Review

Seeing in the dark: vision and visual behaviour in nocturnal bees and wasps

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Summary

In response to the pressures of predation, parasitism and competition for limited resources, several groups of (mainly) tropical bees and wasps have independently evolved a nocturnal lifestyle. Like their day-active (diurnal) relatives, these insects possess apposition compound eyes, a relatively light-insensitive eye design that is best suited to vision in bright light. Despite this, nocturnal bees and wasps are able to forage at night, with many species capable of flying through a dark and complex forest between the nest and a foraging site, a behaviour that relies heavily on vision and is limited by light intensity. In the two best-studied species – the Central American sweat bee _Megalopta genalis_ (Halictidae) and the Indian carpenter bee _Xylocopa tranquebarica_ (Apidae) – learned visual landmarks are used to guide foraging and homing. Their apposition eyes, however, have only around 30 times greater optical sensitivity than the eyes of their closest diurnal relatives, a fact that is apparently inconsistent with their remarkable nocturnal visual abilities. Moreover, signals generated in the photoreceptors, even though amplified by a high transduction gain, are too noisy and slow to transmit significant amounts of information in dim light. How have nocturnal bees and wasps resolved these paradoxes? Even though this question remains to be answered conclusively, a mounting body of theoretical and experimental evidence suggests that the slow and noisy visual signals generated by the photoreceptors are spatially summed by second-order monopolar cells in the lamina, a process that could dramatically improve visual reliability for the coarser and slower features of the visual world at night.

Key words: nocturnal vision, compound eye, bee, wasp, landmark orientation, resolution, sensitivity, spatial summation.

Introduction

To see reliably, an eye must capture sufficient light. For a diurnal (day-active) animal, adapted for vision in bright sunlight, this basic requirement is easily achieved. However, at night, or at tremendous depths in the sea, where light levels may be many orders of magnitude lower, reliable vision cannot be guaranteed. Indeed, many nocturnal and deep-sea animals have simply ceased to rely on vision as their primary sense, depending instead on olfaction, hearing, electroreception and mechanoreception to interpret their environments (Warrant and Locket, 2004; Warrant, 2008). This, however, is by no means the rule: many others have invested heavily in vision, evolving remarkable adaptations to see well in dim light (Laughlin, 1990; Meyer-Rochow and Nilsson, 1998; McIntyre and Caveney, 1998; Warrant, 2004; Warrant, 2006; Warrant, 2008). This review showcases one particular group of such animals – the nocturnal bees and wasps – a group that is starting to reveal some of the basic principles used by animals to process visual information in dim light.

To see well in dim light, a visual system needs to extract reliable information from what may be an unreliable visual signal; that is, to extract information from a visual signal that is contaminated by visual 'noise'. Part of this noise arises from the stochastic nature of photon arrival and absorption: each sample of absorbed photons (or signal) has a certain degree of uncertainty (or noise) associated with it. The relative magnitude of this uncertainty is greater at lower rates of photon absorption, and these quantum fluctuations set an upper limit to the visual signal-to-noise ratio (Rose, 1942; de Vries, 1943; Land, 1981). As light levels fall, the fewer the number of

photons that are absorbed, the greater the noise relative to the signal and the less that can be seen. Signal reliability in dim light can thus be improved with an eye design of high sensitivity to light. In nocturnal insects, including most moths and many beetles, this eye design is typically a refracting superposition compound eye, a design that allows single photoreceptors in the retina to receive focused light from hundreds (and in some extreme cases, thousands) of corneal facet lenses (Fig. 1B). This design represents a vast improvement in sensitivity over the apposition compound eye (Fig. 1A), a design in which single photoreceptors receive light only from the single corneal facet lens residing in the same ommatidium. Not surprisingly, apposition eyes are typical of diurnal insects active in bright sunlight, and this includes all diurnal bees and wasps. Strangely, apposition eyes are also found in several groups of bees and wasps (and also ants) that have evolved a nocturnal lifestyle. Even stranger, despite the poor sensitivity afforded by apposition eyes, these insects invariably see quite well, with well-documented abilities to learn visual landmarks and to use them during foraging and homing (Warrant et al., 2004; Greiner et al., 2007b; Somanathan et al., 2008).

How do nocturnal bees and wasps manage these formidable visual tasks with apposition eyes at night? This paradox, which has ignited considerable recent interest, is the topic of this review. Even though this paradox is not yet fully resolved, we currently have many clues that point to several major strategies that are employed by nocturnal bees and wasps to extract reliable information from an inherently unreliable signal. Based on several years of investigations on the visual system of the Central American sweat bee _Megalopta genalis_
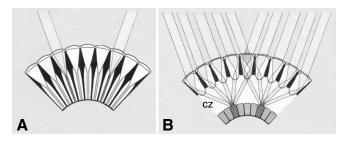
Fig. 1. Compound eye designs. (A) A focal apposition compound eye. Light reaches the photoreceptors exclusively from the small corneal lens located directly above. This eye design is typical of day-active insects. (B) A refracting superposition compound eye. A large number of corneal facets and bullet-shaped crystalline cones collect and focus light – across the clear zone of the eye (cz) – towards single photoreceptors in the retina. Several hundred, or even thousand, facets service a single photoreceptor. Not surprisingly, many nocturnal and deep-sea animals have refracting superposition eyes, and benefit from the significant improvement in sensitivity. Diagrams courtesy of Dan-Eric Nilsson. Adapted from Warrant (Warrant, 2004).

(family Halictidae), we can now conclude that some of these strategies lie within the eye itself, while others appear to be located in specialised neural circuitry in the optic lobe. It is our hope that this remarkable group of nocturnal insects may help us to unravel many of the general principles used by nocturnal animals to see at night.

