrow range (Stone, 1993). The lower limit is defined by the ambient temperature at which the bee can attain the minimum thoracic temperatures required for flight, and the upper limit by the maximum ambient temperature at which flight is possible without critical overheating. If the ambient temperatures encountered during the day in the foraging environment lie outside this range, activity may be constrained to occur within a thermal window.

Lower ambient temperature limits to foraging can be identified by observing female foraging behaviour directly. As the temperature falls towards the lower limit of physiological thermoregulation, bees bask for longer and longer periods until foraging is no longer possible (e.g. Stone, 1994a; Stone *et al.*, 1995). Behavioural thermoregulation in *A. pauperata* was therefore quantified by recording the time females spent basking on stones and the soil surface, and the temperatures achieved by standard operative temperature models placed in the same positions.

Lower ambient temperature limits to foraging can also be assessed indirectly by measuring the rate of endothermic preflight warm-up. Endothermy is general in the genus *Anthophora*, and preflight warm-up rates correlate strongly with the minimum ambient temperature at which *Anthophora* species fly (Stone & Willmer, 1989; Stone,

1994b). Measurement of endothermic ability thus indicates whether a bee is principally adapted to fly at high or low ambient temperatures. The pre-flight endothermic warm-up rates of four female *A. pauperata* (fresh masses 98, 101, 116 and 128 mg, mean mass 111 ± 6 mg) were measured in the laboratory using a fine (40 gauge) thermocouple inserted to a shallow depth (≈ 0.5 mm) in the dorsal flight muscles. All measurements were made in the laboratory at ambient temperatures of between 20 and 22 °C, with the bee out of direct sunlight. These methods have already been applied to 19 other Mediterranean and Middle Eastern *Anthophora* species (Stone, 1994b), allowing direct comparison of the endothermic ability of *A. pauperata* with other *Anthophora* species found in similar habitats.

Upper ambient temperature limits to activity occur when a bee can no longer thermoregulate its thoracic flight muscles. This limit is indicated by a transition from a gradient of body temperature on ambient temperature of significantly less than one (indicating thermoregulation) to a gradient indistinguishable from (or greater than) one (inability to thermoregulate) with increasing ambient temperature. To establish whether the ambient temperature range encountered included this thermoregulatory limit, the thoracic temperatures of bees captured in flight in the field were measured using an inserted thermocouple (Stone & Willmer, 1989) and regressed against ambient air temperatures.

Anthophora foraging

Distinguishing forage types. *Anthophora* females harvest *Alkanna* pollen by inserting their long mouthparts into the corolla tube and sonicating the anthers with vibrations generated by the flight muscles. The loosened pollen accumulates on their mouthparts (Buchmann, 1983; Willmer *et al.*, 1994; Ahmed *et al.*, 1995) and is removed using the legs during flight between sonicating bouts. The buzz made during pollen gathering was clearly audible, and allowed pollen-collecting visits (with or without nectar) to be distinguished clearly from those in which only nectar was harvested. Some females also approached flowers but did not collect floral resources; these were termed approach visits. The distributions of these three visit types over time were compared using Kolmogorov–Smirnov two-sample tests (Sokal & Rohlf, 1981).

Quantifying the flower age preferences of foraging Anthophora. The proportions of flowers of each age group (see below) visited during individual foraging bouts were recorded. Data on the ages of flowers visited by bees were collected for six plants each at the Wadi Tofaha (31 March 1994) and Plain sites (29 and 31 March 1994). If bees visit flowers randomly with respect to age, each class should have been visited in proportion to its occurrence on the plant at that time. The correspondence between the observed and expected frequencies was assessed using *G*-tests for goodness of fit (Sokal & Rohlf, 1981). Total heterogeneity (G_T) was split into variation within (G_p) and between (G_h) bouts (Sokal & Rohlf, 1981).

Floral phenology and floral rewards

Categorizing flower age classes. Changes in floral morphology (colour and shape) associated with ageing were assessed by following a marked cohort of flowers from unopened bud until the corolla fell from the plant (see below). Four flower states of increasing age were recognized: (1) bud: flower a bright yellow, unopened bud; (2) male-phase flower: flower a bright yellow, petals parted but not yet fully open, the stage during which anther dehiscence takes place (Willmer *et al.*, 1994); (3) female-phase flower: flower fully open and still bright yellow, anthers empty and stigma projecting from the open corolla; (4) postreproductive flower: flower fully open, corolla fading to very pale yellow or white, stigma withered and probably unreceptive to pollen.

Observations of marked flowers in Wadi Arbaein ($n=21$) and the Plain ($n=20$) showed that flowers passed from bud to female-phase within a single day. Most flowers spent the second day in the female-phase, and a further 3–4 days as postreproductive flowers.

Temporal changes in flower age structure. Changes throughout the day in the proportion of all flowers on a plant belonging to a particular age class were examined in two similar ways. (1) To examine daily patterns of bud opening, the transition from closed bud to open flowers was followed for all the flowers on eight plants (mean number of flowers 140, range 41–215) in Wadi Arbaein on 25 March 1994. (2) The ages of 100 flowers were scored on a constant part of each of six individual plants at 1.5–2.0 h intervals throughout the day on the Plain on 29 March 1994 and at Wadi Tofaha on 31 March 1994, and each of five individual plants at Wadi Arbaein on 31 March 1994.

Nectar volume and concentration. *Alkanna* nectar accumulates at the base of a deep corolla tube (Gilbert *et al.*, 1996). To sample the nectar, the entire corolla was removed without disturbing the nectar, which was then collected with a micropipette of standard volume (Camlab, Cambridge, U.K.). Each flower was therefore sampled only once. Nectar volume was calculated from the length of the fluid column in the micropipette. The extended mouthparts of *Anthophora* are approximately 10 mm in length, capable of reaching any nectar in *Alkanna* flowers, and the volumes recorded are thus regarded as the volume available to foraging females. Nectar concentration (sucrose, % by mass) was measured immediately after collection with a pocket refractometer modified by the maker to operate with volumes ≥ 0.05 μ l (Bellingham & Stanley Ltd, U.K.). Mean total sucrose per flower was calculated using methods described by Bolten *et al.* (1979).

