Quick guides

Nocturnal bees

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Are there really nocturnal bees? Surprisingly, yes. Most people, if asked about bees, think of those industrious day-active species, like the common honeybee, that harvest sunny meadows of flowers for pollen and nectar. And such images are not misguided — most bees are indeed day active (diurnal). By sundown most bees are safely back in the nest, their day's labours complete. But for some bees, the setting sun instead signals the beginning of a working night. For these nocturnal shift-workers, the gathering of pollen and nectar can occur in near-darkness. Some species forage all night, and these are thus obligately nocturnal. One species, a giant Indian carpenter bee of the genus *Xylocopa* (which remains to be identified), even continues to forage on the darkest moonless nights. Others are crepuscular, meaning that their activity is restricted to the slightly brighter hour (or so) just after sunset and/or before sunrise. Some of these bees may even continue to forage all night if the sky is moonlit. The dim worlds experienced by all of these night-flying bees are actually quite challenging — bees rely heavily on vision during foraging, and recent research shows that nocturnal bees are no exception.

Which bees are nocturnal and where are they found? Nocturnal and crepuscular activity in bees has arisen independently (and on several occasions) in at least four of the seven recognised families of bees, namely in the Colletidae, the Andrenidae, the Halictidae and the Apidae. Most species are tropical or sub-tropical, but many are found in warmer arid areas at higher latitudes. Only one species is known to be obligately nocturnal, and this is the giant Indian carpenter bee mentioned above (*Xylocopa* sp., Apidae), a bee capable of foraging even on the darkest moonless nights. The well-studied Central American sweat bee *Megalopta genalis* (Halictidae) is crepuscular, being active under the thick rainforest canopy during two short time windows shortly after dusk and before dawn. Two species of honeybees (Apidae, genus *Apis*) are known to be crepuscular and to forage throughout the night if a moon half-full or larger is present in the sky — the giant Asian honeybee *Apis dorsata* and the African honeybee *Apis mellifera adansonii*. It is also worth mentioning that even among the wasps, near relatives of bees, many species have become nocturnal.

A tell-tale indicator of nocturnal behaviour in a bee can be found by looking at the ocelli, the three round eyelets located on the dorsal surface of the head between the two compound eyes. These specialised eyes — which likely play a role in flight control — are significantly larger relative to body size in species that fly in dim light. In the giant Indian carpenter bee (*Xylocopa* sp.) they measure almost a millimetre across. The ocelli of the similarly sized sympatric diurnal species *X. ruficornis* are significantly less than half this size. While differing less dramatically, the compound eyes of the nocturnal species are also relatively larger, and typically contain larger numbers of ommatidia, than those of their diurnal relatives. Vision, it seems, plays an important role in nocturnal life.

Why have some bees become nocturnal? There are basically two main reasons that have been hypothesised. The first is reduced competition. In the forested habitats where nocturnal bees are typically found, many species of trees and plants have flowers that open only at night, or that produce nectar both day and night. Compared to diurnal nectar sources, nocturnal flower resources are exploited by comparatively few other animals — only bats and moths are notable competitors. The abundance of nectar and pollen reserves probably drove bees to forage at dimmer light levels, both later into the evening, to exploit the typically generous nectar supplies of nocturnal flowers, and earlier in the morning, when the nectar reserves of newly opened flowers are still relatively untapped.

The second probable reason why bees became nocturnal was to avoid predation and parasitism. Diurnal bees are heavily attacked by predators and parasites alike, and the nocturnal niche may have represented a convenient escape route.

Do nocturnal bees forage like diurnal bees? Essentially yes, although this must be qualified by saying that very few observations have been made of nocturnal bees foraging at flowers, because of the difficulties of watching bees in dim light. We do know, however, that many similarities in foraging strategies exist. Like their diurnal relatives, nocturnal bees visit flowers that may be located at a considerable distance from the nest. This of course implies that they can find their way home again, which is not a trivial undertaking for a small animal like a bee. Diurnal bees rely heavily on vision for this task. Landmarks around the nest entrance, as well as along the foraging route, are identified visually and remembered for later retrieval. The directions and distances flown to and from the foraging site are also determined visually, and in honeybees this information is transferred to other bees in the hive.

