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BEHAVIOR

Possible Foraging Benefits of Bimodal Daily Activity in *Proxylocopa olivieri* (Lepeletier) (Hymenoptera: Anthophoridae)

DAPHNA GOTTLIEB,[1,2] TAMAR KEASAR,[3] AVI SHMIDA,[1] AND UZI MOTRO [1,4]

Department of Evolution, Systematics and Ecology, Hebrew University, Jerusalem 91904, Israel

ABSTRACT   We followed the daily and seasonal foraging patterns of the solitary bee *Proxylocopa olivieri* during two springs and summers in Har Gilo, Israel. During the foraging season, the bees exhibited a clear bimodal daily activity pattern. They foraged mostly before sunrise and after sunset. We hypothesized that this activity schedule entails foraging benefits. We found that snapdragon (*Antirrhinum majus* L.) was a major source of nectar for *P. olivieri*. Nectar production rates in snapdragon were significantly higher during the morning activity period of *P. olivieri* than during mid-day. Bees of numerous other species foraged on snapdragon, but their activity periods hardly overlapped with *P. olivieri*. Foraging activity in *P. olivieri* was highest at a combination of high (25–35°C) temperatures and low (1–100 Lux) illumination levels. We suggest that *P. olivieri* benefits from foraging at dawn and dusk on snapdragon, and possibly additional food plants, because of exploitation of the large amounts of nectar produced. A nectar enrichment experiment revealed that *P. olivieri* does not cease foraging because of lack of available nectar. We suggest that the *P. olivieri's* ability to fly at low light levels enables it to dominate a unique foraging niche.

KEY WORDS   activity rhythm, foraging, interspecific competition, nectar, solitary bee

ACTIVITY RHYTHMS IN INSECTS are affected by extrinsic and intrinsic factors. Extrinsic factors are abiotic (e.g., temperature, illumination, wind) and biotic (e.g., competition, predation) variables. Intrinsic factors include physiological traits (e.g., thermoregulatory activity) and systematic affiliation (Herrera 1990).

In bees, the interplay of these factors defines five broad temporal categories of foraging activity: matinal, diurnal, afternoon, crepuscular, and nocturnal (Pittendrigh 1974). Several bee species, however, forage both during early morning and during late afternoon, thus showing a bimodal activity pattern (Gerling et al. 1983, Willmer 1988).

Several studies attribute bimodal daily activity in bees to thermal constraints. Large bees (>35–50 mg) are often able to raise their body temperature endothermically through shivering (Heinrich 1977, Stone 1994, Willmer and Stone 1997). However, when ambient temperatures are too low, they are not able to generate enough heat to enable initiation of morning flight and prolongation of evening flight (Stone and

Willmer 1989). When air temperatures are too high, bees are not able to dissipate heat generated in flight and may overheat (Chappell 1984, Willmer and Stone 1997). In environments with a wide daily range of ambient temperatures, these constraints often define a thermal window that allows activity only during morning and afternoon hours (Herrera 1990, Stone 1994, Willmer and Stone 1997). Desert and semidesert environments impose a rather narrow window of activity, because of the large temperature differences between day and night. The focus on temperature as a limiting factor to flight implies that bimodal activity may not be the bees' best foraging option, but may rather be imposed on them by their thermal physiology.

In this study, we study bimodal activity in bees as a foraging strategy and test whether it results in efficient foraging. We hypothesized that the foraging benefits of bimodal activity could include access to floral food resources that are produced bimodally (Barthell and Knops 1997, Groman and Pellmyr 1999) or that accumulate during the night and are available to early foragers (Groman and Pellmyr 1999). Such a correlation between the daily pattern of bee activity and food production was recorded for *Anthophora pauperata* (Walker) foraging for pollen on *Alkanna orientalis* L. (Stone et al. 1999). Reduced competition with other foragers could provide an additional foraging benefit to bimodal activity. Such foraging benefits, together

[1] Department of Evolution, Systematics and Ecology and Center for Rationality, Hebrew University, Jerusalem 91904, Israel.
[2] Corresponding author: Department of Life Sciences, Ben Gurion University, POB 653 Beer Sheva 84105, Israel (e-mail: tkeasar@bgumail.bgu.ac.il).
[3] Department of Life Sciences, Achva College, Mobile Post Shikmim 79800, Israel.
[4] Department of Statistics, Achva College, Mobile Post Shikmim 79800, Israel.

