

Light intensity limits foraging activity in nocturnal and crepuscular bees

Almut Kelber,^a Eric J. Warrant,^a Michael Pfaff,^a Rita Wallén,^a Jamie C. Theobald,^a William T. Wcislo,^b and Robert A. Raguso^c

^aDepartment for Cell and Organism Biology—Zoology, Lund University, Helgonavägen 3, S-22362 Lund, Sweden, ^bSmithsonian Tropical Research Institute, Apartado 2072, Balboa, República de Panamá, and ^cDepartment of Biological Sciences, University of South Carolina, Columbia SC29208, USA

A crepuscular or nocturnal lifestyle has evolved in bees several times independently, probably to explore rewarding pollen sources without competition and to minimize predation and nest parasites. Despite these obvious advantages, only few bee species are nocturnal. Here we show that the sensitivity of the bee apposition eye is a major factor limiting the ability to forage in dim light. We present data on eye size, foraging times, and light levels for *Megalopta genalis* (Augochlorini, Halictidae) in Panama, and *Lasioglossum (Sphecodogastra)* sp. (Halictini, Halictidae) in Utah, USA. *M. genalis* females forage exclusively during twilight, but as a result of dim light levels in the rain forest, they are adapted to extremely low intensities. The likely factor limiting their foraging activity is finding their nest entrance on return from a foraging trip. The lowest light intensity at which they can do this, both in the morning and the evening, is 0.0001 cd m⁻². Therefore, they leave the nest at dimmer light levels in the morning than in the evening. *Lasioglossum (Sphecodogastra)* foraging is limited by light intensity in the evening, but probably by temperature in the morning in the temperate climate of Utah. We propose that the evolution of nocturnality in bees was favored by the large variance in the size of females. **Key words:** bees, eyes, foraging, insects, ocelli, sensitivity, visual ecology. [*Behav Ecol*]

Advantages of being nocturnal

Most bees are active during the bright hours of the day but several species from at least four different families within the Apoidea have independently acquired a crepuscular or nocturnal lifestyle. This can have several advantages: some species including *Perdita (Xerophasma)* spp. (Andrenidae) and sweat bees *Lasioglossum (Sphecodogastra)* spp. (Halictidae) are adapted to collect pollen from plants in the Onagraceae, primarily the evening primrose (*Oenothera* spp.), that typically open their flowers just after sunset and provide large amounts of pollen (Bohart and Youssef, 1976; Kerfoot, 1967a). Bees that are able to fly at this time of day can collect large pollen loads very quickly and without competition with other bees or moths, and this is probably of major adaptive value (Bohart and Youssef, 1976). In addition, there might be fewer predators and nest parasites such as satellite flies, ants, sphecids, and parasitic bees active during and after sunset. Effective foraging at this time of day has been suggested as a possible reason for the infrequent parasitism observed in *Sphecodogastra galpinsiae* and *Sphecodogastra texana* (Bohart and Youssef, 1976; Kerfoot, 1967a).

Similar reasons may have led to the matinal activity of the squash bees *Xenoglossa* spp. (Apidae) and *Peponapis* spp. that are able to exploit *Cucurbita* spp. (Cucurbitaceae) flowers 1 or 2 h prior to other bees such as bumblebees (*Bombus* spp.; Linsley et al., 1955). In addition, these bees live in xeric environments. Flying during the colder morning and evening hours minimizes their loss of water (Hurd and Linsley, 1970).

The sweat bee *Megalopta genalis* (Halictidae) forages from more than 40 species of plants but relies heavily on several flower species that are typically bat pollinated (Wcislo et al.,

2004) and also provide large amounts of pollen and nectar. Feeding during dawn and dusk when no competitors are active may be especially important in the Neotropics, where social stingless bees are abundant. *M. genalis* has been shown to suffer to a lesser degree from nest parasitism, and the presence of the bee in her nest reduces predation by ants (Smith et al., 2003; Wcislo et al., 2004).

Problems of vision in dim light

If it is advantageous for bees to be nocturnal, why then are most bees diurnal? We hypothesize that the low sensitivity of their eyes limits crepuscular and nocturnal foraging activity in bees.

Bees are well adapted to a diurnal lifestyle by having apposition compound eyes. The photoreceptors within one ommatidium receive light only through a single tiny facet lens—about 20 µm in diam, in diurnal species (Jander U and Jander R, 2002; Warrant et al., 2004). This lens defines the aperture of the eye, and this is small, compared to the aperture of the dark-adapted human eye (8000 µm) and even compared to the aperture of the superposition compound eye of a nocturnal moth (1000 µm). The sensitivity of the eye is positively correlated to the aperture and to the acceptance angle of the photoreceptors. The acceptance angle, in turn, depends on the area of the receptive structure, the rhabdom, and the focal length. As a result of their small lenses, typical apposition compound eyes therefore do not allow for high absolute sensitivity (Land, 1981). We have recently demonstrated how the eyes of *M. genalis* are adapted to vision in dim light (Warrant et al., 2004). Besides having relatively large facet lenses of up to 40 µm in diam, they also have wide rhabdoms (8 µm in diam, compared to 2 µm in diurnal bees) and thus large acceptance angles. In addition, they have physiological adaptations in the photoreceptors and in subsequent stages of neural processing (Greiner et al., 2004a,b; Warrant et al., 2004).

In addition to their compound eyes, bees have three ocelli that are thought to be involved in flight control (Mizunami,

Address correspondence to A. Kelber. E-mail: almut.kelber@cob.lu.se.

Received 25 April 2005; revised 23 August 2005; accepted 20 September 2005.

1995). Kerfoot (1967b) showed in a comparative study that nocturnal bees have much larger ocelli than diurnal species. As the ocelli have similarly large visual fields and are extremely under focused (Warrant EJ, Kelber A, and Wcislo WT, in preparation), ocellar size effectively correlates to the total amount of light that the retina can collect from an extended scene.

Female bees leave the nest for foraging trips and find their way back home by means of visual landmarks (e.g., Zeil et al., 1996). We have recently demonstrated that this is the case even in *M. genalis* (Warrant et al., 2004). In Panama, *M. genalis* nests in hollow sticks in the rain forest (Wcislo et al., 2004). Finding the tiny dark nest entrance on their return home seems to be the most demanding task for the visual system, with regard to sensitivity. Most nocturnal flowers are rather large and bright and smell strongly. Bees that have nests in the dark understory of the rain forest nevertheless forage mostly in the canopy or at the forest edge where light intensities are up to 500 times higher (Kelber A, unpublished measurements in Panama). Given the same general light conditions, flower detection is therefore less demanding than finding the nest. Ground-nesting bees such as *Lasioglossum* (*Sphécodogastra*) spp. face a similar situation: it is harder for them to detect the dark and small nest hole than the large bright flowers they visit.

During dusk, light levels fall by several logarithmic units within a short period of time (that varies with latitude), and we propose that the light intensity at the return to the nest limits bee activity in the evening. During dawn, a more complicated situation is encountered: in dry and higher elevation climates, the morning temperatures might be too cold for bees to fly. In a lowland tropical rain forest, however, temperature fluctuations are minimal and light intensities probably limit morning flight activity as well.

Crepuscular and nocturnal bees: the subjects of this study

Hitherto, only small data sets, of quite variable nature, are available which describe the time of day and—more importantly—the light intensities at which nocturnal and crepuscular bees are active. Only one species of bee, a large Indian carpenter bee *Xylocopa* sp. (Apidae), has been observed foraging from its pollen host, on moonless nights (Somanathan and Borges, 2001; Somanathan H and Borges R, personal communication). Several other species, including the carpenter bee *Xylocopa* (*Nyctomelitta*) *tranquebarica* (Apidae; Burgett and Sukumalanand, 2000), the giant honeybee *Apis dorsata* (Apidae; Dyer, 1985), the African race of *Apis mellifera* (Fletcher, 1978), and the sweat bee *Lasioglossum* (*Sphécodogastra*) *texana* (Halictidae; Kerfoot, 1967a), have been observed foraging in moonlit nights. The species *Lasioglossum* (*Sphécodogastra*) *galpinski* (Bohart and Youssef, 1976), *Xenoglossa fulva* (Apidae; Hurd and Linsley, 1970; Linsley et al., 1955), *Peponapis* sp. (Apidae; Hurd and Linsley, 1970), *Ptiloglossa guinnae* (Colletidae; Roberts, 1971), *Ptiloglossa jonesi* and *Ptiloglossa arizonensis* (Shelly et al., 1993), *Caupolicana ocellata* and *Caupolicana yarrowi* (Colletidae; Linsley and Cazier, 1970; Rozen and Rozen, 1986), *Martinapis luteicornis* (Apidae; Rozen and Rozen, 1986), and *Xylocopa tabaniformis* (Apidae; Janzen, 1964) forage during dawn or dusk and are thus crepuscular.