To examine patterns of secretion, half the flowers on one plant (a total of 500 flowers) were protected from foragers with white gauze (mesh size 1.5 mm) placed so that it did not contact the flowers. Each day for a week, nectar volume and concentration were recorded for five flowers of each flower stage. Changes in nectar properties over time after exclusion of foragers refer to flowers of a given age, not to the fate of a set

cohort of flowers, and so show what female bees would encounter at an unvisited flower of a given age.

To estimate standing crop in exposed flowers, 10 flowers were sampled randomly from each of six plants at each site and time interval. Means for each flower stage were then calculated in order to describe the resource available to flower visitors when visiting flowers of a particular stage at a particular time.

Pollen. Temporal patterns in the availability of pollen in *Alkanna* flowers were examined by dissection of two randomly chosen flowers of each age class from each of five plants every hour from 08.00 to 15.00 hours at Wadi Arbaein in March 1996. Different plants were used at each time interval. Data obtained for several successive days showed very similar patterns; only summary data for a single day are presented here. *Alkanna* flowers have two sets of anthers, three near the mouth of the corolla tube and two below these inside the corolla tube. For each of the five anthers in a flower, pollen availability was scored on a four point scale: 0=anthers undehisced, no pollen available; 1=pollen available in trace quantities up to <50% of maximum; 2=pollen available between 50% and maximum; 3=full dehiscence and maximum pollen availability. The two anther sets in each flower were scored separately, and the mean scores for each of the two sets added to give a score for the flower as a whole. Each flower could thus have a maximum pollen score of 6. For ease of comprehension, scores are expressed as the proportion of the maximum available. These scores do not allow arithmetical statistical tests, thus the data are presented graphically. Because the differences in pollen availability among the different flower ages observed are sufficiently marked, statistical tests are unnecessary.

Results

Diurnal patterns of female activity at A. orientalis

Female *Anthophora* showed bimodal foraging patterns at all sites, with clearly separated morning and afternoon peaks (Fig. 1). This pattern results from strong bimodality of pollen collection over time, because no bimodality was seen in nectar collection or approach visits. Observation of known nests confirmed the bimodal activity pattern seen at food sources. Females spent between 2 and 240 min away from their nests during foraging trips, which were concentrated in the morning and afternoon (Fig. 2). Female *A. pauperata* spent most of the middle of the day (approximately 3 h between 10.00 and 11.00 hours and 13.00 and 14.00 hours) underground (Fig. 2).

Ambient temperatures and female activity

Comparisons of microclimate and activity among sites. At each site, ambient temperatures rose rapidly after sunrise, and fell rapidly after each site became shaded (i.e. light intensity below 500 lux) (Fig. 3a,b,c). Air and ground surface tempera-

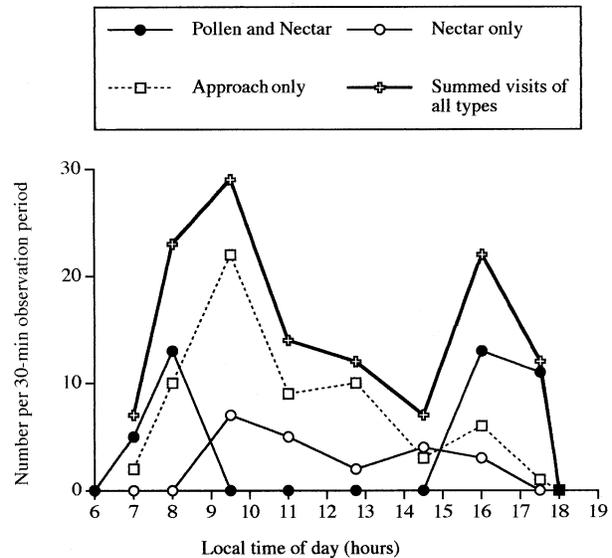


Fig. 1. Distribution of pollen-collecting, nectar-only, and approach visits at the Plain on 29 March 1994. Pollen visits have a significantly different temporal distribution from either nectar (Kolmogorov–Smirnov test $D=0.429$, $P<0.05$) or approach (Kolmogorov–Smirnov test $D=0.460$, $P<0.001$) visits.

tures rose from minima of 2–3 °C before dawn to maxima of 26.5 °C and 42.5 °C, respectively. The air was extremely dry, relative humidity falling from 40–60% before dawn to only 5–15% at approximately midday. There were significant differences among the three sites in the temporal patterns of microclimate (Fig. 3). The Plain was the least shaded by mountains, and received direct sunlight for longest (from ≈07.00–16.30 hours each day). The differing orientation of the wadis containing the other two sites meant that *Alkanna* patches received sunlight earlier in Wadi Arbaein than in Wadi Tofaha (07.50 as opposed to 09.10 hours), but were also shaded earlier (14.45 as opposed to 15.24 hours; Fig. 3a,b,c).

Significant differences in the temporal patterning of female foraging among the sites paralleled the differences in site microclimate (Fig. 3d). At each site, females became active after insolation in the morning, and stopped flying shortly after the sites were shaded in the afternoon. The morning peak in activity occurred earliest at Wadi Arbaein and the Plain and latest in Wadi Tofaha, corresponding to the timing of the arrival of direct sunlight at these sites. The evening peak finished first in Wadi Arbaein and persisted longest at the Plain, corresponding to the departure of direct sunlight from these sites (Fig. 3). The open aspect of the Plain site resulted in the longest exposure to direct sunlight, and correlated with the longest diurnal activity pattern in *A. pauperata*. These responses to site-specific variation in microclimate suggest that activity may be constrained within a thermal window.