Nocturnality in bees and wasps
Activity periods

Nocturnal and crepuscular (dusk and dawn) foraging activity in bees has arisen independently in at least four of the seven recognised families of bees, namely in the Colletidae, the Andrenidae, the Halictidae and the Apidae (Hopkins et al., 2000; Wcislo et al., 2004; Taylor, 2007; Warrant, 2007). 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 *Xylocopa tranquebarica* (Apidae), a bee capable of foraging even on the darkest moonless nights when light levels can be as low as 10^{-5} cd m^{-2} (Burgett and Sukumalanand, 2000; Somanathan and Borges, 2001; Somanathan et al., 2008). Many species are known to be crepuscular, such as *Xylocopa*

tabaniformis, Xenoglossa fulva, *Ptiloglossa guinea* and the well-studied Central American sweat bee *Megalopta genalis* (Linsley et al., 1955; Janzen, 1968; Roberts, 1971; Warrant et al., 2004; Kelber et al., 2006). *Megalopta genalis* (Fig. 2A), for instance, is active under the thick rainforest canopy during two short time windows shortly after dusk and before dawn (Fig. 3) (Warrant et al., 2004; Kelber et al., 2006). Other species, although primarily diurnal or crepuscular, are also capable of foraging throughout the night if a moon half-full or larger is present in the sky. Good examples include two species of honeybees (Apidae, genus *Apis*) – the giant Asian honeybee *Apis dorsata* and the African honeybee *Apis mellifera adansonii* – and the sweat bee *Lasioglossum* (*Sphecodogastra*) *texana* (Kerfoot, 1967a; Kerfoot, 1967b; Fletcher, 1978; Dyer, 1985; Kirchner and Dreller, 1993).

Among the wasps, nocturnal activity has only arisen among the velvet ants (family Mutillidae), and in two vespid genera, the neotropical *Apoica* (Fig. 2B,C; Polistinae – with nine species) and the southeast Asian *Provespa* (Vespinae – with three species). Both *Apoica* and *Provespa* are active nocturnal foragers, with both species collecting arthropod prey and pollen (von Schremmer, 1972; Maschwitz and Hänel, 1988; Hunt et al., 1995; Martin, 1995; Matsuura, 1999). Hunt and colleagues (Hunt et al., 1995) found that *Apoica* forages during the first 4 h of the evening when the moon is new or small, with another small peak of activity just before dawn (due to wasps returning to the nest, possibly because it was too dark to find their way home any earlier). As the moon waxes, *Apoica* also begins to forage all night (Hunt et al., 1995; Nascimento and Tannure-Nascimento, 2005).

Why have some bees and wasps – and many other species of animals – become nocturnal? Two main reasons have been hypothesised. The first is reduced competition (Cockerell, 1923; Roubik, 1992; Hopkins et al., 2000; Kronfeld-Schor and Dayan, 2003; Wcislo et al., 2004). In the forested habitats where nocturnal bees and wasps 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 with 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 and wasps
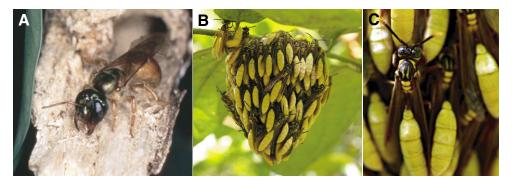

Fig. 2. Nocturnal bees and wasps. (A) The Central American sweat bee *Megalopta genalis* (Halictidae), whose sensitive apposition eyes allow them to forage at night by visually learning landmarks along the foraging route and around the nest entrance. Reproduced with the kind permission of the photographer, Dr Michael Pfaff. (B,C) The pale-yellow coloured Central American paper wasp *Apoica pallens* (Vespidae), which congregates on the outside of the nest (B) to create a distinctive pale object that may be visible to returning foragers at night. Photographs in B and C were reproduced with the kind permission of the photographer, Gillian Little, and Daniel Marlos from 'What's That Bug?', a website devoted to popular entomology (www.whatsthatbug.com).

became nocturnal was to avoid predation and parasitism (Bohart and Youssef, 1976; Smith et al., 2003; Kronfeld-Schor and Dayan, 2003; Wcislo et al., 2004). Diurnal bees and wasps are heavily attacked by predators and parasites alike, and the nocturnal niche may have represented a convenient escape route.

Eye size, ocellus size and nocturnality

Despite being nocturnal, our discussion above indicates that light levels – and by implication visual reliability – nonetheless limit foraging activity in bees and wasps active at night (Kelber et al., 2006). Some species are clearly crepuscular, requiring slightly brighter twilight skies to see well enough to negotiate obstacles during flight and to find their way home following a foraging trip. Those that fly all night often require the presence of bright moonlight. Light levels are thus limiting – a species 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.

This light-level limitation has led to the evolution of proportionately larger compound eyes and ocelli that have an improved capacity to capture light. The ocelli, the three round eyelets located on the dorsal surface of the head between the two compound eyes, are significantly larger relative to body size in species that fly in dim light (Kerfoot, 1967b; Kelber et al., 2006; Warrant et al., 2006). These specialised eyes – which probably play a role in flight control (Berry et al., 2007) – are a tell-tale indicator of nocturnal behaviour in bees and wasps. In the giant nocturnal Indian carpenter bee (*Xylocopa tranquebarica*) 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 (Jander and Jander, 2002). Interestingly, the common European hornet *Vespa crabro*, which has also been suggested to have nocturnal activity (Blackith, 1958; Spiewok and Schmolz, 2006), lacks all such optical enlargements (F. Jonsson, A. Kelber and E.J.W., in preparation).

Nocturnal visual behaviour in bees and wasps

Despite the fact that the visual systems of nocturnal bees and wasps are clearly operating near their limits, these insects are capable of quite sophisticated visual behaviours. Recent studies have shown that they are capable of visually learning landmarks around their nest entrances, and using them for homing, although the capacity to fly quickly and accurately in the vicinity of the nest is nevertheless affected by light level, and ultimately limited by it.

Homing, foraging and visual navigation

Bees and wasps are well known for their ability to forage at significant distances from their nests, and to routinely and repeatedly return to the nest with pollen and other provisions. In diurnal species this ability to 'home' is known to be a predominantly visual task. The location of the nest, and favoured routes to flowers or other resources, are recognised by landmarks that are learned visually and stored for later retrieval (reviewed in Collett et al., 2003). The directions and distances flown to and from the foraging site are also determined visually (reviewed in Srinivasan et al., 2006), and in honeybees this information is transferred to other bees in the hive.