Roberts (1971) reports from a nest site in Costa Rica that the first *P. guinnae* started foraging in the morning and the last bee returned from the last foraging trip in the evening, at light intensities of 10 lx. For most other nocturnal or crepuscular bees, no exact data on the light intensities during foraging times are available. In a recent study, we found that *M. genalis* forages only during dawn and dusk (Warrant et al., 2004), but in a previous study using light traps, small numbers

of *M. genalis* were caught throughout the night (Roulston, 1997). In the same study, the related species *Megalopta ecuadoria* was caught only during late dawn (Roulston, 1997).

We have collected combined data sets of light intensity and flight activity for two species of halictid bees belonging to two tribes within the subfamily Halictinae, *M. genalis* (Augochlorini) and *Lasioglossum* (*Sphécodogastra*) *lusoria* (Halictini). We relate these data to data on eye and ocellus size, in the study species and several closely related diurnal species, and compare our data to those found in the literature. We propose that the light levels encountered by bees when they return to the nest and the sensitivity of their eyes limit the foraging activity of bees, in dim light.

MATERIALS AND METHODS

Observations of flight activity

Observations of *M. genalis* were made on Barro Colorado Island (BCI), Republic of Panama, from 10 to 25 February 2000, and from 9 March to 2 April 2001. Some additional observations were made in May and June 2001. In both years, several nests were collected and positioned close enough together for observation on stands in the forest near the back edge of the old laboratory clearing. We observed the bees when they were leaving and returning to the nest (Figure 1A). We collected data from 7 different nests, during 15 evenings and 15 mornings, in 2000, and from 10 nests, during 23 evenings and 20 mornings, in 2001. We used infrared-sensitive night vision goggles (ITT Industries Night Quest 5001) and video cameras (Sony DCR-TRV310E, equipped with night shot) for observations between 1800 and 2200 h in the evenings and between 0400 and 0800 h in the mornings. On some days, headlights or flashlights were used to set up equipment. This did not affect bees in the evenings but it had a major effect in the mornings (see Results).

In 2001, four artificial nests were used in addition to natural nest sticks. These nests consisted of a layer of balsa wood placed between two glass panes (following Michener and Brothers, 1971, but substituting wood for soil). Each nest measured 10 × 25 cm and housed one wild-caught female bee. The entrances of the artificial nests were equipped with bee counters. A bee counter consisted of an inner and an outer pair of infrared light barriers, each built from an infrared-emitting diode and an infrared sensor and an electronic circuit connected to a computer. When a bee left the nest, the inner sensor sent a signal prior to the outer sensor and vice versa when a bee returned and entered the nest. When a bee stayed very close to the nest entrance without leaving the nest, a signal was registered from the inner sensor only. In this way, we registered when a bee left or returned to the nest, 24 h a day. Bee counter data were collected over 6 days in a row, from 22 March 2001, 1700 h, to 28 March 2001, 0700 h, with only 2 h (23 March, from 1730 to 1930 h) missing as the result of a technical problem.

L. (S.) lusoria were observed while foraging from their pollen hosts, *Oenothera caespitosa* (Figure 3A) and *Oenothera pallida*, in Logan, Cache County, Utah, from 13 to 17 June 2003. The plants grew on an open meadow, on a westerly exposed hillside. Bohart and Youssef (1976) observed the related species *L. (S.) galpinski* at a very similar site. According to their observations, nests were close to the flowers, but we were unable to find nests at either study site.

Light measurement

At both study sites, light levels were measured in candela per square meter with a highly sensitive silicon detector attached

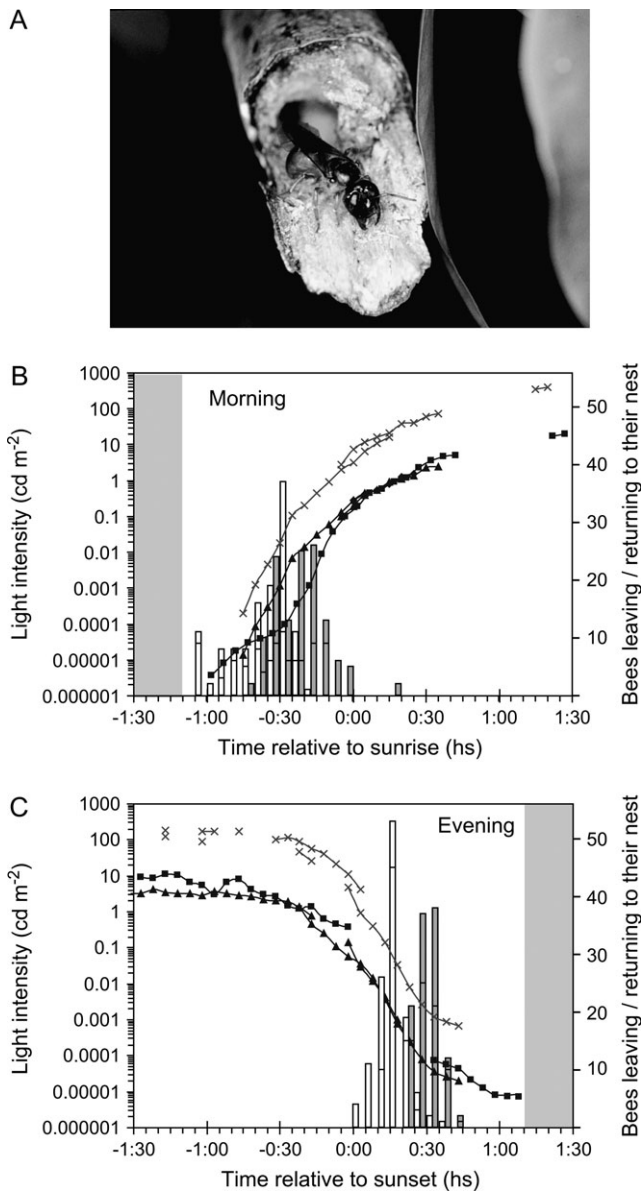


Figure 1
 (A) The tropical bee *Megalopta genalis* (Augochlorini, Halictidae) at the entrance of her nest in a rotting stick. (B, C) Timing of foraging trip of *M. genalis* and light intensity at the nest site (curves with triangles and squares) and at the forest edge (curves with crosses), on BCI, Panama. White bars, number of bees leaving the nest, during each 5-min interval; gray bars, number of bees returning to the nest in each 5-min interval. The stacked bars give counts obtained in 2000 in the lower and those obtained in 2001 in the upper part. (B) Timing of the first foraging trip in the morning. The gray-shaded area of the graph indicates the time before astronomical twilight. (C) Timing of the last foraging trip in the evening. The light gray-shaded area of the graph indicates the time after astronomical twilight.

to a radiometer (InternationalLight, Newburyport, MA, IL1700). In Utah, temperatures were also measured at the study site. All light measurements were taken in the shadows, and in Panama, we took measurements both at the forest edge and at the nest site. Sunset and sunrise, moonset and moonrise, and astronomical twilight data were obtained for the study sites as well as for the study site of Bohart and Youssef (1976), from the National Aeronautics and Space Administration database

(<http://aa.usno.navy.mil/>). Flight activity could thus be related to sunrise and sunset hours, for each study site. Light levels during the flight activity reported by Bohart and Youssef (1976) were estimated from the measured curves, sunset and sunrise data, and geographical and topographical locations. The study site where Bohart and Youssef (1976) observed *S. galpinsiae* between 1968 and 1973 was an open place, very similar to our study site in Logan, so we can assume very similar light conditions. In contrast, *A. dorsata* and *X. tranquebarica* were studied in the forest (Burgett and Sukumalanand, 2000; Dyer, 1985) where light intensities cannot easily be reconstructed.