Thermal physiology of *A. pauperata*. *Anthophora pauperata* is highly endothermic, with a mean preflight warm-up rate of

$7.4 \pm 0.6^\circ\text{C min}^{-1}$. This is similar to the rates of much larger temperate bumblebees and other Mediterranean and Middle Eastern desert *Anthophora* species of a similar size (Stone & Willmer, 1989; Stone, 1994b). Measurements of thoracic temperatures in flight indicate that *A. pauperata* is also an excellent thermoregulator; it regulates its thoracic temperature at approximately 37°C , and the gradients of the relationships between thoracic temperature and ambient temperature, whether measured as air temperature or standard operative temperature, are both close to zero (least squares linear regressions, with 95% confidence limits of slope in parentheses: shade air temperature: $y = 0.122(0.015\text{--}0.230)x + 35.44$, $n = 42$, $r^2 = 0.117$, $P < 0.05$; standard operative temperature: $y = 0.081(0.008\text{--}0.153)x + 35.97$, $n = 42$, $r^2 = 0.113$, $P < 0.05$).

At the onset of flight activity in the morning, females must raise thoracic temperatures approximately 20°C above ambient temperatures in order to fly. Long bouts of basking at low ambient temperatures suggest that in the morning and evening endothermy alone does not generate the required thoracic temperatures for flight. Bouts of basking on exposed soil and stones became longer as ground temperature decreased (the measurement considered most appropriate to the basking microhabitat; ANOVA across sites and days; $F_{1,93} = 5.46$, $P < 0.05$), reaching 5–10 min between flights at ground temperatures approaching 10°C . The importance of behavioural ectothermy in the morning and evening supports the conclusion that *A. pauperata* is largely unable to forage without direct sunlight on its food plants.

The maximum midday air temperatures recorded (26.5°C) are very moderate, and no loss of thermoregulation was

observed at these temperatures. Thus, *A. pauperata* probably does not decrease activity during the middle of the day to avoid thermal stress.

Floral resource availability

Flower age structure. All flower stages (bud to postreproductive) were present throughout the day on all the *Alkanna* plants observed, and microclimatic differences among the sites did not affect flower stage distributions on plants detectably. The only flower stages to vary in their proportional contribution to the total throughout the day were buds and male-phase flowers. The proportion of unopened buds decreased during the middle of the day, and the proportion of male-phase flowers peaked in the early afternoon (Fig. 4a,b). Averaged over time and across sites, a mean of $14.5 \pm 1.0\%$ of all flowers were buds and $7.8 \pm 0.5\%$ were male-phase. The proportions of the total number of flowers in female or postreproductive phases neither changed significantly through the day nor differed among the sites; across sites and times, means of $42.0 \pm 1.8\%$ were in the female-phase and $35.5 \pm 0.6\%$ were postreproductive.

Pollen release. Anther dehiscence in *A. orientalis* began during the transition from bud to male-phase, and occurred synchronously in the sampled population throughout the morning to generate maximum pollen availability per flower at approximately 14.00 hours (Fig. 5). After dehiscence, bee foraging (described below) rapidly reduced the pollen standing crop in male-phase flowers to low levels. Male-phase flowers

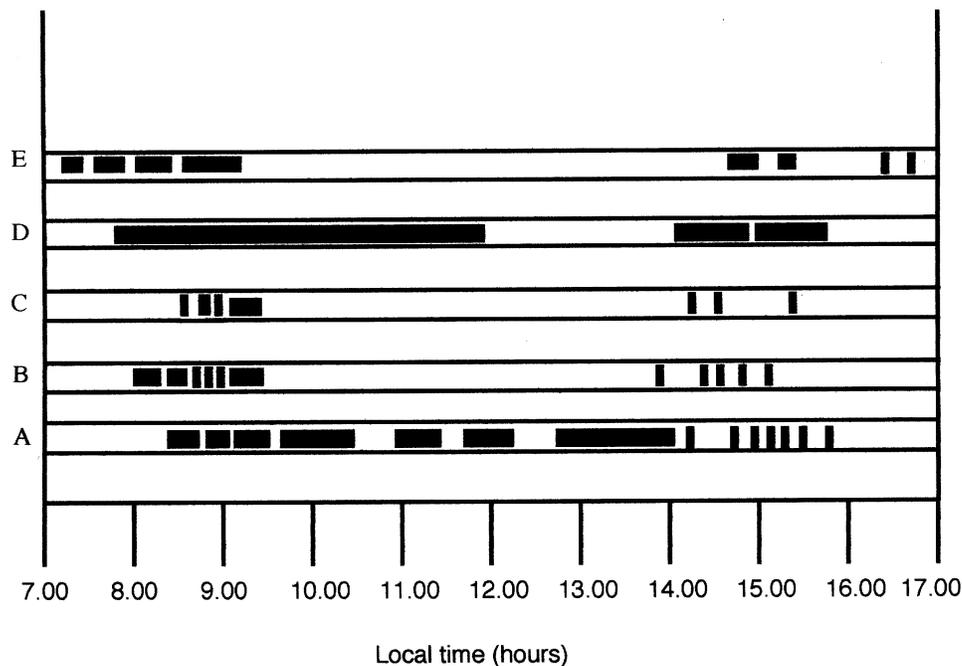


Fig. 2. Activity patterns of five females (A–E) observed throughout their activity period at Wadi Arbaein on (A) 29 March 1994 (B, C) 1 April 1994 and (D, E) 5 April 1994. Each shaded bar indicates a period away from the nest.

were the only age category to show a clear change in pollen standing crop throughout the day. Although female-phase flowers contained small quantities of pollen early in the morning, both female-phase and postreproductive flowers contained little pollen at any time compared to male-phase flowers (Fig. 5). Thus, the pollen standing crop in male-phase flowers represented almost the entire pollen resource available to foragers. These data show that pollen release is highly structured in time and strongly associated with flowers of a particular age.