In order to locate and recognise its nest after returning from a foraging trip, diurnal bees learn the arrangement of landmarks around the nest entrance. This is done by performing an 'orientation flight' (Becker, 1958; Zeil et al., 1996; Lehrer, 1996; Capaldi and Dyer, 1999): as a bee flies from its nest, it turns to face the nest
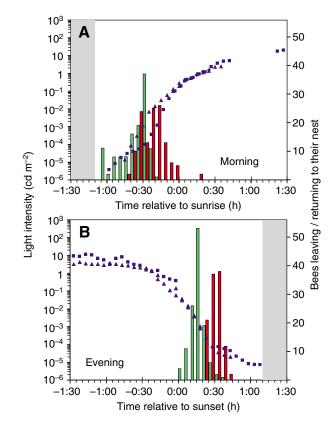

Fig. 3. The daily timing of foraging flights in the nocturnal bee *Megalopta genalis. Megalopta* is active during two short time intervals each day, once in the morning (A) and once in the evening (B), when light levels at the nest (blue symbols) can be lower than 10^{-4} cd m^{-2}. The number of bees leaving the nest (green bars) and returning to the nest (red bars) in 5 min intervals is shown relative to sunrise or sunset (0:00 h). Data were collected over several nights from several nests during two successive years on Barro Colorado Island (Panama). (A) The timing of foraging trips in the morning. The grey area indicates the time before astronomical twilight. (B) The timing of foraging trips in the evening. The grey area indicates the time after astronomical twilight. During the time interval between the onset of astronomical twilight in the evening and its offset in the morning, no light from the sun is present in the night sky. Modified with kind permission from Kelber et al. (Kelber et al., 2006).

entrance and begins to fly backwards in increasingly larger arcs to survey (and learn) the field of local landmarks. In the sweat bee *Megalopta genalis* and the carpenter bee *Xylocopa tranquebarica*, both active in extremely dim light, recent behavioural investigations have revealed that both species perform such orientation flights (Fig. 4A) and use them to visually learn landmarks around the nest entrance at night (Fig. 4B,C) (Warrant et al., 2004; Somanathan et al., 2008). For experiments on *Megalopta*, five nest sticks were placed beside one another on a small stand in the rainforest and, of these, only the middle nest was occupied (marked by a stars in Fig. 4B,C). The bee left its nest at 18:48 h (16 min after sunset), performed an orientation flight for a few seconds (presumably learning the spatial arrangement of the five nests), and then left (Fig. 4B, upper panel). While the bee was away, the positions of the bee's nest and an empty nest were swapped (Fig. 4B, lower panel). Upon return at 18:58 h, the bee flew without hesitation into the central unoccupied nest – the 'spatially correct' nest – but after a couple of seconds flew out again. After re-surveying the nests, the bee returned to the central nest, again immediately flying out. Presumably the aroma or some other feature of the nest was repellent
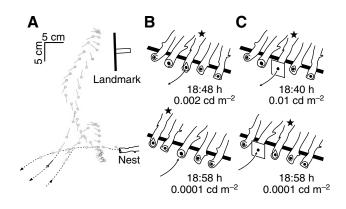
Fig. 4. Nocturnal landmark orientation in the nocturnal halictid bee *Megalopta genalis*. (A) A typical nocturnal orientation flight, as seen from below. The bee leaves her nest, and quickly returns to face the nest entrance. Flying in short arcs, she investigates the nest entrance and a neighbouring landmark to learn their spatial arrangement before departing on her foraging trip. Each 'ball-and-stick' represents the position of the head (ball) and body (stick) at 40 ms intervals. (B,C) Landmark learning. Bees leaving for a foraging trip learn the position of their nest relative to others (B), or learn the presence of a white square card attached to their nest (C). Upon return, bees enter the nest marked by the landmarks they have previously learned, not their actual nests (which are marked by stars). The rear side of the square card was attached to a Perspex cylinder that slipped neatly over the end of the nest stick to hold the card in place over the nest entrance. Times and light intensities at departure and return are also shown. Adapted from Warrant et al. (Warrant et al., 2004).

to the bee, and it was not until the bee's actual nest was retuned to the central position that the bee ceased to re-emerge. In a second experiment, a moveable white card was instead used as a landmark – the bee's nest in this case remained in its original location. Prior to the bee's departure, the landmark was placed over the entrance of the central, occupied nest (Fig. 4C, upper panel). The bee departed its nest at 18:40h, performed an orientation flight, and left. While the bee was away, the white card was placed over the entrance of a neighbouring unoccupied nest. The bee returned at 18:58h and flew directly into the landmarked unoccupied nest (Fig. 4C, lower panel). As before, the bee flew out almost immediately, due to the foreign internal environment of the landmarked nest. This continued until the landmark was returned to the bee's actual nest, after which it no longer emerged. These two experiments show that *Megalopta* are capable of using visually learned landmarks at night to find their way home, an ability that nocturnal carpenter bees also share (Somanathan et al., 2008).

Just like their diurnal relatives (reviewed in Collett et al., 2003), nocturnal bees and wasps probably also have the ability to learn visual landmarks along the foraging route. One possible system of landmarks is the characteristic pattern of bright patches of sky visible through the canopy. For a human observer standing in a dark rainforest at night this is the only visible landmark! Its complexity – due to the overlapping silhouettes of tens of thousands of small leaves and branches – is, however, overwhelming, and it is difficult for a human observer to see any order or pattern. However, if seen through the poor spatial resolution of an ocellus or compound eye, this complexity disappears and the pattern becomes much more obvious (H. Malm and E.J.W., in preparation). If, in addition, the pattern is sufficiently different at different places in the rainforest, this would allow its use as a landmark for an insect flying or walking beneath it. Indeed, it has been found that both nocturnal (Hölldobler and Taylor, 1983; Klotz and Reid, 1993;