Capture of bees with lights

M. genalis and *M. ecuadoria* were captured on a large white cotton sheet, suspended between two trees in the rain forest, using a standard UV-enriched black light for insect collection. This apparatus was set up every morning between 0400 and 0430 h from 13 to 23 April 2004. Collection proceeded until about sunrise (approximately 0610 h). Soon after the lights were switched on, several bees (typically between one and five) were attracted immediately to the sheet, presumably lured from nearby nests by the light. No further bees came until approximately 0445 h, after which time bees came regularly to the sheet for slightly more than an hour.

Measurements of body and eye size

Bees from collections in Utah and at Smithsonian Tropical Research Institute (STRI), Panama, and bees caught during experiments were measured to determine body size, eye size, ommatidial diameter, and the diameter of the median ocellus. Head-thorax lengths (HT) were measured as in an earlier study (Jander U and Jander R, 2002, Figure 1) for using as a body-size parameter. For eye size, the dorso-ventral linear length was measured. The diameter of ommatidia was always determined at the same fronto-ventral position on the eye where ommatidia are largest (see Greiner et al., 2004a). Eye size and HT were determined from photos taken under dissection microscopes and ocellar and ommatidial diameters were measured using either the same method or using photos taken by the Scanning Electron Microscope (SEM). For some bees, we also determined the number of ommatidia in one eye, either from nail polish replicas (van Praagh et al., 1980) or from photos taken under the SEM. We used linear regression statistics and Student's *t* test to compare nocturnal and diurnal bees with respect to different eye and ocellar parameters, relative to body size.

RESULTS

***M. genalis*: flight activity determined at the nest site**

For *M. genalis*, we observed 181 foraging trips in the mornings and 131 foraging trips in the evenings. We observed only eight occasions, where more than one bee left the nest at the same time, and all these observations were made on three nests (in 2001). All other observations were made on nests where only a single female foraged. This was confirmed in some cases where nests were opened after the completion of observations.

Typically for this sample, *M. genalis* made one single foraging trip in the evening and between one and four foraging trips in the morning. Only three bees (all in 2001), on seven occasions, left the nest two or more times in the evening but only for short periods of time, and it was not always clear whether these were foraging trips. In some other cases, bees did not forage at all in the evenings, but on most evenings, a bee left and returned to the nest just once.

Figure 1C summarizes data for the last foraging trip of all bees, on all evenings. The number of bees leaving and returning to their nests within a period of 5 min is given together with the light intensities, relative to sunset. In both years, the majority of bees (more than 70%) returned to the nest within a very short time window of only 15 min. Activity was thus restricted to the early twilight period. All bees returned to the nest at least 25 min before astronomical twilight ends—the time when the sun is so far beyond the horizon (18°) that it no longer contributes any significant amount of light to the sky. Astronomical twilight ends 70 min after sunset, at the study site in Panama, and the very last bee returned to her nest about 45 min after sunset. Because of the dense vegetation cover in the forest, the light intensities were then already extremely dim, equaling the light intensities experienced under the open sky, on a starlit night (0.0001 cd m^{-2}).

In the mornings, most bees performed one foraging trip, but some bees performed up to four flights (see below and Figure 2B). Only the first flights are shown in Figure 1B. With the exception of a small group (see below), bees never left the nest before astronomical twilight begins, which in Panama occurs 70 min before sunrise. No bee returned to the nest earlier than 45 min before sunrise. Bees that performed more than one foraging trip during a single morning left the nest earlier for the first trip, compared to bees that performed only a single foraging trip. Thus, in the mornings, some bees left the nest at much dimmer light intensities than in the evenings but returned to the nest at about the same light intensities (0.0001 cd m^{-2}) at both times of the day. This indicates that the light intensity that prevails on the return to the nest is limiting the timing of their foraging activity.

Nine bees left the nest extremely early, before astronomical twilight began, when light levels in the forest were lower than $0.00001 \text{ cd m}^{-2}$. In all these cases, bright artificial light had been used at the nest site. On the first occasion, this happened accidentally, when observers used headlights at the arrival to the nest site. Two bees left their nests almost immediately. In another case (shown by the arrow in Figure 2B), a flashlight was purposely pointed directly toward the nest entrance, and the bee left the nest within 2 min. This happened 90 min before sunrise, a time at which we never saw an undisturbed bee leave her nest. In the other cases, bright lights were used close to the nest entrance for several reasons. When we carefully avoided bright light at the nests, we never observed a bee this early.

Foraging flights that were not elicited by light lasted between 2 and 34 min, with an average of 10.5 min in the mornings (136 flights, SD of sample 6.4 min, median 9 min) and 12.6 min in the evenings (99 flights, SD of sample 4.8 min, median 12 min). In contrast, all flights that had been elicited by light prior to astronomical twilight lasted much longer than normal flights, with a minimum of 35 min, a maximum of 106 min, and an average of 72 min (9 flights, SD of sample 25 min, median 70 min). All bees that left the nest prior to astronomical twilight returned at similar times as the other bees, the earliest arriving 36 min before sunrise when light levels had already reached 0.0001 cd m^{-2} . This clearly suggests that *M. genalis* is unable to return to the nest earlier because light intensities are too dim for them to find the nest entrance hole by means of visual cues.

We mostly observed the nests during dawn and dusk hours but only rarely during day and never between 2200 and 0400 h in the night. The bees' activity during bright daylight and in the night was studied using bee counters. Bees from four artificial nests were studied during 6 days and nights. They never left the nest at night, in the time interval between the end of astronomical twilight in the evening and the start of astronomical twilight in the morning, when no sunlight is

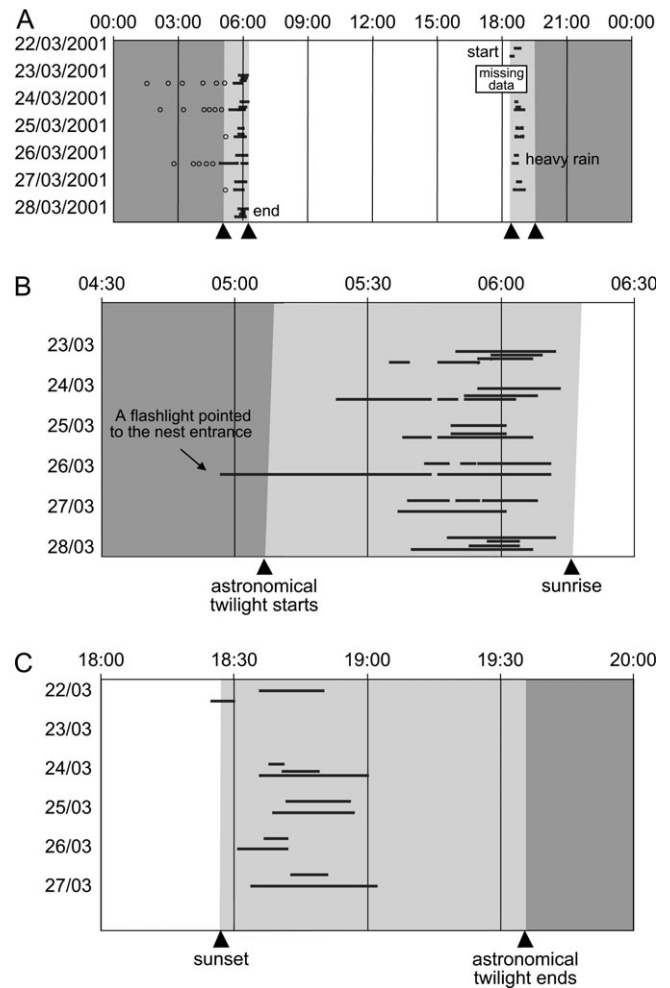


Figure 2

The foraging activity of four females of *Megalopta genalis* as registered with bee counters. Bold lines mark periods during which a bee was outside the nest, the same four bees are shown in the same order for each of the observation days. Twilight periods are shaded in light gray. Arrows mark (from left to right) the onset of astronomical twilight, sunrise, sunset, and the end of astronomical twilight. Foraging activity was restricted to the second half of the twilight period before sunrise and the first half of the crepuscular period after sunset. No activity was recorded during the days (white areas) and nights (dark gray-shaded areas). (A) 24-h tracks. Open circles are associated with one of the four bees and indicate when this bee was moving forward and backward in the nest entrance during the second half of the night. (B) Activity during dawn. Bees that performed several foraging trips (including the bee that moved in the nest entrance before leaving the nest) left the nest earlier than the others. (C) Activity during dusk.