Nectar standing crop. Nectar volume and concentration varied with flower age, but did not show a daily pattern of variation as marked as that seen in pollen supplies. Exclusion of foragers by bagging flowers rapidly stabilized age-characteristic nectar standing crops. Closed buds had the

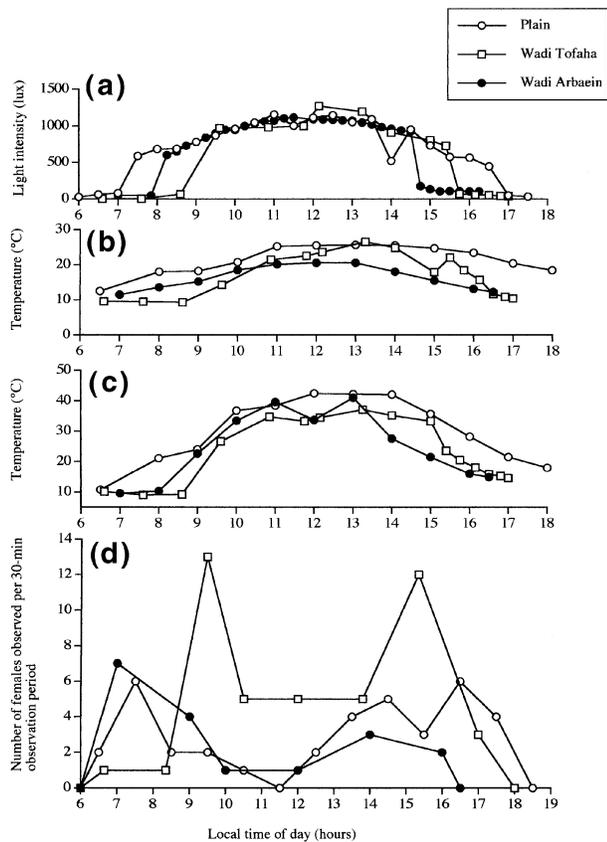


Fig. 3. (a) Light intensity (b) shade air temperature, and (c) ground surface temperature for the Plain, Wadi Tofaha, and Wadi Arbaein sites on 31 March 1994. (d) Summed flower visits [nectar only, pollen (with or without nectar) and approaches] over time for female *A. pauperata* at the three study sites used in 1994 on 31 March 1994. Temporal patterns of activity differed significantly between Wadi Arbaein and the Plain (Kolmogorov–Smirnov test, $D=0.329$, $P<0.05$), and between Wadi Arbaein and Wadi Tofaha (Kolmogorov–Smirnov test, $D=0.469$, $P<0.001$). Wadi Tofaha and the Plain did not differ significantly (Kolmogorov–Smirnov test, $D=0.212$, $P=NS$).

lowest mean volume and concentration per flower ($\approx 1 \mu\text{L}$ at 15–20% sucrose). Both volume and concentration increased during the transition to male-phase ($1.5 \mu\text{L}$ at $\approx 20\%$ sucrose),

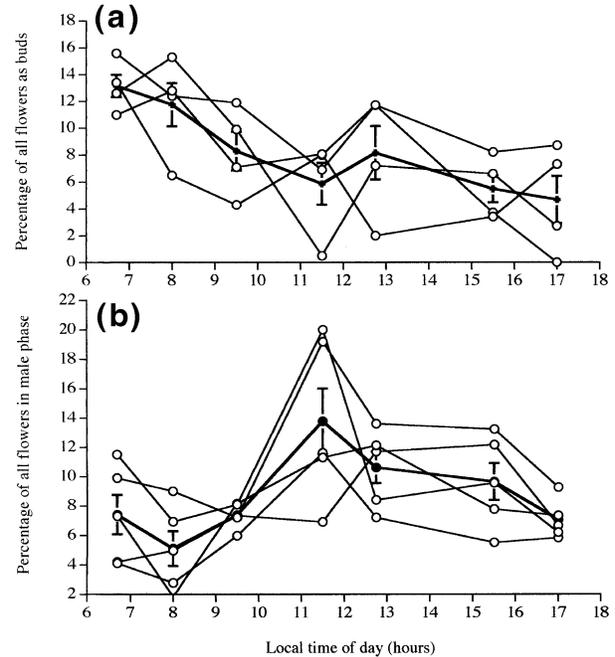


Fig. 4. Changes in the proportions of flowers in (a) bud and (b) male-phase over time for individual *A. orientalis* plants at the Plain site on 29 March 1994. The bold line represents the mean ± 1 SE.

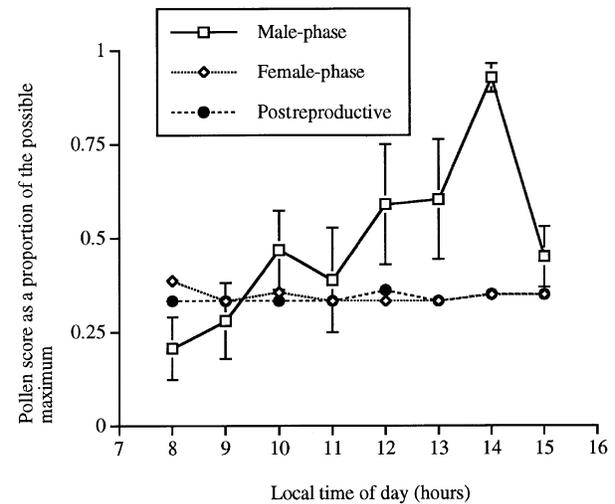


Fig. 5. Progress of anther dehiscence and changes in pollen standing crop over time for *A. orientalis* in Wadi Arbaein. Scores increase from 0 (anthers undehiscent) to 1 (full dehiscence, no pollen removal by foragers). The asymptotic values in female-phase and postreproductive flowers represent only trace amounts. Values are means ± 1 SE, $n=10$ for each sample.