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with thermal constraints, may constitute a selective force favoring bimodal activity rhythms.

We tested our hypothesis using the solitary anthophorid bee, *P. olivieri*, as a model. This is a multivoltine species with palearctic distribution in desert and semidesert habitats. Newly emerged females forage for nectar only and typically mate shortly after emergence (Kronenberg 1984). After mating, they concentrate their activity on nest construction, provisioning, and oviposition. Females nest communally in slopes of clay-rich soils. They generally construct three to six cells in each nest and provide them with pollen and nectar. A single egg is laid in each cell. *P. olivieri* is well suited for our study question because it shows a clearly bimodal daily foraging pattern (Malyshev 1931, Kronenberg 1984). In addition, it is relatively large, conspicuous, and active for several months a year, facilitating observations.

Materials and Methods

Study Site. The study was carried out in Har Gilo, Israel, located southwest of Jerusalem, at an altitude of 900 m. The location is characterized by a semidesert climate, with cold winters and dry hot summers. Mean annual precipitation is 600 mm. The site has a rich fauna of pollinators (Shmida and Dukas 1990). The vegetation includes wild Mediterranean phrygana plants and cultivated plants. The main bee forage plants during the study period were *A. majus* L., *Abelia x grandiflora* (Rovelli ex Andr'), *Rosmarinus officinalis* L., *Teucrium creticum* L., and *Vitex agnus-castus* L.

Observations of Bee Activity. Field observations were carried out between April and October of 1998 and 1999. Snapdragon, a major food source for *P. olivieri* (see Figs. 2 and 3), was the main plant species observed. Forager composition at the study site was sampled at weekly intervals throughout the season. We walked along a fixed route for half an hour, four times daily, and recorded all visitors seen foraging on the flowers of snapdragon (total, 145 observations). The results of walking the strip once represent a "count." The sampling unit used here in the analyses of forager abundance is "foragers/count" (Herrera 1990).

Proxylocopa olivieri foraging activity on snapdragon was observed once a week at 15-min intervals throughout activity hours (total, 438 observations). In each 5-min observation, we recorded the number of flowers visited by a single, randomly selected, individual. In rare cases, when a bee could not be followed for 5 min (usually because it was foraging in a shady part of its food plant), we calculated its expected number of visits per 5 min based on the observed visitation rates. Observations of <30 s were discarded. We observed both males and females. We calculated "bee visitation rate," defined as the number of visits per bee per 5 min. The number of individuals observed depended on bee activity and our ability to follow single foragers. Because we usually observed only a few conspicuous foragers at a time, each individual could generally be tracked throughout the 5-min observation period. We

therefore estimated that most individuals were observed only once; hence, independence of data can be assumed. In a different set of 5-min observations, we recorded the number of flowers visited by all *P. olivieri* foraging individuals in a snapdragon patch of a known size (total, 508 observations). We used these data to calculate "flower visitation rates," defined as the number of visits per 100 flowers per 5 min. This measure is affected by the total number of foraging bees and by their rate of foraging at the time of observation.

Temperature and Illumination Recording. Temperature and light were recorded at 15-min intervals during the activity period of the bees on the same days that bees were observed. We recorded shade air temperature at the ground and light levels in the shade, 50 cm above ground. Both measurements were taken at the observation site.

Nectar Volume Sampling. Nectar was extracted from snapdragon flowers (20 per sample) using 1- or 5-μl micropipettes of standard length (Vitrex, Modulohum I/S, Denmark). Nectar volumes were calculated from the length of the fluid column in the micropipette. Nectar was measured at biweekly intervals throughout the season. We did not record bee activity on days of nectar sampling to prevent possible effects of sampling on foraging conditions.

Both nectar production rates and nectar yields were recorded five times daily: before the beginning of *P. olivieri* morning activity, at the end of the morning activity, at mid-day, before the beginning of evening activity, and at the end of evening activity. Nectar production is the amount produced by plants in the absence of exploitation. Nectar yield (or standing crop) reflects the amount of nectar actually available to the bees and is affected by the production rate of the plant and the exploitation rate of foragers. Production rates were measured by emptying marked flowers (using a micropipette), covering them with fine-mesh gauze bags (mesh size, 1.5 mm) for a predetermined time, and measuring the accumulated nectar volume. Nectar yield was measured in uncovered flowers.