available (Figure 2). One of the four observed bees was very actively foraging during this 6-day period, with up to four foraging trips on several mornings. This bee was sitting close to the nest entrance (where one of the light barriers was positioned) for several hours (indicated by open circles in Figure 2) before she actually left the nest. On one of the mornings, a flashlight was pointed toward her nest entrance, and the bee left the nest before the start of astronomical twilight (arrow in Figure 2B). As in similar cases when bees left the nest early, this bee stayed away for a very long time (Figure 2B).

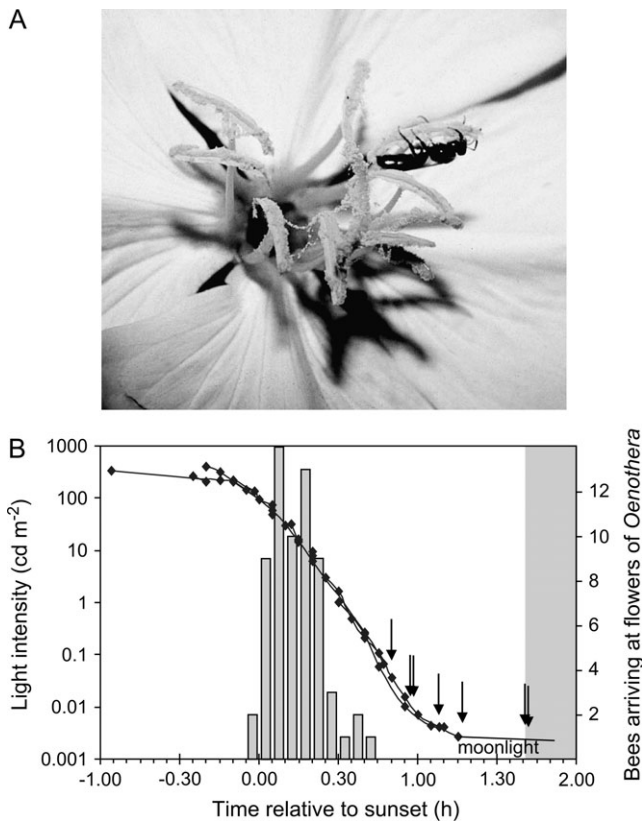


Figure 3
 (A) The temperate bee *Lasioglossum* (*Sphecodogastra*) spp. (Halictini, Halictidae) collecting pollen from a flower of *Oenothera caespitosa* subsp. *marginata*. (B) Activity of *Lasioglossum* (*Sphecodogastra*) *lusoria* and *Lasioglossum* (*Sphecodogastra*) *galpinskiæ* and light intensities at the flower site during dusk. Gray bars: number of *L. (S.) lusoria* observed in Logan, during 5-min intervals, at the flowers. Lines with diamonds: light intensities at the flower site. Arrows relate to the times at which *L. (S.) galpinskiæ* were observed foraging, by Bohart and Youssef (1976), at a similar site in Utah (see text for details).

L. (S.) lusoria: observations at the pollen host plant

During four evenings of observation, the first *S. lusoria* females visited the flowers of *O. pallida* as soon as they opened around sunset (Figure 3A). We observed bees for about 30 min at the flowers. At this time, most flowers were stripped of pollen, and we continued our observations at the flowers of *O. caespitosa* that opened about half an hour later than those of *O. pallida*. The latest bee was observed 45 min after sunset, when the light intensity had fallen to 0.02 cd m⁻² (Figure 3B). At this time, the temperature was around 15°C, well above the threshold temperature of 11°C–12°C that Bohart and Youssef (1976) found for the closely related species *L. (S.) galpinskiæ*. The first hawk moths (*Hyles lineata* and *Sphinx vashti*) visited the flowers about 30 min after sunset. We did not watch the bees in the morning because the data by Bohart and Youssef (1976) clearly indicate that morning activity was limited by temperature or other factors rather than light intensity.

In Figure 3B, we compare our data to the data of Bohart and Youssef (1976) on the closely related species *L. (S.) galpinskiæ* that were observed on several evenings in the years 1968–1973. These authors observed the last foraging trips of these bees about 100 min after sunset (arrows in Figure 3B) on some moonlit nights. A comparison with our light measurements shows that light intensity must have been lower than in our own observations, closer to 0.005 cd m⁻². However,

these last foraging trips still occurred before astronomical twilight ended (110 min after sunset, in Logan), and in addition the moon was up. The matinal activity of *L. (S.) galpinskiæ* always began well after astronomical sunrise. At the field site, the sun might still have been behind mountains, but light intensities must have been rather high at this time, suggesting that the bees' morning activity was limited by temperature rather than light intensity.

Eye and ocellus measurements in diurnal and nocturnal Augochlorini, Halictini, and Andrenid bees

The eyes of *M. genalis* have been studied to some extent (Greiner et al., 2004a; Warrant et al., 2004). The diameters of eyes, ommatidia, and ocelli of *M. genalis*, *M. ecuadoria*, *Megalothea diurnalis*, as well as for several diurnal and one crepuscular augochlorine bees (see Table 1) are presented in Figures 4 and 5 and in Table 1. *M. genalis* is referred to as nocturnal because the light intensities at which the females fly equal those experienced under the open sky, in a moonless night (see above). Similar sets of data are given for a diurnal and a nocturnal species of *Perdita* (Andrenidae) and for four halictine bees *L. (S.) texanum*, *L. (S.) lusoria*, *Lasioglossum* (*Lasioglossum*) *sisymbrii*, and *Lasioglossum* (*Lasioglossum*) *leucozonium*. *L. (S.) texanum* is truly nocturnal and forages on moonlit nights (Kerfoot, 1967a), *L. (S.) lusoria* is crepuscular as described above, and *Lasioglossum* (*Lasioglossum*) is a related diurnal subgenus.

For all three groups of related species, the nocturnal bees have vastly larger ocelli, slightly larger eyes, and larger ommatidia, relative to body size (Figures 4 and 5; Table 1). With respect to ocellar diameters, our measurements confirm those of Kerfoot (1967b). The ocelli of diurnal species are smallest, with a mean of 0.21 mm (± 0.04 mm, SD of sample). The ocelli of the nocturnal species have more than twice this diameter (0.49 ± 0.03 mm, different from the diurnal ones, *t* test, $p < .001$)—and thus capture more than four times as much light. The ocellus diameter is very similar and almost independent of body size in all nocturnal bee species (Figure 5D; regression: $0.4 \text{ mm} + 0.02 \text{ HT}$, $n = 4$, $R^2 = .35$), whereas in diurnal bees, it scales with body size (regression: $-0.05 \text{ mm} + 0.07 \text{ HT}$, $n = 11$, $R^2 = .53$). Those of the crepuscular species fall in between.