Taylor, 2007) and diurnal (Hölldobler, 1980) ants navigate to and from their nests using the rainforest canopy pattern as a visual landmark.
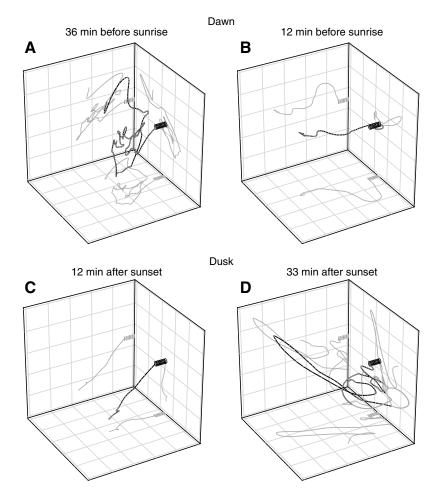
The canopy patches also contain a second possible navigational cue – polarised skylight, either due to the setting sun, or formed around the moon, a cue used by other crepuscular and nocturnal insects for navigation (Dacke et al., 2003a; Dacke et al., 2003b; Dacke et al., 2004). During the hour directly after sunset or before sunrise, the sun's pattern of skylight polarisation is very simple, with the dominant direction of polarisation identical in all parts of the sky, and oriented roughly north–south (Cronin et al., 2006). The degree of polarisation is also very high (Cronin et al., 2006). Thus, in addition to its characteristic pattern, the patches of sky visible through the canopy after dusk and before dawn are each rich in a single direction of highly aligned polarised light. The two cues together – a spatial pattern of canopy landmarks and a single directional compass cue defined by the plane of polarised skylight – might be sufficient to allow homing in nocturnal bees and wasps. This would require that the ocelli and/or the compound eyes are sensitive to polarised light. The dorsal areas of compound eyes in many insects have long been known to contain photoreceptors sensitive to polarised light (Wehner and Labhart, 2006). *Megalopta* also has such a 'dorsal rim' area, and the ommatidia located there have enormous rhabdoms with photoreceptors that are highly sensitive to polarised light (Greiner et al., 2007a).

Nocturnal flight performance

Foraging on foot at night, as many nocturnal ants do (e.g. Klotz and Reid, 1993; Greiner et al., 2007b), while demanding, is nonetheless made easier by several sensory cues: olfactory, mechanosensory and visual cues all cooperate to guide ground-based nocturnal navigation (Klotz and Reid, 1993). A walking nocturnal insect can make use of navigational guides provided by topographical landmarks in the substrate, or by scent trails left there by conspecifics, whereas nocturnal flying insects rarely experience such cues. Instead, they tend to rely on visual cues, a considerable challenge in dim light. How well, then, do nocturnal bees and wasps fly?

In the only study of nocturnal flight performance in insects (Theobald et al., 2007), the nocturnal bee *Megalopta* was filmed returning to the nest at different times relative to sunrise or sunset (and thus at different light intensities). Several interesting things were discovered. Firstly, bees always flew quickly, irrespective of the level of illumination. This is surprising because one might have suspected that as light levels fell, failing visual reliability and longer visual integration times may have demanded slower flight [as seen in honeybees (Menzel, 1981; Rose and Menzel, 1981)]. This, however, is apparently not the case. Secondly, at brighter light levels, *Megalopta* was typically found to return to the nest and to enter it quickly and confidently (Fig. 5B,C) whereas at dimmer light levels, returns were usually found to be more circuitous (thus taking longer) and less confident, often involving several aborted landing attempts (Fig. 5A,D). Thus, decreasing light level does indeed seem to worsen flight performance and landing success, but remarkably at all intensities, even at the dimmest, there were exceptions: some bees flew quickly and confidently into the nest without hesitation. These exceptional individuals may, by chance, have succeeded in landing on their first attempt. Alternatively, these bees may have reliably detected large-scale landmarks, such as the canopy pattern or larger (or closer) bushes and trees, successfully relaying the sequence of retinal images required to match the stored memory 'snap-shots' that allow the bee to accurately home in on the otherwise invisible

Dawn

A 36 min before sunrise

B 12 min before sunrise

Dusk

C 12 min after sunset

D 33 min after sunset

Fig. 5. The flight paths of four individual nocturnal bees (*Megalopta genalis*) returning to the nest at dimmer (A,D) and brighter (B,C) light levels during dawn (A,B) and dusk (C,D). In each plot, the three-dimensional flight path (black) is shown together with two-dimensional projections (grey shadows on the right, left and bottom walls) of the flight path onto the imaginary walls of a cubical space centred on the nest entrance (which is shown as a cylinder on the right wall). Luminance in the early dawn (A) was 1.1×10^{-4} cd m^{-2} and the landing lasted 11.4 s; late dawn (B), 1.9×10^{-3} cd m^{-2} and the landing lasted 4.7 s; early dusk (C), 3.9×10^{-3} cd m^{-2} and the landing lasted 1.8 s; and late dusk (D), 3.9×10^{-4} cd m^{-2} and the landing lasted 16.2 s. Note that during both the dawn and the dusk, landing flights were more circuitous and took longer in dimmer light. Each grid square is 10 cm×10 cm. Adapted with kind permission from Theobald et al. (Theobald et al., 2007).

nest entrance (Cartwright and Collett, 1983; Stürzl and Zeil, 2007). Thus, even though light level clearly affects flight performance, bees are capable of accurate visual navigation at all light levels within their normal range. Interestingly, an analogous situation has also been found in bumblebees: at lower light levels bumblebees spend more time visually searching for flowers than at higher light levels (Skorupski et al., 2006).