We now know that, like diurnal bees, nocturnal bees can see polarised light and can visually learn the arrangement of landmarks around the nest entrance. They do this as they fly from the nest, turning in mid air to face the nest, and then flying in increasingly larger arcs to survey the field of local landmarks. Even though we currently do not know whether landmarks along the foraging route are learned

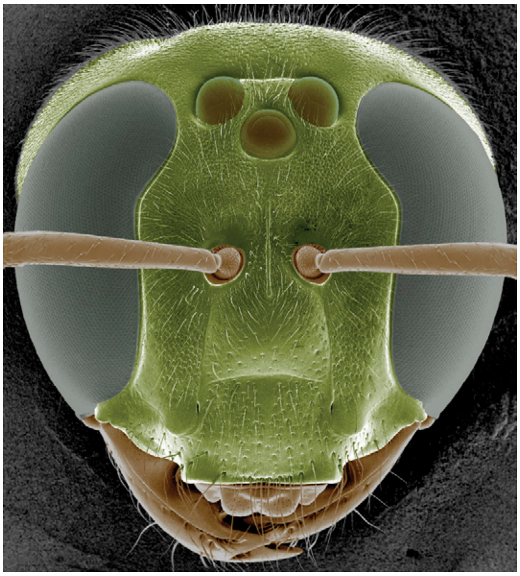

Figure 1. The head of the nocturnal bee *Megalopta genalis*, showing the relatively large compound eyes and ocelli.

visually, nor whether vision is used to determine directions and distances travelled to the foraging site, there is no reason to rule out the possibility.

Can nocturnal bees really see so well with such tiny eyes?
Remarkably yes. But there is no question that their visual systems are operating near the limit and that only the coarser and slower features of the world can be seen. Light intensity plays a deciding role in whether a particular bee species is able to forage or not — many species of bees that are capable of visual foraging in the early dusk may be forced back to the nest just a short time later before light levels have become unacceptably dim. Those able to forage at the very dimmest light levels (such as *Megalopta genalis* (Figure 1) and the giant Indian carpenter bee *Xylocopa* sp.) typically have visual specialisations that permit nocturnal foraging. Apart from giant ocelli, these bees have very large ommatidial facet lenses and massive photoreceptors, adaptations that maximise light capture and improve vision. Moreover, it is very likely that nocturnal bees (and indeed many other nocturnal insects) are also able to enhance vision at a higher level in the visual system by neurally summing photons in space and time. This strategy, which improves visual sensitivity at the expense of spatial and temporal resolution, requires the presence of specialised circuits in the optic lobes of the brain. Even though we have considerable evidence for the presence of such circuits, their existence remains to be established with certainty. But the remarkable visual abilities of nocturnal bees — which allow landmark-based homing at light levels where humans are practically blind — are beyond question.

Further reading

Burgett, D.M., and Sukumalanand, P. (2000). Flight activity of *Xylocopa (Nyctomelitta) tranquebarica*: a night flying carpenter bee (Hymenoptera: Apidae). J. Apic. Res. *39*, 75–83.
Dyer, F.C. (1985). Nocturnal orientation by the Asian honeybee, *Apis dorsata*. Anim. Behav. *33*, 769–774.
Kelber, A., Warrant, E.J., Pfaff, M., Wallén, R., Theobald, J.C., Wcislo, W., and Raguso, R. (2006). Light intensity limits the foraging activity in nocturnal and crepuscular bees. Behav. Ecol. *17*, 63–72.
Kerfoot, W.B. (1967). The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee. Anim. Behav. *15*, 479–486.
Warrant, E.J., Kelber, A., Gislén, A., Greiner, B., Ribi, W., and Wcislo, W.T. (2004). Nocturnal vision and landmark orientation in a tropical halictid bee. Curr. Biol. *14*, 1309–1318.
Wcislo, W.T., Arneson, L., Roesch, K., Gonzalez, V., Smith, A., and 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. Linnean Soc. *83*, 377–387.

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Columbines

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What are columbines?
Columbines are compact, herbaceous, flowering plants belonging to the genus *Aquilegia* which have long been of interest to both garden enthusiasts and scientists. Species of *Aquilegia* are found primarily in mountainous regions of Europe, Asia and North America. Their flowers are usually brightly coloured and each petal is modified to have a tubular outgrowth, the nectar spur (Figure 1). Nectar is made at the very tip of the spur, filling it partially. Animals probe the spurs to obtain the nectar, thereby achieving pollination of the flowers. Species of *Aquilegia* can differ dramatically in flower color and shape, yet they can usually be hybridized, which has resulted in both natural hybrid zones and a startling number of horticultural varieties. In the Figure, panels A and B show the species *A. formosa* and *A. pubescens*, respectively, while C shows a naturally occurring hybrid of the two. The ability of very divergent columbines to hybridize also piqued the interest of Darwin, as he discussed the concept of species in letters with J.D. Hooker during the 1850s, and continued to attract scientific interest throughout the twentieth century, resulting in classic studies such as Munz's taxonomic treatment in the 1940s, Verne Grant's analysis of ecological and pollinator isolation in the 1950s and Prazmo's genetic studies of floral differences in the 1960s.

How have columbines evolved?
Aquilegia has about 70 species that vary in their flower color and shape as well as the habitats in which they grow. Despite their geographic, morphological and ecological diversity, very few genetic differences can be found among the species. This has led to columbines becoming a textbook example of a recent adaptive radiation, where speciation has occurred rapidly to produce a variety of species, each