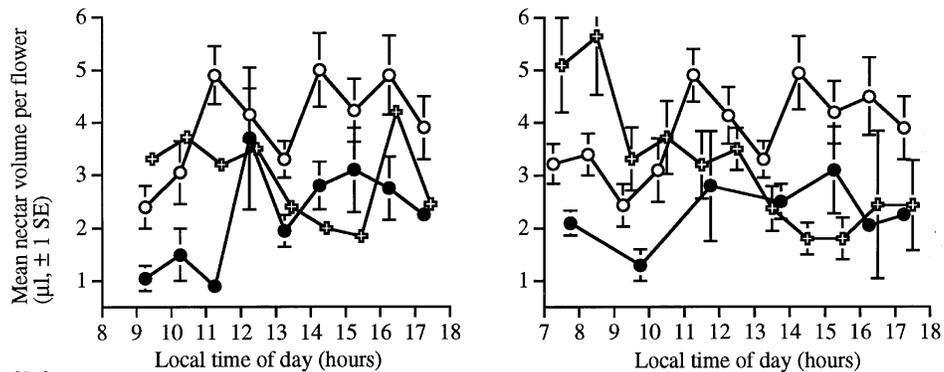
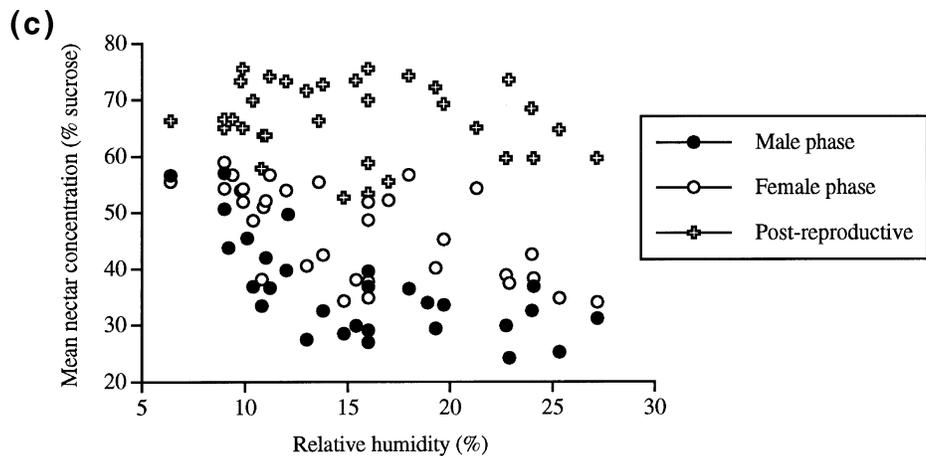
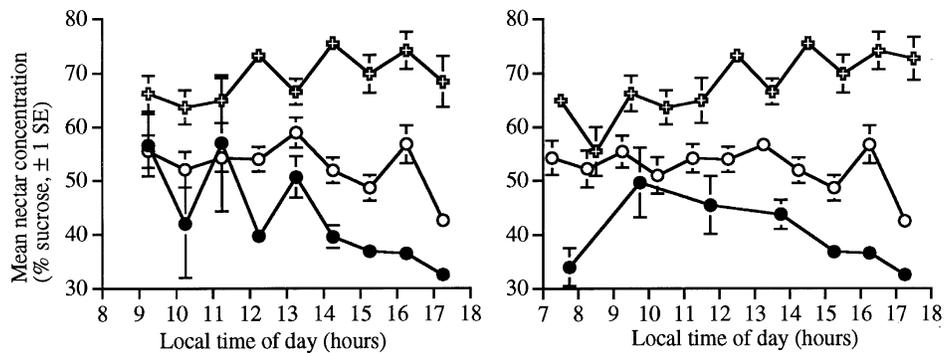
(a) Nectar volume**(b) Nectar concentration**

Fig. 6. Nectar standing crop in *A. orientalis* for flowers in male-, female-, and postreproductive-phases at the Plain. The two graphs on the left are for three plants on 31 March 1994; those on the right are for three different plants on 29 March 1994. (a) Nectar volume and (b) nectar concentration over time. Each point represents the mean $\pm 1 \text{ SE}$ for flowers of a given age from a total of 30 flowers (10 from each plant) sampled at each time interval. (c) Relationships between relative humidity and nectar concentration. Male-phase: $n=29$, $r^2=0.62$, $P<0.001$; the relationship is curvilinear, with significant x ($P<0.001$) and x^2 ($P<0.005$) terms. Female-phase: $n=33$, $r^2=0.383$, $P<0.001$. There is no significant relationship for postreproductive flowers.

and then again more substantially in the transition to female-phase ($\approx 4.5 \mu\text{L}$ at $\approx 25\%$ sucrose), indicating that nectar secretion continues up to and including the female-phase. Nectar in postreproductive flowers showed a continuing

decrease in volume and increase in concentration, suggesting that nectar secretion had stopped.

These patterns were repeated in the nectar standing crops of exposed flowers (Fig. 6). Throughout the day, male-phase