Eye size closely correlates with body size (all species, $n = 19$, $R^2 = .769$) and moreover, nocturnal species have only slightly longer eyes than closely related diurnal species (no significant difference between diurnal and nocturnal bees; see Figure 5C and Table 1). More importantly, nocturnal bees have larger ommatidia than diurnal bees, contributing to a higher sensitivity of their eyes (Figure 5F, Table 1; the ratio of ommatidial diameter/HT is significantly higher in the nocturnal bees, *t* test, $p < .001$). The number of ommatidia in the eye increases with body size (Figure 5E, Table 1; see also Jander U and Jander R, 2002). However, nocturnal Augochlorini bees (five individuals of *M. genalis* and one individual of *M. diurnalis*) have smaller numbers of ommatidia relative to body size than diurnal species of the same tribe. Figure 5F shows the number of ommatidia as a function of a measure for body surface (HT², for a similar graph, see Jander U and Jander R, 2002; linear regressions fit data about as logarithmic regressions; $R^2_{\text{diurnal species}} = .71$; $R^2_{\text{nocturnal species}} = .77$; mean ratio ommatidial number/HT² differs significantly between both groups, *t* test, $p < .001$). Being large bees with accordingly large eyes, both species invest more in the sensitivity (by having a smaller number of larger ommatidia) than in the spatial resolution of their eyes. These results supply additional evidence for the hypothesis that light levels limit the foraging activity of crepuscular and nocturnal bees.

Table 1

Head-thorax length (HT), eye length (Eye), ommatidial diameter (Omm), diameter of the median ocellus (OC), number of ommatidia (Num), lifestyle (N, nocturnal; C, crepuscular; D, diurnal), and habitat (f, forest; o, open field) of bees

Bee species	Lifestyle, habitat	HT (mm)	Eye (mm)	Omm (μm)	Num	OC (μm)
Halictidae, Halictini						
<i>Lasioglossum (Sphecodogastra) texanum</i>	N, o	3.3	1.83	27.0	—	0.442
		3.7	1.92	27.5	—	0.468
<i>Lasioglossum (Sphecodogastra) lusoria</i>	C, o	3.3	1.56	25.1	—	0.238
<i>Lasioglossum (Sphecodogastra) aberrans</i>	C, o	2.9	1.51	23.8	—	0.238
<i>Lasioglossum (Lasioglossum) sisymbrii</i>	D, o	3.3	1.58	18.2	—	0.171
		3.0	1.62	17.6	—	0.177
<i>Lasioglossum (Lasioglossum) leucozonium</i>	D, o	3.2 ^a	1.35	20 ^a	3421 ^a	0.175
Halictidae, Augochlorini						
<i>Megalopta genalis</i>	C, f ^b	4.40 ^a	3.2	36 ^a	4883 ^a	0.492
		4.06	2.83	33	4212	—
		4.40	2.74	39	4849	—
		4.09	2.54	38	4632	—
		4.40	—	36	4575	—
		4.08	2.76	36	4729	—
<i>Megalopta ecuadoria</i>	C, f	3.3	2.33	34.5	—	0.358
		3.1	2.32	32.3	—	0.336
<i>Megalopta diurnalis</i>	N, f	4.7	2.75	38.4	5134	0.525
<i>Rhinotula dentricus</i>	C ^c , f	4.8	2.60	32.5	3626	0.316
<i>Augochloropsis hebescens</i>	D, f	3.8	2.03	23.9	4699	0.234
<i>Neocorynura</i> sp.5	D, f	3.9	1.91	21.8	4642	0.206
<i>Caenaugochlora</i> sp.4	D, f	3.2	1.83	22.8	4075	0.219
<i>Caenaugochlora costaricensis</i>	D, f	3.6	2.08	25.6	—	0.262
<i>Augochlora nigrocyanea</i>	D, f	3.2	1.79	22.0	4024	0.199
<i>Augochloropsis fuscognatha</i>	D, f	4.0	2.08	20.9	4674	0.235
<i>Neocorynura</i> sp.	D, f	3.3	1.81	24.8	4077	0.228
<i>Pseudaugochloropsis graminea</i>	D, f	4.0	2.06	25.9	5425	0.302
Andrenidae						
<i>Perdita bequaertiana</i>	N, o	3.0	1.62	27.8	—	0.484
<i>Perdita bohartorum</i>	D, o	3.0	1.25	19.9	—	0.167

^a Data from Greiner et al., 2004a.

^b *M. genalis* is referred to as nocturnal in Figure 5 because it encounters nocturnal light intensities.

^c See Wolda and Roubik, 1986.

Eye size and ocellar diameter of 81 *M. genalis* and 52 *M. ecuadoria* females are given in Figure 5A,B. Within each species and between both congeneric species, both eye size and ocellar diameter are correlated to body size. These bees were captured in the morning with light, the largest bees first and the smallest bees last (Warrant EJ and Theobald JC, personal observations). In addition, most bees of the larger species *M. genalis* were captured earlier and at dimmer light intensities than most *M. ecuadoria*.

DISCUSSION

Dim light sets a limit

Our data show that light intensity limits the foraging activity of bees. Whether a bee—with a given sensitivity of her eyes and ocelli—is able to fly and forage all night, or only during dawn and dusk, and whether it can forage on moonless nights also depend on the exact light intensity at the nest site. The critical importance of light intensity explains the seemingly paradoxical situation that bees with relatively small and insensitive eyes—such as *L. (S.) texanum*—can forage in moonlit nights in the open areas where it lives, whereas *M. genalis*, with its highly sensitive eyes, is restricted to foraging during the brighter part of twilight, in the dim rain forest. To call *M. genalis* a nocturnal bee species is correct with regard to the light intensities at which the species forages—these light

intensities equal those experienced under the open sky on a starlit night.

M. genalis left the nest before astronomical twilight, in the morning, but never returned at these dim light intensities. Bees never performed orientation flights when they left the nest very early (Kelber A, personal observations), which would demand light for landmark vision (Warrant et al., 2004). However, they can easily find their way to the canopy where it is 500 times brighter than at the nest site by phototaxis. On the return trip, they need visual landmarks to find the tiny hole that forms the nest entrance (Warrant et al., 2004). Occasional observations by scientists watching bats, as well as light capture data, indicate that small numbers of *M. genalis* can be found at any time of the night (Roulston, 1997). Our results clearly demonstrate that *M. genalis* does not forage after astronomical twilight in the evening or before astronomical twilight in the morning. Concerning their temporal activity window, they are clearly crepuscular rather than nocturnal, at our study site in Panama.

There are several possible explanations to account for the truly nocturnal observations and captures. First, bees that are actively foraging (with up to four foraging trips in the morning, see Figure 2) sit near the nest entrance during most of the second half of the night (Figure 2A). A bright light at the nest entrance—such as the headlights of bat observers or a light trap—tricks them into believing that it is time for a first foraging trip, and they may leave the nest. They may also take the