The length of the tongue of *P. olivieri* (12.3 ± 2.3 mm length from the base of the prementum to the end of glossa, $N = 4$) should allow access to any nectar in the corolla of snapdragon, and the volume recorded is assumed to approximate the volume available to foragers.

Nectar Enrichment Experiment. To test whether *P. olivieri*'s activity is limited by nectar availability, we manipulated flower patches to supply nectar for a longer time. During 20 d in August 1999, *P. olivieri* were allowed to forage in an *Abelia X grandiflora* patch, in which 1,000 flowers had been previously covered by fine-mesh gauze bags (mesh size, 1.5 mm). The covered flowers were revealed and made accessible to the bees 15 min before the end of natural morning foraging period. This created an additional nectar supply for bees in the patch. We compared the ending hour of the foraging activity between the nectar-enriched patch and an adjacent control patch without nectar manipulation. The *Abelia* patch was
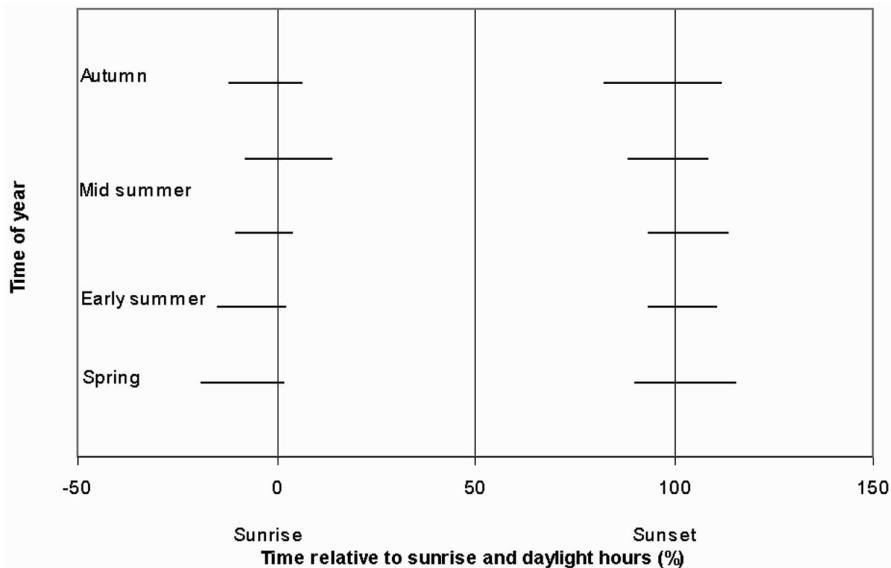
Fig. 1. Seasonal changes in the timing and duration of morning (top) and evening (bottom) foraging activity. Morning and evening activity hours are plotted relative to the times of sunrise and sunset (0 in the x-axis), respectively. Length of days (y-axis) is divided according to increasing and reducing daylength, 13–14 and 14–11 h of light, respectively. Data included only above the threshold of one visit per 5 min in 100 flowers.

visited more frequently than snapdragon at the time of the experiment and was therefore chosen as observation site.

Data Analysis. *Proxylocopa olivieri* activity was clearly correlated with daylight hours, peaking around dawn and dusk. The number of daylight hours varied between 11 and 14 during *P. olivieri*'s activity season. We corrected for this variation by presenting bee activity times relative to the time since sunrise and to the number of daylight hours on each observation day. For example, a record of activity at 0800 hours on a 14-h daylight day with sunrise at 0600 hours is reported at 14.28% of day length.

We tested the effects of temperature and light on foraging activity using two-way analysis of variance (ANOVA). We grouped light levels into three categories (1–10, 11–100, and 101–1,000 lux) and temperature records into four categories (15–20, 21–25, 26–30, and 31–35°C).

Results

Daily and Seasonal Activity Patterns. The bees showed a strongly bimodal daily foraging pattern. Foraging took place in early morning and in the evening and stopped during mid-day. Timing and duration of foraging, relative to sunrise and sunset, changed as the season progressed (Fig. 1). One apparent exception is the end of the evening activity period, which occurred between 0.75 and 1 h after sunset throughout the season (Fig. 1). In addition, duration of night nesting (according to maximal duration of activity) shortened gradually from spring (9.25 h) to autumn (7.72 h).