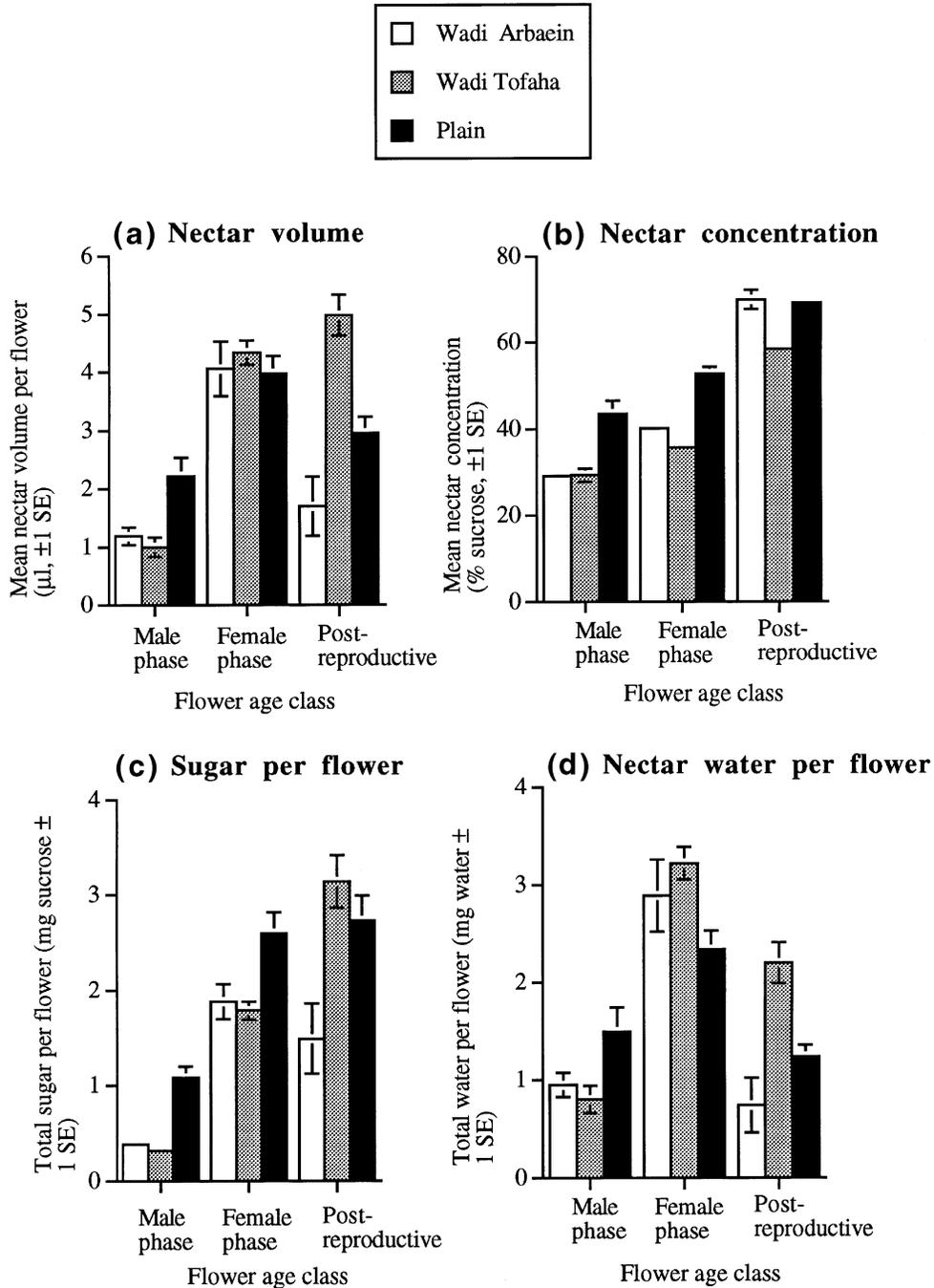


Fig. 7. A summary of nectar characteristics of flowers of each age class for the three study sites on 31 March 1994. (a) Nectar volume, (b) nectar concentration, (c) total sugar, (d) total water. Values are means ± 1 SE of all the data for flowers of a particular age throughout the day.

flowers showed consistently lower nectar volume and concentration than female-phase flowers. Postreproductive flowers consistently contained the most concentrated nectar, exceeding 70% sucrose. In both male- and female-phase flowers, nectar concentration correlated negatively with relative humidity (Fig. 6c), suggesting that evaporative

water loss increases nectar concentration during flower ageing.

Differences in nectar characteristics among flower stages were generally consistent across sites (Fig. 7). ANOVA, with site and flower age as independent variables (Table 1), revealed significant effects of site, flower age and the site \times flower age

Table 1. Two way ANOVAs of floral nectar characteristics across sites and flower age classes 2, 3, and 4. $n=69$ overall, with $n=13$ for each flower age for the Plain, $n=8$ for each flower age for Wadi Tofaha, and $n=6$ for each flower age for Wadi Arbain. SS = sum of squares, MS = mean squares.

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Nectar volume per flower					
Site	2	8.6	4.3	5.62	<0.01
Flower age	2	79.2	39.6	51.8	<0.001
Interaction	4	20.6	5.1	6.74	<0.001
Error	60	45.9	0.76		
Nectar concentration					
Site	2	2548	1274	51.4	<0.001
Flower age	2	12118	6059	244	<0.001
Interaction	4	530	132	5.34	<0.001
Error	60	1487	24.8		
Sugar per flower					
Site	2	8.51	4.25	13.1	<0.001
Flower age	2	43.5	21.8	66.95	<0.001
Interaction	4	7.6	1.9	5.8	<0.005
Error	60	19.5	0.3		
Water per flower					
Site	2	3.4	1.7	5.05	<0.01
Flower age	2	37.8	18.9	56.7	<0.001
Interaction	4	10.5	2.6	7.9	<0.001
Error	60	20	0.33		

interaction on nectar properties. Although significant interaction terms show that the effects of flower age vary among sites (Table 1), at all sites female-phase flowers contained a greater volume of more concentrated nectar than did male-phase flowers, and postreproductive flowers contained either as much or more total sugar as female-phase flowers, but in the form of much more concentrated nectar.

Anthophora pauperata foraging preferences

Pollen foraging. Pollen foraging by female *Anthophora* in both the morning and afternoon was highly nonrandom with respect to the flower ages visited. In each case, the preferred flower age represented the richest pollen source available at the time.

In the early afternoon, pollen-collecting bees preferred male-phase flowers significantly; these received $59.5 \pm 10.3\%$ of visits, compared to a random expectation (flower age-independent) of 10%. Female-phase flowers received the remaining 40.5% of visits, and bees ignored tightly closed buds and postreproductive flowers ($n=9$ foraging bouts, each with a mean of 43.1 ± 12.7 flowers; $G_p=963.5$ on 3 d.f., $P<0.001$). Immediately following dehiscence, females sonicated the same flower up to six times successively, removing pollen during brief flights in front of the flower between each sonication. The number of sonications per male-phase flower by individual females decreased rapidly over a short period (Fig. 8a), suggesting that most of the pollen available to females was removed quickly. This occurred over the same

time period as the reduction in pollen standing crop demonstrated by flower dissection (Fig. 5). Bees usually sonicated female-phase flowers, which contained very little pollen by the afternoon (Fig. 5), only once (Fig. 8a).

Overnight, flowers harbouring any remaining pollen aged from male-phase to female-phase. These changes were reflected in female *Anthophora* foraging behaviour in the morning, which was also highly nonrandom with respect to flower age ($G_p=305.5$ on 3 d.f., $P<0.001$) (Fig. 8b). In particular, $91 \pm 3\%$ of visits involved female-phase flowers, in contrast to the expected mean frequency for age-independent foraging of 45%. Male-phase flowers formed the remaining 9% of visits, with significant preference for this age during one bout.