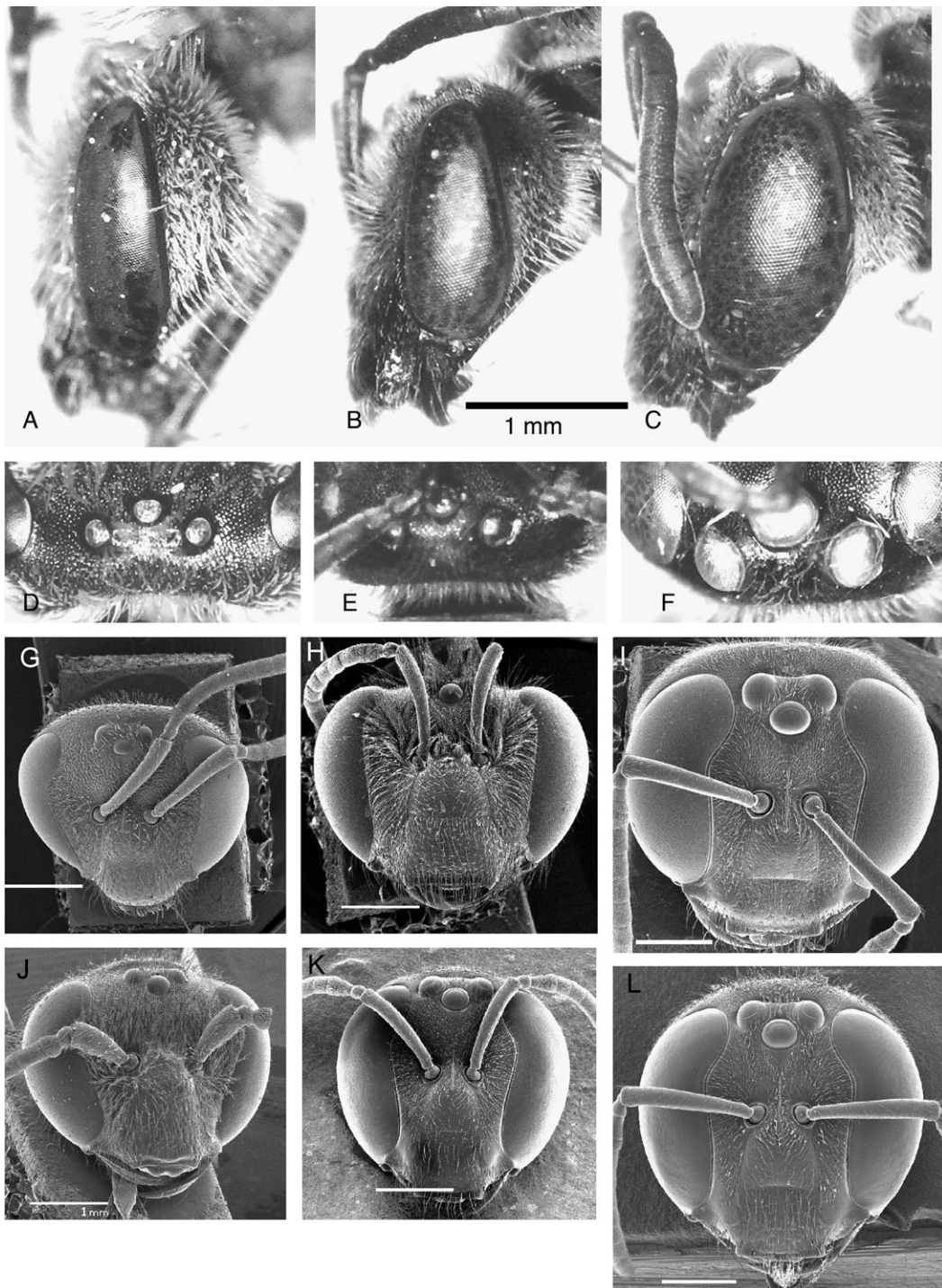


Figure 4

The eyes and ocelli of bees flying at diurnal (left column), crepuscular (central column), and nocturnal (right column) light intensities. All scale bars are 1 mm. (A–C) Eyes and (D–F) ocelli of three species of the halictid tribe Halictini, photographed in an optical microscope. The same scale applies to (A–F). (A, D) *Lasioglossum sisymbrii*, (B, E) *Sphecodogastra lusoria*, (C, F) *Sphecodogastra texanum*. (G–L) Six species of the halictid tribe Augochlorini. (G) *Augochloropsis hebescens*, (H) *Rhimetus dentricus*, (I) *Megalopta genalis*, (J) *Pseudaugochloropsis graminea*, (K) *Megalopta ecuadoria*, (L) *Megalopta diurnalis*.

artificial light as a piece of open sky guiding them to the canopy where flowers are to be expected. Roulston (1997) captured almost only bees without pollen, strongly suggesting they were on their way from the nest to a foraging site.

In the evening, even late after sunset, bees never left the nest when we pointed a flashlight toward the nest entrance (Kelber

A, personal observations). This may explain why Roulston (1997, Figure 1) caught more bees in the second half than in the first half of the night. It remains to be studied how bees decide when to leave the nest. Our observations indicate that they use different criteria in the evening and the morning, but we can only hypothesize that they use decreasing light

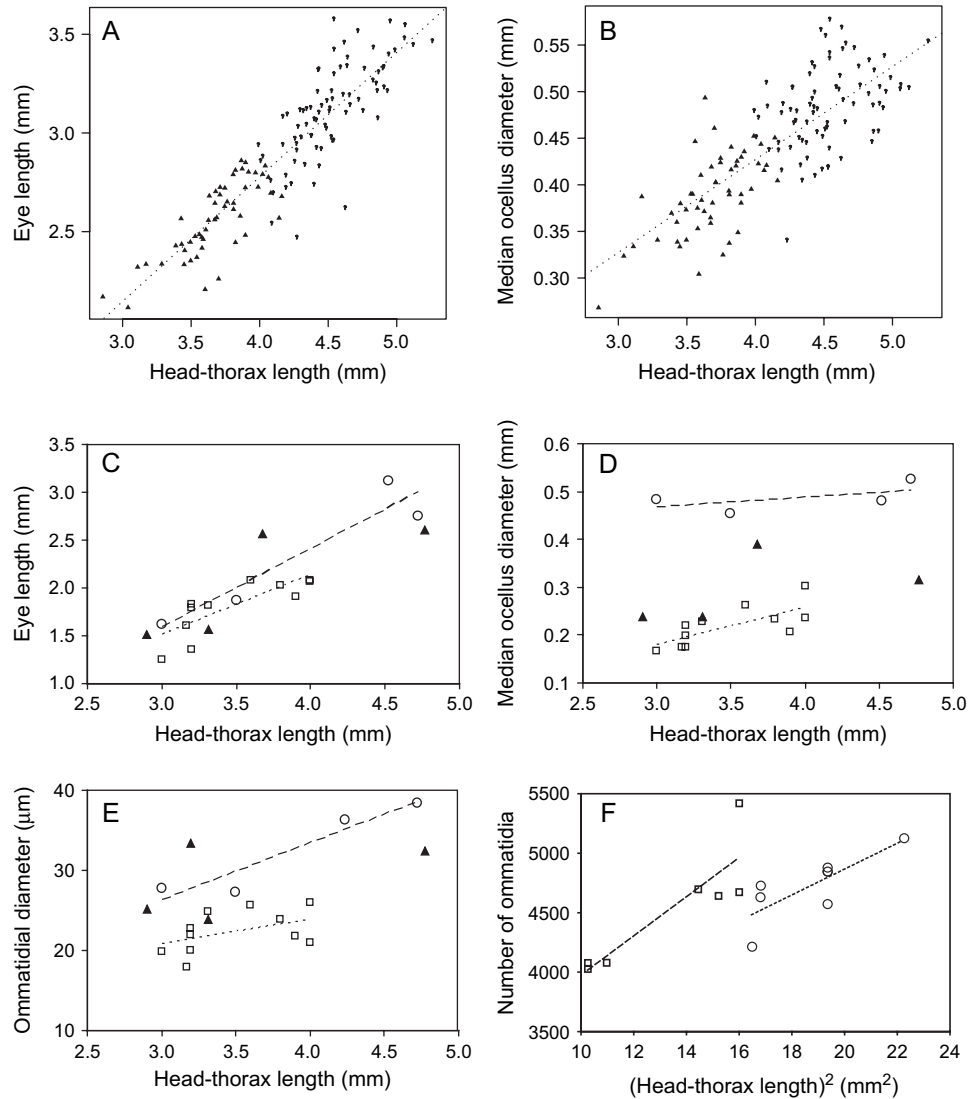


Figure 5

(A) Eye length and (B) diameter of the median ocellus in 81 *Megalopta genalis* and 52 *M. ecuadoria*, as a function of body size. *M. genalis*—HT: mean = 4.525, SD = 0.2835, SEM = 0.0315; eye length: mean = 3.113, SD = 0.2438, SEM = 0.02709; ocellus diameter: mean = 0.4798, SD = 0.06652, SEM = 0.007391. *Megalopta ecuadoria*—HT: mean = 3.678, SD = 0.2767, SEM = 0.03837; eye length: mean = 2.564, SD = 0.1911, SEM = 0.0265; ocellus diameter: mean = 0.3912, SD = 0.04432, SEM = 0.006146. In both species, eye length ($R^2 = .811$) and ocellus diameter ($R^2 = .61$) depend on body size. (C–E): Eye length (C), diameter of the median ocellus (D), and ommatidial diameter (E) of different species of halictid and andrenid bees that forage in nocturnal (open circles), crepuscular (filled triangles), and diurnal (open squares) light intensities. Regression lines are given for nocturnal (dashed) and diurnal (dotted) bees. Average values are given for species where more than one animal was measured. For measurements of individual bees please see Table 1. (F) Number of ommatidia of nocturnal (open circles) and diurnal (open squares) augochlorine bees as a function of a body-surface parameter, the square of HT. Each data point represents an individual bee (see Table 1).

intensities in the evening and increasing light intensities in the morning as cues. In addition, they might strongly rely on a circadian clock—at latitudes where sunset and sunrise times vary as little as half an hour over the year, this might be a rather reliable cue.