Proxylocopa olivieri's Food Sources. Snapdragon was a major food source for *P. olivieri* in our site,

because of its long flowering period (Fig. 2) and high attraction for the bees (Fig. 3).

Nectar production in snapdragon was significantly higher before sunrise than during daytime, with the exception of after sunset (ANOVA, $F_{(4,535)} = 4.67; P < 0.002$), correlating well with the morning peak in *P. olivieri* activity (Fig. 4). Nectar yields in snapdragon were not significantly affected by the time of day. The proportion of snapdragon flowers that did not contain any measurable nectar significantly increased during the day (ANOVA, $F_{(4, 305)} = 3.21, P = 0.013$), from 18% at dawn to 38% at sunset.

Activity Period of Potential Competitors. Snapdragon was visited by numerous other foragers, mainly bees. These included honey bees (*Apis mellifera* L.), bumblebees (*Bombus terrestris* L.), carpenter bees (*Xylocopa violacea* L.), and large and small solitary bees. Body and tongue lengths for the bee species found at Har Gilo are listed in Shmida and Dukas (1990). These visitors foraged mainly during late morning and noon, with little overlap with *P. olivieri*'s activity (Fig. 5). As a consequence, food rewards per forager visit were probably higher during *P. olivieri*'s activity periods than during the rest of the day (Fig. 4).

In the nectar enrichment manipulation, there was no significant change in the behavior of *P. olivieri*. Their activity stopped at the same time as in control patches (Fig. 6).

Abiotic Correlates of *Proxylocopa olivieri*'s Foraging Activity. High rates of foraging activity, i.e., flower visitation rates, were correlated with high air temperatures, 25–30°C ($F_{(3,365)} = 5.543; P < 0.001$), and low light levels, 1–100 Lux ($F_{(2,365)} = 3.708; P = 0.025$; Fig. 7). Mean ambient temperatures were 19.95 ± 2.99 and
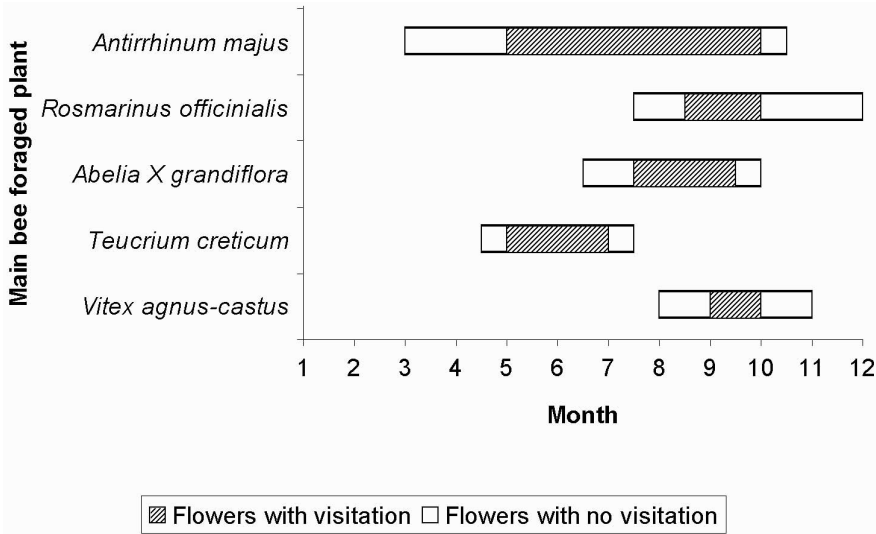
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Fig. 2. Seasonal changes in flowering of the main bee forage plants and in the bees' foraging preferences. Bars indicate the flowering seasons. Periods of *P. olivieri* visitation to the flowers are indicated by the full portions of the bars. Data included only above the threshold of one visit per 5 min in 100 flowers.

20.61 ± 3.45°C (SD) at the beginning and the end of morning activity, respectively. Mean temperatures at the beginning and the end of evening activity were, respectively, 23.82 ± 4.98 and 21.40 ± 4.89°C. The significant interaction ($F_{(3,565)} = 4.09; P < 0.001$) between temperature and light suggests that intensity of light and temperature have a combined effect on flower visitation rates.