Temporal variation in pollen availability was also reflected in the time required to collect a pollen load. Foraging trips were shortest after females emerged from their nests to begin the afternoon pollen-foraging period, when collection of a full pollen load took as little as 2 min (mean duration 10.3 ± 2.2 min, $n=21$). Trips during the morning were significantly longer than those in the afternoon (07.00–10.00 hours, mean duration 31.8 ± 11.6 min, $n=20$). The few trips recorded during the middle of the day (10.00–14.00 hours) had the longest duration (mean 74.1 ± 26.2 min, $n=7$). All of the differences between these three sets of visits are significant (Mann–Whitney *U*-test: morning and middle of the day, $z=-2.66$, $P<0.01$; morning and afternoon, $z=-2.94$, $P<0.005$; middle of the day and afternoon, $z=-3.76$, $P<0.001$).

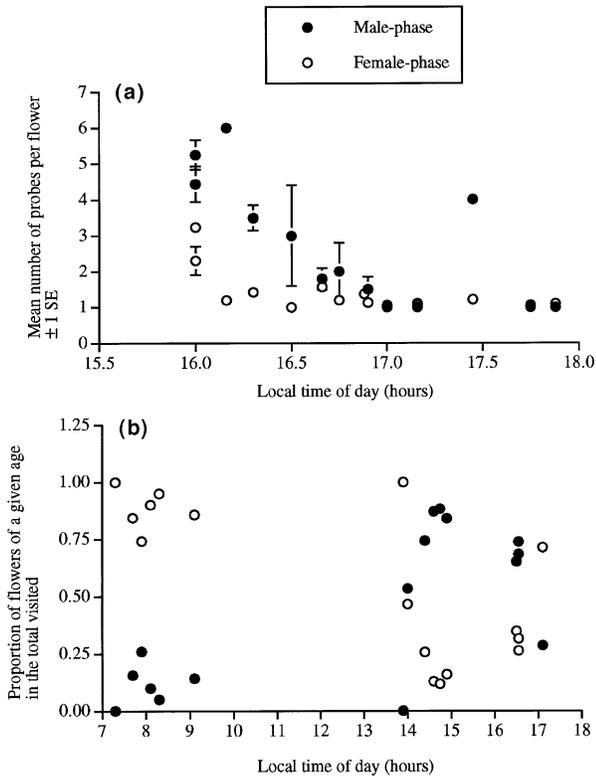


Fig. 8. (a) Changes over time in the mean number of probes per flower for flowers in male- and female-phase for the Plain site on 29 March 1994. Values are means ± 1 SE. (b) Changes in flower age preference over time by female *A. pauperata* for the Plain on 31 March 1994.

Nectar foraging. In twelve nectar-only foraging bouts (from all times of day), females visited 69 female-phase flowers, 13 male-phase flowers, four postreproductive flowers and no buds, representing an overall significant departure from random foraging ($n = 12$ bouts, $G_p = 36.66$ on 3 d.f., $P < 0.001$). Overall, the 15% of visits observed to male-phase flowers did not differ significantly from the 10% expected (the mean proportion of male-phase flowers across times and sites), but the observed preference for female-phase flowers (observed 80%, expected 45%) is highly significant. Nectar foraging *Anthophora* very rarely harvested the abundant but highly concentrated nectar in post-reproductive flowers. Unlike the pattern seen in pollen foraging, there was no evidence that the flower ages preferred by nectar-collecting bees changed throughout the day.

Discussion

Factors structuring the activity patterns of female solitary bees

Activity patterns of female bees result from the interaction among the physiology of the pollinator, microclimatic changes in the environment and temporal patterns of floral resource

availability, together with factors that may affect the timing of nest construction. General evidence for the roles of these factors is discussed in turn, then the *A. pauperata*/*A. orientalis* system is considered in detail.

Because of the physiological difficulties associated with foraging at both high and low ambient temperatures, bimodal activity patterns may well result in environments with considerable diurnal temperature ranges. In highly endothermic bees that generate a high thoracic temperature in flight, high ambient temperatures during the middle of the day may lead to the generation of intolerable heat loads in flight, and abandoning of the foraging site (Chappell, 1982, 1984; Willmer, 1983, 1985; Herrera, 1990). In some cases, a return to forage sources in the cool of the evening generates a bimodal activity pattern. Most of the bee species in which bimodal activity patterns have been demonstrated are either known to be highly endothermic (*Bombus*, *Xylocopa*, *Anthophora*; Linsley *et al.*, 1963; Janzen, 1964; Gerling *et al.*, 1983; Posey *et al.*, 1986) or good potential candidates in which the presence of this phenomenon has yet to be investigated (e.g. the colletid solitary bee genera *Ptiloglossa* and *Caupolicana*; Linsley, 1962; Linsley & Cazier, 1970).

Times of nectar and pollen release by flowers impose ultimate limits on the times when female bees can forage. Many plants release pollen and nectar in the morning or evening at relatively low ambient temperatures, and successful exploitation of these resources under such conditions may be associated with the widespread endothermy seen in bees (Stone & Willmer, 1989). When the resource becomes available in the late afternoon, some bees forage into the evening, then return to collect remaining resources in the morning (e.g. *Anthophora* and *Andrena* collecting pollen from evening primrose; Linsley & MacSwain, 1959; Linsley *et al.*, 1963; Hurd & Linsley, 1975). Temporal patterns of resource availability can thus generate a bimodal activity pattern.

The resources offered by a particular plant may change significantly during the day, and where alternative floral sources exist females may switch among sources during the day (Willmer, 1988; Herrera, 1990; Gilbert *et al.*, 1991; Stone *et al.*, 1996, 1998). The activity patterns shown by provisioning females will then be site-dependent. For example, Linsley *et al.* (1963) described a mass shift by *Andrena omninigra clarkiae* (Andrenidae) from *Clarkia*, visited for pollen during the middle of the day, to *Brassica*, visited for nectar in the evening. A similar shift from one forage source to another has also been observed in *Anthophora* (Stone, 1994a). Observation of *A. pauperata* nests rules out such a food-source switch in this bee; periods away from *Alkanna* were spent underground rather than at an alternative food source.