Visual adaptations for reliable nocturnal vision

Our discussions above clearly indicate that nocturnal bees and wasps are able to see well in very dim light. What visual adaptations have allowed this? Part of the answer is embodied in the optical sensitivity (*S*) of an eye to an extended source of broad-spectrum light. *S*, expressed in units of µm^2 sr, is given by (Kirschfeld, 1974; Land, 1981; Warrant and Nilsson, 1998):

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 \left(\frac{kl}{2.3 + kl}\right), \qquad (1)$$

where, in an apposition eye, *A* is the diameter of the corneal facet lens, *l* is the length of the rhabdom, *k* is the peak absorption coefficient of the visual pigment, *f* is the focal length of the ommatidium and *d* is the diameter of the rhabdom. This equation predicts that good sensitivity to an extended scene results from a facet of large area ($\pi A^2/4$) and photoreceptors that each view a large solid angle of visual space ($\pi d^2/4f^2$ sr) and absorb a substantial fraction of the incident light [$kl/(2.3+kl)$]. The apposition eyes of nocturnal bees and wasps show all three trends. Moreover, recent

work has shown that even their photoreceptors have special neural adaptations for life in dim light.

Optical adaptations in the compound eyes and ocelli

To see how nocturnal life has affected the optical structure, and sensitivity, of the apposition eyes and ocelli of bees and wasps, we can compare nocturnal and diurnal species. For instance, the nocturnal sweat bee *Megalopta* has larger eyes and larger facets (diameters up to 36 µm) than the strictly day-active European honeybee *Apis mellifera* (diameters up to 20 µm). Moreover, in *Apis* the rhabdoms have a width of only 2 µm, whereas in *Megalopta* they reach an extraordinary 8 µm, resulting in a receptive field of more than 7 times greater solid angular extent (Greiner et al., 2004a; Warrant et al., 2004). Similar differences are also seen in the ocelli: nocturnal bees and wasps have much larger ocellar lenses and rhabdoms than their diurnal relatives (Warrant et al., 2006). In the compound eyes, these differences in receptive field and facet size allow *Megalopta* an optical sensitivity that is roughly 27 times greater than in *Apis*: 2.7 µm^2 sr *versus* 0.1 µm^2 sr. Similar differences in sensitivity can be seen in the apposition eyes of nocturnal and diurnal carpenter bees (H. Somanathan, R. M. Borges, A. Kelber and E.J.W., in preparation), wasps (Greiner, 2006) and ants (Menzi, 1987; Moser et al., 2004; Greiner et al., 2007b). Even though nocturnal species experience a significant improvement in optical sensitivity over diurnal species, it is still very modest compared with that found in a typical superposition eye, such as those of the nocturnal moth *Deilephila elphenor* (*S*=69 µm^2 sr). This shows up the inherent limitations of the apposition design for vision in dim light, and begs the question – how can nocturnal bees and wasps nonetheless navigate using landmarks at night? Part of the answer lies in the properties of the photoreceptors, the topic to which we turn next.

Neural adaptations in the photoreceptors

Slowly flying nocturnal crane flies (Laughlin and Weckström, 1993), and slowly walking nocturnal ants (de Souza and Ventura, 1989), tend to have slow vision, with photoreceptors having long integration times compared with the photoreceptors of faster moving and distantly related species active in bright light. These studies conclude that the slow vision of the nocturnal species might be correlated with a slower locomotory speed, or a dimmer habitat, or both.

What is the situation in fast-flying nocturnal bees? Do their photoreceptors reveal properties that are uniquely suited to a life in
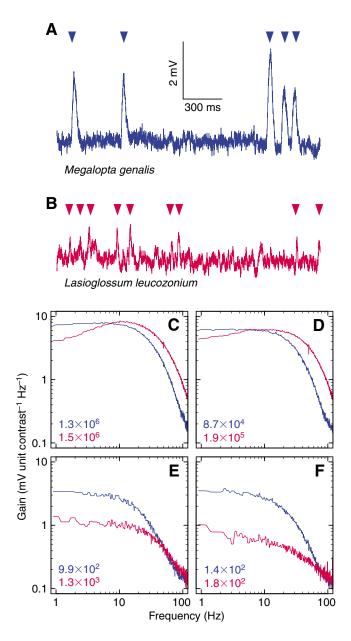
Fig. 6. Adaptations for nocturnal vision in the photoreceptors of the nocturnal sweat bee *Megalopta genalis*, as compared to photoreceptors in the closely related diurnal sweat bee *Lasioglossum leucozonium*. (A,B) Responses to single photons (or 'photon bumps': arrowheads) recorded from photoreceptors in *Megalopta* (A) and *Lasioglossum* (B). Note that the bump amplitude is larger, and the bump time course much slower, in *Megalopta* than in *Lasioglossum*. (C–F) Average contrast gain as a function of temporal frequency in *Megalopta* (blue curves, N=8 cells) and *Lasioglossum* (red curves, N=8 cells) at different adapting intensities, indicated as 'effective photons' per second in each panel for each species [for each species, each stimulus intensity was calibrated in terms of 'effective photons'; that is, the number of photon bumps per second the light source elicited, thereby eliminating the effects of differences in the light-gathering capacity of the optics between the two species, which is about 27 times (Lillywhite and Laughlin, 1979)]. In light-adapted conditions (C,D), the two species reach the same maximum contrast gain per unit bandwidth although *Lasioglossum* has a broader bandwidth and a higher corner frequency (the frequency at which the gain has fallen off to 50% of its maximum). In dark-adapted conditions (E,F), *Megalopta* has a much higher contrast gain per unit bandwidth. All panels adapted with kind permission from Frederiksen et al. (Frederiksen et al., 2008).
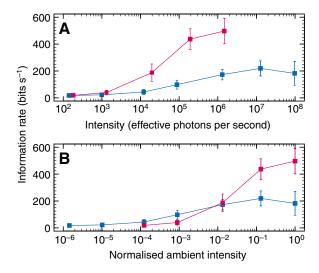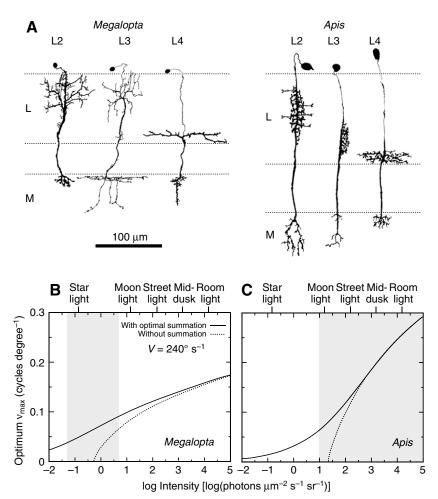