Discussion

The bees in our study accessed their main forage plant, snapdragon, before dawn and after dusk. Nectar production in snapdragon peaked before dawn, providing the bees with a rich food source. This nectar production pattern might be a consequence and at the same time a cause of the early morning activity of the pollinator, as shaped by co-evolution.

Daily nectar and pollen production patterns in other food plants visited by *P. olivieri* vary widely among species (Rathcke and Real 1991, Cane 2001). It is quite possible that *P. olivieri* used more than one plant species that produces rich reward during its activity period. In addition, early morning foraging may enable *P. olivieri* to use nectar and pollen that have accumulated in flowers during the night (Groman and Pellmyr 1999). Nectar yields in snapdragon were constant throughout the day and do not seem to build up overnight. Such build-up may occur in other forage plants visited by *P. olivieri.*
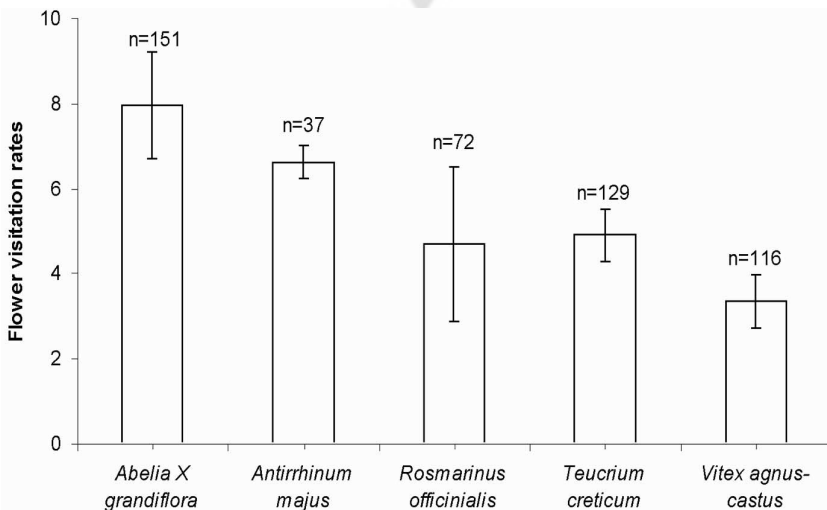
Fig. 3. Flower visitation rates at main bee foraged plants. Error bars are 1 SD.
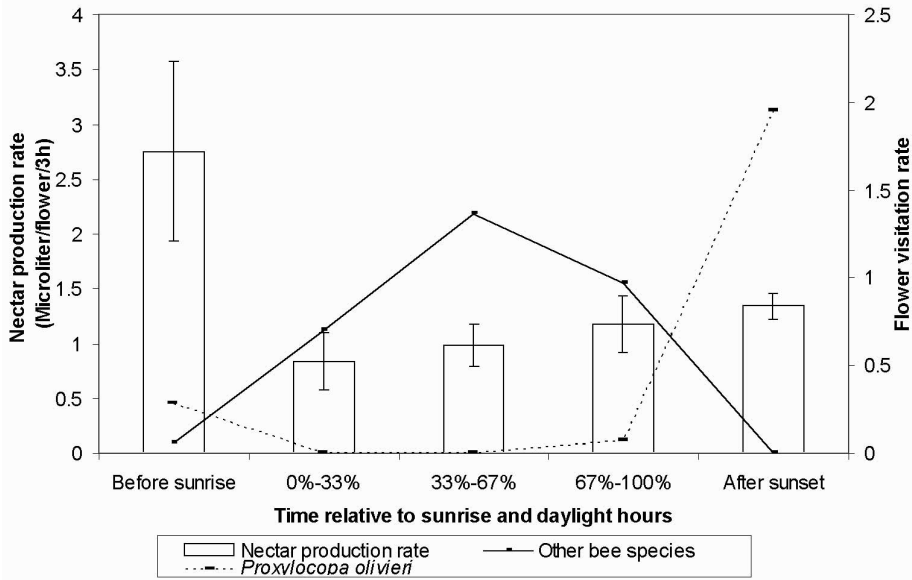
Fig. 4. Flower visitation rates and nectar production rates at different times in the day. Time plotted relative to the time since sunrise and to the number of daylight hours on each observation day. Bars: nectar production rate. Solid line: flower visitation rate for all foragers (excluding *P. olivieri*) Dotted line: flower visitation rate for *P. olivieri* (based on flower visitation rate). Error bars are 1 SD.