Second, some newly eclosed females leave the natal nest (Wcislo et al., 2004), and it presumably takes them some time to find their own appropriate nest stick. Especially during the dry season, there presumably are homeless bees in the forest. In addition, even if we have no reliable observation of this, bees might occasionally stay out too late in the evening and get lost. And finally, it is possible that some bees have nests very close to the forest edge where it is bright enough for them to fly later than any bee we have observed at our nest

site in the forest. Any of these reasons can account for the bees occasionally observed by scientists watching bats and the small numbers of bees that Roulston (1997) captured during the first half of the night.

Other limits to nocturnal foraging

Are there other limits to nocturnal foraging activity in bees, in addition to light intensity? Temperature has already been mentioned as a factor that probably limits morning activity in *L. (S.) galpinsiae* and possibly also in *L. (S.) lusoria*. The same may apply to a larger number of bees in climates with huge diurnal temperature changes. However, the colletid bee *P. arizonensis* can warm up the thorax to temperatures

considerably higher than ambient temperature (Shelly et al., 1993) and is thus able to start foraging before sunrise. Indian carpenter bees (*Xylocopa* sp., Somanathan and Borges, 2001; Somanathan H and Borges R, personal communication) are able to forage at temperatures as low as 2°C. In the tropical rain forest of Panama, temperature can be excluded as a limiting factor.

Food availability and competition may be another factor strongly influencing foraging schedules of bees. The foraging behavior of bees generally tracks diel availability of pollen, and foragers cease activity when floral resources are depleted (e.g., Minckley et al., 1994; Wcislo and Cane, 1996). However, for both *M. genalis* and *L. (S.) lusoria*, it is highly unlikely that foragers cease activity in the evening due to the depletion of resources. Pollen sources for *M. genalis* include emergent canopy trees that are associated with bats, such as *Ceiba pentandra* (Bombacaceae) and *Pseudobombax septenatum* (Bombacaceae) (Wcislo et al., 2004). Quantitative data on diel resource availability are lacking for Panamanian populations of these genera, although data from other localities are consistent with our hypothesis. In the Mexican *Pseudobombax ellipticum*, for example, flowers open at 1800 h and availability of pollen and nectar peaks at 2000 and 2200 h, respectively, and both resources are present throughout the night (Eguiarte et al., 1987). At their study site, bats did not begin foraging until 1930 h (Eguiarte et al., 1987). Likewise, cumulative nectar production for *C. pentandra* in Amazonia is greatest at 1900 h, approximately half of the nectar is still available at midnight (2400 h), and residual pollen and nectar were still present in the morning (Gribel et al., 1999). Assuming that flowering phenologies do not vary dramatically among localities (see Lobo et al., 2003), it is likely that there are similar patterns of resource availability in central Panama, and thus floral resources are likely to be most abundant after *M. genalis* females have already ceased foraging in the evening. *L. (S.) lusoria* collected pollen from two species of *Oenothera*. They removed most pollen from the flowers of *O. pallida* within half an hour and may have exhausted this pollen source for the evening. However, the flowers of *O. caespitosa* opened about half an hour later than those of *O. pallida* and received only few visits by the bees (white bars in Figure 3B) before the latest bee was seen, and pollen was left in most of the flowers. Some flowers did not open before bees ceased to visit. Few hawk moths were present at that time, and the moths, being nectar feeders, did not remove large pollen masses. We are therefore confident that food availability was not the reason for either of the bees to stop foraging in the evening.

Another possible factor is the hour of day—some bees may have a strict circadian activity rhythm forcing them to forage at certain hours of day, independent of light intensities. Even if the circadian rhythm is most likely controlled by the diurnal light intensity rhythm, it may thus only indirectly control foraging activity. For *M. genalis*, most data were collected between 25 February and 2 April. The sunrise times on the first and last day differ by 20 min, and between both years of observations, they differ on average by 10 min. Figure 1B shows that matinal foraging activity in both years (lower and upper parts of bars) starts at the same time relative to sunset, and thus very similar light intensities, and does not differ between both years. In laboratory flight facilities, *M. genalis* females become active in the evening as soon as the bright day illumination is switched off and the dim night illumination is switched on, even if the rhythm is changed between 2 days.

Some of the above-mentioned factors, such as temperature and the availability of pollen, may limit foraging activity in other nocturnal or crepuscular bees. Some of them may also be the reasons why bees forage at night. Bees of the genera *Peponapis* and *Xenoglossa*, for instance, avoid both, the heat of the day and competition with larger bees, by foraging in the early morning.

Body size matters

Obviously, large bees have large eyes, and large eyes are advantageous for being nocturnal (e.g., Jander and Jander, 2002). Why do not all large bees fly at night, and how can small bees be nocturnal? Some species may indeed be limited by strict behavioral patterns, by temperature, or by their dependence on a narrow spectrum of hosts. Other larger bees such as the African race of *A. mellifera* are facultatively crepuscular.

The halictini species are interesting because they are of similar body size but nonetheless differ considerably in ommatidial and ocellar size, indicating that the nocturnal and even the crepuscular species invest more in vision than the diurnal bees do. *L. (S.) texanum*—flying in moonlit nights—have larger ocelli and ommatidia than the crepuscular and the diurnal species, clearly indicating that they have evolved higher sensitivity in both of their visual organs. It is also obvious that ocellus diameters, and thus sensitivity, differ more between diurnal and nocturnal bees than do ommatidial diameters.

Compared to lens eyes, it is more difficult in a compound eye to maintain both high spatial resolution and good sensitivity: other than in lens eyes, these two parameters cannot easily be decoupled. At equal eye size and focal length, a compound eye can either have many small ommatidia or few large ommatidia. At the same body size, the nocturnal species have larger ommatidia (Figure 5E) but fewer of them (Figure 5F). They invest less in spatial resolution than diurnal bees of similar size. Moreover, many nocturnal species have a large body size, and thus larger and more sensitive eyes and an advantage in flying under dimmer light conditions, relative to small bees.

Within the species *M. genalis* and its smaller congener *M. ecuadoria*, both eye and ocellar size correlate with body size (Figure 5A,B). Body size variation is very common among bees and may have facilitated the evolution of dim light foraging in bees. Social halictids in temperate regions typically have a spring generation of relatively large females, which then produce one or more summer generations of smaller daughters (e.g., Wcislo and Danforth, 1997). If temperature did not set limits to their foraging activity, the larger females should be able to fly earlier in the morning. Observations of *Lasioglossum malachurum* near Tübingen, Germany, indicate that bees are too cold to fly from the ground during early mornings (Kelber A, unpublished data), so it is likely that temperature limits their morning activity at this site. In contrast, the colletid bee *P. arizonensis* can warm up the thorax (Shelly et al., 1993) and is thus able to start foraging before sunrise.

In the tropical rain forest, temperature does not limit bee activity at any time of the day. *M. genalis* and *M. ecuadoria* females vary extensively in body size, and the size—and thus sensitivity—of their eyes is closely correlated to body size (Figure 5A), although it varies considerably. Within very few generations, the advantage of foraging in dim light would have selected for larger bodies and relatively larger eyes (Nilsson and Pelger, 1994). The timescale for the evolution of a nocturnal lifestyle is not known for any bee, but nocturnality seems to be a rather new trait in all of them (Engel, 2000).