Fig. 7. The average rates of information transmission (in bits s^{-1}) in the photoreceptors of the nocturnal and diurnal sweat bees *Megalopta genalis* (blue curves, N=8 cells) and *Lasioglossum leucozonium* (red curves, N=8 cells). (A) When the photoreceptors alone are considered (*via* a light source calibration in 'effective photons' absorbed by the photoreceptor per second), it is evident that at all intensities *Lasioglossum* has a higher information rate than *Megalopta*. (B) When light sources are instead calibrated to external ambient intensities (a normalised intensity of 100 corresponds to the light intensity on an overcast day, or around 180 cd m^{-2}), *Megalopta* has a higher information rate in dim light. This, however, is due to its 27 times more sensitive optics and is not due to an intrinsic adaptation present within the photoreceptors. Error bars show ±s.d. Both panels adapted with kind permission from Frederiksen et al. (Frederiksen et al., 2008).

dim light? This question was investigated by intracellularly recording the responses of photoreceptors to Gaussian-distributed white-noise light stimuli in closely related nocturnal and diurnal sweat bees: the nocturnal *Megalopta genalis* and the diurnal *Lasioglossum leucozonium* (Frederiksen et al., 2008). Two important differences in photoreceptor performance were found between these two species, each of which highlights an adaptation for vision in dim light.

Firstly, the photoreceptor's dark-adapted responses to single photons – so-called 'quantum bumps' – are much larger in nocturnal *Megalopta* than in diurnal *Lasioglossum* (Fig. 6A,B). These larger bumps, which have also been reported from other nocturnal arthropods [e.g. crane flies, cockroaches and spiders (Laughlin et al., 1980; Laughlin and Weckström, 1993; Heimonen et al., 2006; Pirhofer-Walzl et al., 2007)] indicate that the photoreceptor's gain of transduction is greater in *Megalopta* than in *Lasioglossum*. This higher transduction gain manifests itself as a higher contrast gain; that is, in a greater photoreceptor voltage response per unit change in light intensity (or contrast). Contrast gain is plotted as a function of temporal frequency in Fig. 6C–F: at all levels of light and dark adaptation, for the frequency range both species can discriminate, the visual gain of *Meglopta* is always higher than that of *Lasioglossum*, and at the lowest intensities (Fig. 6E,F) is up to five times higher. This higher gain results in greater signal amplification. Unfortunately, it also amplifies the noise, and thus on its own, the higher gain does not alter the visual signal-to-noise ratio. However, because the noise (including photon shot noise, the noise associated with the random nature of photon absorption in the retina) is uncorrelated between different photoreceptors and ommatidia, a subsequent spatial summation – as we propose for nocturnal bees

A *Megalopta*   *Apis*

100 μm

B

C

log Intensity [log(photons μm^{-2} s^{-1} sr^{-1})]

Fig. 8. Spatial summation in nocturnal bees. (A) Comparison of the first-order interneurons – L-fibre types L2, L3 and L4 – of the *Megalopta genalis* female (left) and the worker honeybee *Apis mellifera* (right). Compared with the worker honeybee, the horizontal branches of L-fibres in the nocturnal halictid bee connect to a much larger number of lamina cartridges, suggesting a possible role in spatial summation. L, lamina; M, medulla. Reconstructions from Golgi-stained frontal sections. Adapted from Greiner et al. (Greiner et al., 2004b) and Ribi (Ribi, 1975). (B,C) Spatial and temporal summation modelled at different light intensities in *Megalopta genalis* (B) and *Apis mellifera* (C) for an image velocity (*V*) of 240° s^{-1} [measured from *Megalopta genalis* during a nocturnal foraging flight (Warrant et al., 2004)]. Light intensities are given for 540 nm, the peak in the bee's spectral sensitivity. Equivalent natural intensities are also shown. The finest spatial detail visible to flying bees (as measured by the maximum detectable spatial frequency, v_{max}) is plotted as a function of light intensity. When bees sum photons optimally in space and time (continuous lines), vision is extended to much lower light intensities (non-zero v_{max}) compared with when summation is absent (broken lines). Note that nocturnal bees can see in dimmer light than honeybees. Grey areas denote the light intensity window within which each species is normally active (although honeybees are also active at intensities higher than those presented on the graph). Adapted from Theobald et al. (Theobald et al., 2006).

(see below) – has the potential to average out the noise and amplify the signal even further, thereby greatly improving the visual signal-to-noise ratio. Thus, a high visual gain, followed by spatial summation, could represent a significant strategy for vision in dim light.

Secondly, as in slowly moving nocturnal ants and flies, the dark-adapted photoreceptors of fast-flying nocturnal *Megalopta* are slow. In the frequency domain, this is equivalent to saying that temporal corner frequency is low – this is the frequency at which the gain has fallen to 50% of its maximum value, and lower values indicate slower vision. In *Megalopta* it is around 7 Hz in dark-adapted conditions (Fig. 6F). This can be compared with values of between 16 and 19 Hz in slowly flying nocturnal crane flies (Laughlin and Weckström, 1993). In diurnal *Lasioglossum*, the dark-adapted corner frequency is nearly three times the value found in *Megalopta*, at around 20 Hz (Fig. 6F), a value that is nonetheless considerably less than that typical of the diurnal, highly manoeuvrable and rapidly flying higher flies [50–107 Hz (Laughlin and Weckström, 1993)]. Since the two bees fly at similar speeds, their difference in temporal properties – most probably due to different photoreceptor sizes, and different numbers and types of ion channel in the photoreceptor membrane (Laughlin, 1996) – can only be related to the difference in light intensity experienced by the two species. The nocturnal *Megalopta* has clearly evolved slower vision, and this must be beneficial at night. Indeed, van Hateren (van Hateren, 1993) has convincingly shown that slower vision in dim light – despite compromising temporal resolution – is beneficial because it increases the visual signal-to-noise ratio and improves contrast discrimination