We also found that most of *P. olivieri's* daily activity period did not overlap with other bee species, suggesting that their activity rhythm allowed them to evade interspecific interference competition. Interspecific competition affects the composition of bee communities and the success of invasive bee species (Buchmann 1996, Steffan-Dewenter and Tscharntke 2000, Goulson 2003). *P. olivieri*, because of its ex-

tremely bimodal activity rhythm, seems to occupy a niche that is almost competitor-free, improving its foraging prospects. The following findings imply that *P. olivieri* received a larger share of the available nectar resources by foraging early. (1) Nectar yields in snapdragon were fairly constant throughout the day, whereas nectar production was highest during *P. olivieri's* foraging hours. The difference between
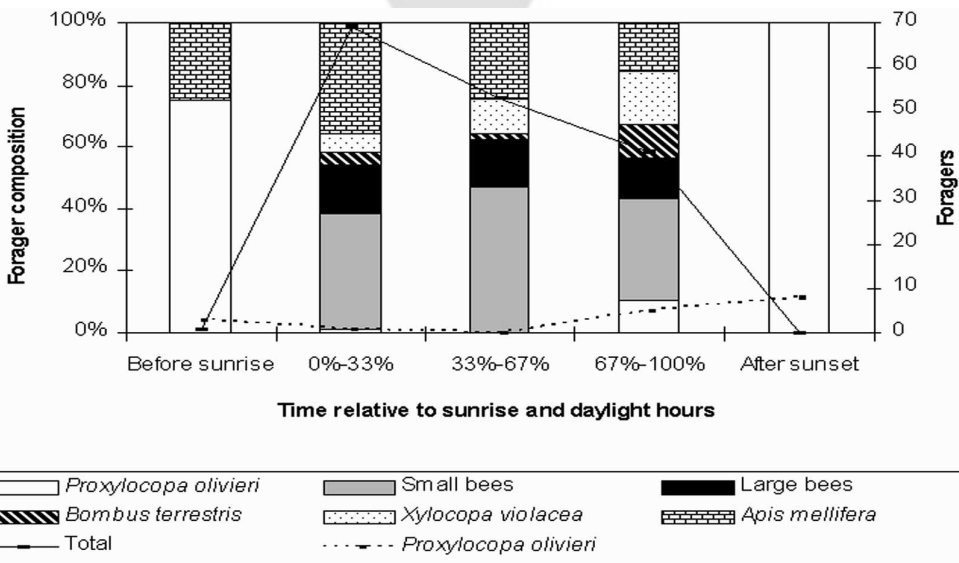

Fig. 5. Foragers/count at different times in the day, based on strip data. Time plotted relative to the time since sunrise and to the number of daylight hours on each observation day. Bars, composition of appearances by forager type; solid line, foragers/count for all foragers (excluding *P. olivieri*); dotted line, foragers/count for *P. olivieri*.
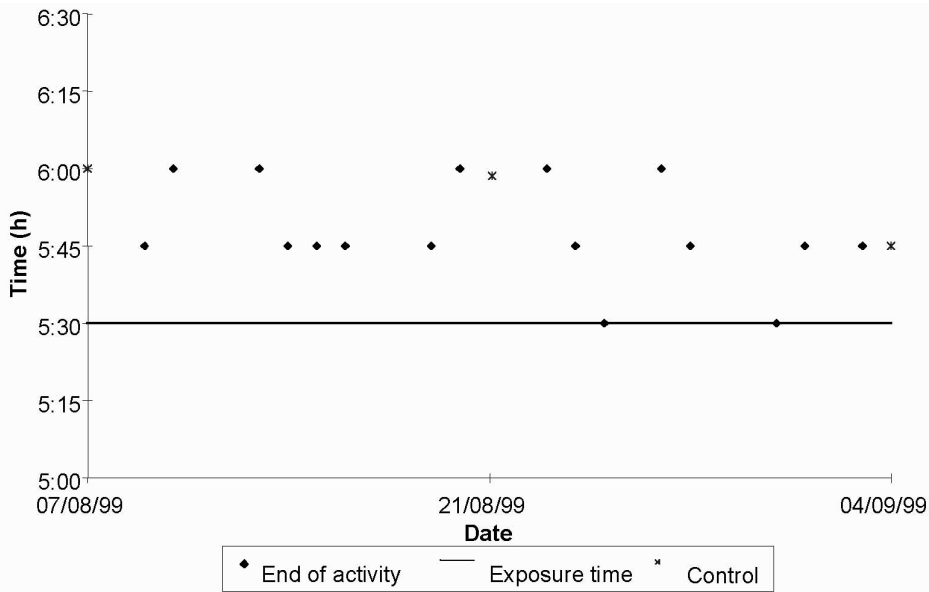
Fig. 6. End of morning foraging activity under experimental and controlled conditions. Every point represents 1 d.