As well as provisioning their cells with pollen and nectar, female bees must construct and seal their cells. These activities preclude foraging for at least some of their active period, and periods of activity inside the nest may constitute a considerable proportion of the total activity period (Fig. 2, Willmer, 1986; Willmer & Stone, 1988; Stone, 1994a). Where floral resource availability is highly structured in time, females may construct nest cells during periods of low resource availability (Willmer & Stone, 1988). The factors that affect female activity may

also change if there are phases of different behaviour over a female's life (Stone, 1994a).

The interactions among these factors are complex, and daily cycles of pollinator activity and floral resource availability may be hard to reconcile (Herrera, 1990). The *A. pauperata*/*A. orientalis* system is free of many of the complications seen in other systems, and provides an opportunity to tease apart the effects of temperature and resource availability.

Thermal limitations on the activity patterns of Anthophora pauperata

The behaviour and activity patterns of *A. pauperata* females suggest strongly that inability to cope with low ambient temperatures, rather than avoidance of heat stress, has the greater impact on *Anthophora* activity patterns. Even slight differences in daily patterns of temperature at the different study sites affected the time of morning arrival, time of afternoon departure, and overall duration of activity of foraging *A. pauperata* populations. Although correlation with temperature changes need not imply that temperature caused the observed among-site differences, no changes were observed in any other factor to which foraging females might be sensitive (e.g. nectar or pollen quantity or quality) on such a fine time scale. *Anthophora pauperata*, in common with other *Anthophora* spp. (Stone, 1993, 1994b), regulates thoracic temperatures during flight, and is capable of considerable endothermic heat generation independent of external sources. Detailed studies of a similar-sized *Anthophora* species have shown that at morning temperatures similar to those experienced by female *A. pauperata*, endothermic heat generation alone can generate the minimum thoracic temperatures required for flight. However, preflight warm-up under such conditions is lengthy and metabolically costly (Stone, 1993). Supplementing internal heat generation with external solar warming reduces the cost of preflight warm-up under the same conditions considerably (Stone *et al.*, 1995), and has been observed in *Anthophora plumipes* (Stone, 1994a; Stone *et al.*, 1995). It is likely that the ambient temperatures at the study sites before and after exposure to direct sunlight were sufficiently low that the metabolic cost of purely endothermic regulation became prohibitive at these times.

Several lines of evidence suggest that avoidance of thermal stress is unlikely to underlie reduced activity by *A. pauperata* in the middle of the day. First, *A. pauperata* is an excellent thermoregulator and there is no indication of breakdown in this ability at ambient temperatures associated with the midday drop in activity. Second, females were clearly able to carry out nectar foraging and approach visits throughout the day. Third, ambient temperatures in the early afternoon pollen foraging period were no lower than those encountered in the middle of the day (Fig. 3). It is more likely that *A. pauperata* spends the midday period underground in response to other constraints on foraging activity imposed by resource availability, and meanwhile completes other necessary tasks in the nesting cycle (see below).

Temporal patterns of floral resource availability and foraging preferences

Female *A. pauperata* require two floral resources, nectar and pollen. The nectar standing crop of preferred female-phase flowers did not change significantly throughout the day, hence there is no evidence that variation in nectar provision by *Alkanna* causes the bimodal activity pattern. In contrast, pollen availability varied considerably, because male-phase flowers reached their maximum proportion of all flowers on an *Alkanna* plant in the early afternoon. Pollen per male-phase flower peaked at the same time. These two effects combined to produce a peak in available pollen. Unlike nectar, which was secreted throughout the male and female phases of a flower's life, pollen is nonrenewable for a given cohort of flowers. The afternoon peak of pollen collection in *Anthophora* was tightly coupled to the schedule of pollen release in *Alkanna*, and females visited male-phase flowers preferentially at this time. Each female required only a matter of minutes to collect a full pollen load, decreasing the available pollen standing crop rapidly (shown both by direct scoring of anthers and by observations of female foraging behaviour). Bees then visited anthers that they had missed on the previous day or that had dehisced in the evening, during a poorer morning pollen-gathering period the following day, completing the observed bimodal pollen foraging cycle. In the morning, females collected the leftovers of dehiscence from the previous day, and pollen availability in the morning was far lower than peak levels in the afternoon. Lower pollen standing crops per flower in the morning were probably responsible for the significant increase in forage trip duration relative to the afternoon period. The tight synchrony of afternoon pollen collection and dehiscence, and pollen collection in the morning despite low standing crops, both suggest that pollen is a limiting resource in this system.

The rapid exhaustion of most of the available pollen supplies may provide an adaptive explanation for the approach visits to *Alkanna* made by female *Anthophora* in the middle of the day. Oils on the surface of pollen grains commonly include volatiles whose release accompanies dehiscence. Approach visits may allow the females to assess the onset of anther dehiscence, either directly through visual inspection of the corollas, or through detection of volatiles released during dehiscence (D'Arcy *et al.*, 1990; Dobson & Groth, 1990). Under conditions in which pollen is depleted rapidly, bees would benefit by beginning to collect it as soon as it becomes available.

Completion of the nesting cycle within constraints imposed by temperature and resource availability

Under adequate conditions, female *Anthophora* typically construct one nest 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 completed cell. 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. The temperate species *A. plumipes* digs new cells predominantly in the evening, and collects pollen and nectar throughout the day (Stone, 1994a). *Anthophora pauperata* shows a different pattern (Willmer *et al.*, 1994); digging takes place in the middle of the day. Although *Alkanna* pollen and nectar are scarce at this time, some does remain available. Why, then, do female *A. pauperata* not fly throughout the day and complete cell construction activities in the evening, as *A. plumipes* does? One possible explanation is that the rapid drop in ambient temperature following sunset not only constrains flight activity, but also constrains the activity of females underground. If this is the case, digging during the middle of the day could represent efficient use of a period during which digging is possible while foraging would be relatively unproductive.

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