at lower temporal frequencies by suppressing photon noise at frequencies that are too high to be reliably resolved. Despite comprising temporal resolution, this low-pass filtering (which is evident in Fig. 6C–F), improves visual reliability in dim light. However, the narrower bandwidth possessed by nocturnal *Megalopta* (Fig. 6C–F) has a devastating effect on the visual information rate (calculated in bits s^{-1}): at all intensities, the intrinsic rate of visual information in the photoreceptors of *Lasioglossum* is significantly greater than in those of *Megalopta* (Fig. 7A). It is only when the approximately 27 times greater optical sensitivity of the apposition eyes of *Megalopta* is accounted for (Fig. 7B) that the rate of information transmission in *Megalopta* is greater than that in *Lasioglossum*, but then only at the very lowest intensities. Information, it seems, has been sacrificed in *Megalopta* for a greater absolute sensitivity. Again, this sacrifice only makes sense in the light of a subsequent strategy of spatial summation, the topic to which we turn next.

Spatial and temporal summation

As we saw above, the apposition eyes of nocturnal bees and wasps are not especially sensitive to light. Even if the eyes of nocturnal species have 10 to 50 times the optical sensitivity of those in diurnal species (Eqn 1), this may still not be enough to guarantee reliable vision. There is, however, an additional strategy, thought to reside in the neural circuits processing the incoming visual signal, which can potentially solve the problem: the neural summation of light in space and time (Snyder, 1977; Snyder et al., 1977a; Snyder et al., 1977b; Laughlin, 1981; Laughlin, 1990; Warrant, 1999). We

have already discussed summation in time above: when light gets dim, the visual systems of nocturnal animals can improve visual reliability by integrating signals over longer periods of time (Laughlin, 1990; van Hateren, 1993). In the eye, this can be achieved by having slower photoreceptors. Even slower vision could be obtained by neurally integrating (summing) signals at a higher level in the visual system. This temporal summation only comes at a price: it can drastically degrade the perception of fast-moving objects, potentially disastrous for a fast-flying nocturnal animal (like a nocturnal wasp or bee) that needs to negotiate obstacles. Not surprisingly, temporal summation is more likely to be employed by slowly moving animals.

Summation of photons in space can also improve image quality. Instead of each visual channel collecting photons in isolation (as in bright light), the transition to dim light could activate specialised laterally spreading neurons that couple the channels together into groups. Each summed group – themselves now defining the channels – could collect considerably more photons over a much wider visual angle, albeit with a simultaneous and unavoidable loss of spatial resolution. Despite being much brighter, the image would become necessarily coarser.

Evidence for laterally spreading neurons has been found in the first optic ganglion (lamina ganglionaris) of nocturnal cockroaches (Ribi, 1977), fireflies (Ohly, 1975) and hawkmoths (Strausfeld and Blest, 1970), and these have been interpreted as an adaptation for spatial summation (Laughlin, 1981). The nocturnal bee *Megalopta genalis* also appears to have such neurons (Greiner et al., 2004b; Greiner et al., 2005) (Fig. 8A). The wide lateral branches of its laminar monopolar cells L2, L3 and L4, which spread to 12, 11 and 17 lamina cartridges, respectively, are considerably wider than the homologous cells of *Apis*, which spread to 2, 0 and 4 cartridges, respectively (Ribi, 1981; Greiner et al., 2004b; Greiner et al., 2005) (Fig. 8A).

Even though their role in summation is yet to be shown, the morphologies of these cells in *Megalopta* are well suited to the task of summation. If one investigates the possible improvement afforded by optimal spatial and temporal summation using theoretical methods (Warrant, 1999), then both *Megalopta* (Fig. 8B) and *Apis* (Fig. 8C) are able to resolve spatial details in a scene at much lower intensities with summation than without it (Theobald et al., 2006). These theoretical results assume that both bees experience a rotational velocity during flight of $240°\,s^{-1}$, a value that has been measured from high-speed films of *Megalopta* fixating the nest entrance during orientation flights at night. At the lower light levels where *Megalopta* is active, the optimum visual performance shown in Fig. 8B is achieved with an integration time of about 30 ms and summation from about 12 ommatidia (or cartridges). This integration time is close to the photoreceptor's dark-adapted integration time (Warrant et al., 2004), and the extent of predicted spatial summation is very similar to the number of cartridges to which the L2 and L3 cells branch (Greiner et al., 2004b), thus strengthening the hypothesis that the lamina monopolar cells are involved in spatial summation.

Even in the honeybee *Apis*, summation can improve vision in dim light (Fig. 8C). As we mentioned above, the Africanised race, *Apis mellifera scutellata*, and the closely related south-east Asian giant honeybee *Apis dorsata*, both forage during dusk and dawn, and even throughout the night, if a moon half-full or larger is present in the sky. Behavioural experiments show, however, that even the strictly day-active European honeybee is capable of seeing course habitat features, like large pale flowers, at moonlight intensities. This ability can be explained only if bees optimally sum photons over space and time (Warrant et al., 1996), and this is also revealed in Fig. 8C (for an angular velocity of $240°\,s^{-1}$). At the lower light levels where *Apis* is active, the optimum visual performance shown in Fig. 8C is achieved with an integration time of about 18 ms and summation from about three or four cartridges. As in *Megalopta*, this integration time is close to the photoreceptor's dark-adapted value (Warrant et al., 2004), and the extent of predicted spatial summation is again very similar to the number of cartridges to which the *Apis* L2 and L3 cells actually branch.

In addition to simply capturing more light, spatial summation in nocturnal bees is ideally suited to take advantage of the special signal characteristics of the photoreceptors. As we mentioned above, the high voltage gain present in the photoreceptors amplifies both the signal and the noise. Because the noise is uncorrelated across ommatidia, spatial summation could effectively average out the noise, and dramatically increase the visual signal-to-noise ratio in dim light, albeit for a lower range of spatial frequencies. Whether the cellular circuits of the nocturnal bee lamina actually perform this task remains to be seen.