production and yield, which is consumed by foragers, was therefore highest during early morning. (2) The total number of active bees was lowest during *P. olivieri*'s activity hours, allowing a higher nectar intake per foraging individual. The competititive advantage of early morning activity may be even larger for pollen foraging. This is because pollen is a depleting food resource that is likely more abundant during early morning than later in the day, whereas nectar is renewed to some extent during the day.

The working hypothesis that early morning foraging entails foraging advantages for P. *olivieri* is thus supported by high nectar production rates of its main food plant and by the low activity of its potential competitors. However, P. *olivieri*'s foraging behavior may also be constrained by its evolutionary history. For example, the mid-day heat may be a limiting factor in *P. olivieri*'s native desert habitats. Evolutionarily, bees may have been selected to be active in early morning, a pattern that persisted under the milder
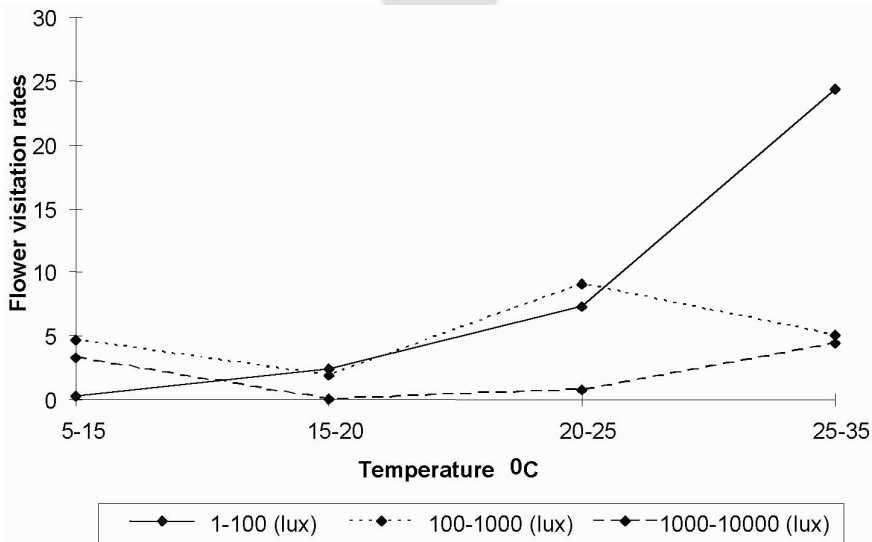
Fig. 7. Flower visitation rate at different temperatures and light intensities. Light intensities were grouped into low (1–100 Lux, bold line), medium (100–1,000 Lux, dotted line), and high (1,000–10,000 Lux, broken line). Observations <15°C were pooled into a single category because of small sample sizes.

climate conditions in this study. Such a constraint may have prevented the bees from responding to increased nectar supplies in the enrichment experiment, although temperatures were optimal. However, *P. olivieri* is active for several months a year, during which abiotic and biotic conditions change. This is expected to select for flexible foraging patterns that allow efficient performance at a wide range of environmental conditions, rather than a rigid behavioral repertoire.

Proxylocopa olivieri spends only 4–5 h/d foraging, a relatively short period compared with other bees (Dafni et al. 1987). The rest of the time is spent on nest construction and guarding. Predators and parasites are important mortality factors for broods of solitary bees (Linsley 1958, Linsley and MacSwain 1959, Stone 1994). Hence, a solitary female's nesting success is likely to be increased by a time-minimizing foraging strategy: collecting the nectar and pollen needed to provision a brood cell as quickly as possible and spending the rest of the day at the nest. Such a strategy is compatible with *P. olivieri's* foraging pattern.