OUTLOOK

Eye size and the apertures (lens diameters) of ocelli and ommatidia are not the only measures of sensitivity. We have recently shown that *M. genalis* has a receptor anatomy and physiology and a neuronal anatomy in the first optic neuropile (the lamina) that are adapted to enhance sensitivity (Greiner et al., 2004a,b; Warrant et al., 2004). We expect spatial and temporal pooling to be more important in smaller

than in larger species of crepuscular and nocturnal bees. In line with this, we also expect that small nocturnal bees have a much coarser spatial resolution and must fly more slowly to avoid motion blur while they approach the nest hole. Additional behavioral, physiological, and ecological studies on other closely related diurnal and nocturnal species are required to understand how different bees are adapted for flying and foraging in dim light habitats.

We thank Laura Arneson, Victor Gonzalez, Birgit Greiner, and Kari Roesch for help with fieldwork. Victor's skills in setting up artificial nests are also greatly acknowledged. Thanks to the STRI staff on BCI for making work there both effective and pleasant. David Roubik, STRI, kindly allowed us to use Augochlorini bees of his collection for the SEM studies. Special thanks to Jim Cane and Terry Griswold for sharing their knowledge on *Sphecodogastra* and for their hospitality at the Utah State University/US Department of Agriculture bee lab in Logan. Financial support from the Swedish Research Council (VR), the Royal Swedish Academy of Sciences (KVA), the Swedish Foundation for International Cooperation in Research and Higher Education (STINT), the Wenner-Gren foundation, all in Stockholm, the Science Faculty of Lund University, the Company of Biologists in Cambridge, the US NSF (DEB-0317217), the Baird Restricted Endowment from the Smithsonian Institution, and general research funds from the STRI is gratefully acknowledged.

REFERENCES

- Bohart GE, Youssef NN, 1976. The biology and behaviour of *Evyllaes galpimsiae* Cockerell (Hymenoptera: Halictidae). *Wasmann J Biol* 34:185–234.
- Burgett DM, Sukumalanand P, 2000. Flight activity of *Xylocopa (Nyctimelitta) tranquebarica*: a night flying carpenter bee (Hymenoptera: Apidae). *J Apic Res* 39:75–83.
- Dyer FC, 1985. Nocturnal orientation by the Asian honeybee, *Apis dorsata*. *Anim Behav* 33:769–774.
- Eguarte L, Martínez del Rio C, Arita H, 1987. El néctar y el polen como recursos: el papel ecológico de los visitantes a las flores de *Pseudobombax ellipticum* (H.B.K.) Dugand. *Biotropica* 19:74–82.
- Engel M, 2000. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bull Am Mus Nat Hist* 50:1–89.
- Fletcher GJC, 1978. The African bee, *Apis mellifera adansonii*, in Africa. *Annu Rev Entomol* 23:151–171.
- Greiner B, Ribí WA, Warrant EJ, 2004a. Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*. *Cell Tissue Res* 316:377–390.
- Greiner B, Ribí WA, Wcislo WT, Warrant EJ, 2004b. Neural organisation in the first optic ganglion of the nocturnal bee *Megalopta genalis*. *Cell Tissue Res* 318:429–437.
- Gribel R, Gibbs PE, Queiróz AL, 1999. Flowering phenology and pollination biology of *Ceiba pentandra* (Bombacaceae) in Central Amazonia. *J Trop Ecol* 15:247–263.
- Hurd PD, Linsley EG, 1970. A classification of the squash and gourd bees *Peponapis* and *Xenoglossa* (Hymenoptera: Apoidea). In: University of California Publications in Entomology, vol. 12. Berkeley: University of California Press; 1–39.
- Jander U, Jander R, 2002. Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct Dev* 30:179–193.
- Janzen DH, 1964. Notes on the behavior of four subspecies of the carpenter bee, *Xylocopa (Notoxylocopa) tabaniformis*, in Mexico. *Ann Entomol Soc Am* 57:296–301.
- Kerfoot WB, 1967a. The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee (Hymenoptera: Halictidae). *Anim Behav* 15:479–486.
- Kerfoot WB, 1967b. Correlation between ocellar size and the foraging activities of bees (Hymenoptera, Apoidea). *Am Nat* 101:65–70.
- Land MF, 1981. Optics and vision in invertebrates. In: Handbook of sensory physiology, Vol VII/6B (Autrum H, ed). New York: Springer-Verlag; 471–592.
- Linsley EG, MacSwain JW, Smith RF, 1955. Biological observations on *Xenoglossa fulva* Smith with some generalizations on biological characters of other Eucerine bees. *Bull South Calif Acad Sci* 54:128–141.
- Linsley EG, Cazier MA, 1970. Some competitive relationships among maternal and late afternoon foraging activities of caupolicanine bees in southeastern Arizona (Hymenoptera, Colletidae). *J Kansas Entomol Soc* 43:251–261.
- Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herrerías-Diego Y, Rojas J, Saborío G, 2003. Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *Am J Bot* 90:1054–1063.
- Michener CD, Brothers DJ, 1971. A simplified observation nest for burrowing bees. *J Kans Entomol Soc* 44:236–239.
- Minckley RL, Wcislo WT, Yanega D, Buchmann SL, 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. *Ecology* 75:1406–1419.
- Mizunami M, 1995. Functional diversity of neural organisation in insect ocelli. *Vision Res* 35:443–452.
- Nilsson D-E, Pelger S, 1994. A pessimistic estimate of the time required for an eye to evolve. *Proc R Soc Lond B* 256:53–58.
- van Praagh JP, Ribí W, Wehrhahn C, Wittmann D, 1980. Drone bees fixate the queen with the dorsal frontal part of their compound eyes. *J Comp Physiol* 136:263–266.
- Roberts RB, 1971. Biology of the crepuscular bee *Ptiloglossa guinnæ* n. sp. with notes on associated bees, mites and yeasts. *J Kans Entomol Soc* 44:283–294.
- Roulston TH, 1997. Hourly capture of two species of *Megalopta* (Hymenoptera: Apoidea: Halictidae) at black light in Panama with notes on nocturnal bees. *J Kans Entomol Soc* 70:189–196.
- Rozen JR, Rozen BL, 1986. Bionomics of crepuscular bees associated with the plant *Psorothamnus scoparius* (Hymenoptera: Apoidea). *J New York Entomol Soc* 94:472–474.
- Shelly RTE, Villalobos EM, Buchmann SL, Cane JH, 1993. Temporal patterns of floral visitation for two bee species foraging on *Solanum*. *J Kans Entomol Soc* 66:319–327.
- Smith AR, Wcislo WT, O'Donnell S, 2003. Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera, Halictidae). *Behav Ecol Sociobiol* 54:14–21.
- Somanathan H, Borges R, 2001. Nocturnal pollination by the carpenter bee *Xylocopa tenuiscafa* (Apidae) and the effect of floral display on fruit set of *Heterophragma quadriloculare* (Bignoniaceae) in India. *Biotropica* 33:78–89.
- Warrant EJ, Kelber A, Gislen A, Greiner B, Ribí W, Wcislo WT, 2004. Nocturnal vision and landmark orientation in a tropical halictid bee. *Curr Biol* 14:1309–1318.
- Wcislo WT, Arneson L, Roesch K, Gonzalez V, Smith A, Fernandez H, 2004. The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biol J Linn Soc* 83:377–387.
- Wcislo WT, Cane JH, 1996. Resource utilization by solitary bees (Hymenoptera: Apoidea), and exploitation by their natural enemies. *Annu Rev Entomol* 41:257–286.
- Wcislo WT, Danforth BN, 1997. Secondarily solitary: the evolutionary loss of social behavior. *Trends Ecol Evol* 12:468–474.
- Wolda H, Roubik DW, 1986. Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* 67:426–433.
- Zeil J, Kelber A, Voss R, 1996. Structure and function of learning flights in ground-nesting bees and wasps. *J Exp Biol* 199:245–252.