The nectar manipulation experiment that maintained artificially high levels of nectar beyond *P. olivieri's* normal foraging hours did not change the bees' behavior. Their activity stopped at the same time as it did without the manipulation. This result supports the suggestion that *P. olivieri* does not use nectar depletion as a proximate cue to stop foraging. We assume that bees in the enriched patch were not nectar-limited, but do not know whether bees in the control patch experienced nectar shortage. Thus, one way to interpret the results is that nectar-limited and -unlimited bees have similar activity schedules. An alternative interpretation (assuming no nectar limitation in the control patch) is that foraging stopped in both patches while nectar was still abundant. In either case, we conclude that the bees used some other environmental cue (such as light intensity) to stop their morning foraging session. Although nectar depletion did not have an important proximate effect on the bees' behavior in our study, it may have been an important selective factor during the bees' evolution. In addition, it may act as a stronger proximate cue in harsher habitats, such as natural desert environments.

Foraging rates in *P. olivieri* were highest at air temperatures of 25–30°C (at low levels of illumination). Air temperatures at midday at Har Gilo are frequently within the same range, suggesting that *P. olivieri's* inactivity at midday is not caused by bees reaching their upper thermal limit. Similarly, morning activity started, and evening activity ended, at air temperatures of 20°C, well above the lower thermal limit measured for other Mediterranean anthophorids (Stone 1994, Willmer and Stone 1997, Stone et al. 1999). We therefore suggest that ambient temperature was not a major constraint on *P. olivieri's* activity in our study. Nevertheless, fluctuations in temperature may have caused corresponding fluctuations in nectar quality, such as nectar solute concentration (20–40 g sucrose/100 g solution), which could have affected *P. olivieri's* behavior (Corbet 1990).

Intensity of light plays a major role not only in illumination but also in heat reflection (Corbet et al. 1993). According to this hypothesis, body temperature of bees is affected by ambient temperature and intensity of light. Direct sun is very efficient in heating up the body in comparison to heating up by ambient temperature (Stone et al. 1995). Therefore, one way of avoiding overheating of the body is to avoid direct sun (Linsley 1958). Our results agree with this suggestion, because activity increased with ambient temperature at low illumination levels only (Fig. 7). Higher light levels may bring *P. olivieri* closer to their upper thermal limit.

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Foraging activity, i.e., flower visitation rates, at high temperatures was highest at very low light levels. This suggests that *P. olivieri* activity was not constrained by low levels of illumination. The ability to fly at low light levels may be better developed in *P. olivieri* than in most other bee species (Briscoe and Chittka 2001) and may allow it to occupy its unique foraging niche. However, although honey bees were not observed foraging at night at Har Gilo, they do have the ability to do so (Briscoe and Chittka 2001), hinting at a possible potential competitive interaction between *P. olivieri* and *A. mellifera.*

Exogenic factors that have been found correlating to foraging activity can act as a physiologically limiting factor to activity, but can also serve as Zeitgebers (Saunders 1982, Moore and Rankin 1993), i.e., cues that synchronize the daily cycle with external events (Saunders 1982). In this study, we have noticed two lines of evidence that may imply the existence of Zeitgebers in *P. olivieri.* (1) Evening foraging activity stopped at approximately the same time after sunset throughout the season; this suggests that sunset may serve as a Zeitgeber that couples *P. olivieri* activity pattern with a 24-h cycle. (2) Although *P. olivieri* individuals do not have continuous information on the rate of nectar production during the night, they initiate foraging before sunrise while nectar production rates are highest. To initiate foraging at the most profitable time without extrinsic information, the bee would need an inner clock.

It is possible that additional Zeitgebers can influence the timing foraging in a similar manner as light (e.g., temperature). Light/temperature manipulations are required to estimate the combined effects of these factors on the daily activity as Zeitgebers (Saunders 1982).

Acknowledgments

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AQ: 4

AQ1: Please provide reference or delete citation here.

AQ2: Please provide reference or delete citation here.

AQ3: Linsley 1878 changed to 1958 to match reference list.

AQ4: Please provide first initial of first author and all authors names. et al is not allowed.

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