Finally, it must be pointed out that all of these nocturnal visual investments – larger eyes, more numerous ommatidia, larger corneal lenses, wider rhabdoms and more extensively branching lamina monopolar cells – are unavoidably costly, in terms of both the extra weight (payload) that must be carried during flight, and the extra energy (measured in terms of ATP molecules consumed) that is required to power (and maintain) an improved nocturnal visual capacity (Laughlin et al., 1998; Laughlin, 2001; Niven et al., 2007). Even though the cost per bit of nocturnal visual information remains to be determined, it is likely to be high, and almost certainly higher than the equivalent cost of diurnal visual information. This greater cost – like the significant visual investments described in this review – all indicate that for bees and wasps, and certainly for many other nocturnal animals, the evolutionary benefits associated with seeing well at night are significant indeed.

Conclusions

Despite their tiny and relatively insensitive apposition eyes, several groups of bees and wasps have successfully conquered the nocturnal niche, and taken advantage of the benefits that this niche provides for foraging and the avoidance of enemies. Like their diurnal relatives, these insects successfully learn visual landmarks and use them for homing, a feat that requires reliable vision in dim light. This reliability is the result of the combined action of a variety of adaptations within the eyes, and also most probably in the optic lobes, particularly in the lamina. Greatly enlarged corneal facets and rhabdoms, and slow photoreceptors with high contrast gain, ensure that visual signal strength is maximal as it leaves the eye and travels to the lamina. Even though it remains to be shown conclusively, anatomical and theoretical evidence suggests that once the visual signals from large groups of ommatidia reach the lamina, they are spatially summed by the second-order monopolar cells, resulting in an enhanced signal and reduced noise. The greatly improved signal-to-noise ratio that this strategy could afford, whilst confined to a narrower range of spatial and temporal frequencies, would ensure that nocturnal visual reliability is maximised for the slower and coarser features of the world. Those features that are faster and finer – and inherently noisy – would be filtered out. However, for a nocturnal bee or wasp struggling to find its way home in the dark, the ability to see a slow and coarse world, rather than nothing at all, would probably mean the difference between a successful return to the nest and becoming hopelessly lost.

References

Becker, L. (1958). Untersuchungen über das Heimfindevermögen der Bienen. *Z. Vergl. Physiol.* **41**, 1-25.

Berry, R., van Kleef, J. and Stange, G. (2007). The mapping of visual space by dragonfly lateral ocelli. *J. Comp. Physiol. A* **193**, 495-513.

Blackith, R. E. (1958). Visual sensitivity and foraging in social wasps. *Insectes Soc.* **5**, 159-169.

Bohart, G. E. and Youssef, N. N. (1976). The biology and behaviour of *Evylaeus galpinsiae* Cockerell (Hymenoptera: Halictidae). *Wasmann J. Biol.* **34**, 185-234.

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.

Capaldi, E. A. and Dyer, F. C. (1999). The role of orientation flights on homing performance in honeybees. *J. Exp. Biol.* **202**, 1655-1666.

Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees. Experiments and models. *J. Comp. Physiol. A* **151**, 521-543.

Cockerell, T. D. A. (1923). Two nocturnal bees and a minute *Perdita*. *Am. Mus. Nov.* **66**, 1-4.

Collett, T. S., Graham, P. and Durier, V. (2003). Route learning by insects. *Curr. Opin. Neurobiol.* **13**, 718-725.

Cronin, T. W. and Greiner, B. and Warrant, E. J. (2006). Celestial polarization patterns during twilight. *App. Optics* **45**, 5582-5589.

Dacke, M., Nilsson, D.-E., Scholtz, C. H., Byrne, M. and Warrant, E. J. (2003a). Insect orientation to polarized moonlight. *Nature* **424**, 33.

Dacke, M., Nordström, P. and Scholtz, C. H. (2003b). Twilight orientation to polarised light in the crepuscular dung beetle *Scarabaeus zambesianus*. *J. Exp. Biol.* **106**, 1535-1543.

Dacke, M., Byrne, M., Scholtz, C. H. and Warrant, E. J. (2004). Lunar orientation in a beetle. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 361-365.

de Souza, J. M. and Ventura, D. F. (1989). Comparative study of temporal summation and response form in hymenopteran photoreceptors. *J. Comp. Physiol. A* **165**, 237-245.

de Vries, H. (1943). The quantum character of light and its bearing upon threshold of vision, the differential sensitivity and visual acuity of the eye. *Physica* **10**, 553-564.

Dyer, F. C. (1985). Nocturnal orientation by the Asian honeybee, *Apis dorsata*. *Anim. Behav.* **33**, 769-774.

Fletcher, G. J. C. (1978). The African bee, *Apis mellifera adansonii*, in Africa. *Annu. Rev. Entomol.* **23**, 151-171.

Frederiksen, R., Wcislo, W. T. and Warrant, E. J. (2008). Visual reliability and information rate in the retina of a nocturnal bee. *Curr. Biol.* (in press).

Greiner, B. (2006). Visual adaptations in the night-active wasp *Apoica pallens*. *J. Comp. Neurol.* **495**, 255-262.

Greiner, B., Ribi, W. A. and Warrant, E. J. (2004a). Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*. *Cell Tissue Res.* **316**, 377-390.

Greiner, B., Ribi, W. A. and Warrant, E. J. (2004b). Neuronal organisation in the first optic ganglion of the nocturnal bee *Megalopta genalis*. *Cell Tissue Res.* **318**, 429-437.

Greiner, B., Ribi, W. A. and Warrant, E. J. (2005). A neural network to improve dim-light vision? Dendritic fields of first-order interneurons in the nocturnal bee *Megalopta genalis*. *Cell Tissue Res.* **323**, 313-320.

Greiner, B., Cronin, T. W., Ribi, W. A., Wcislo, W. T. and Warrant, E. J. (2008). Polarisation vision in the nocturnal bee *Megalopta genalis* and its possible role in homing behaviour. *J. Comp. Physiol. A* **193**, 591-600.

Greiner, B., Narendra, A., Reid, S. F., Dacke, M., Ribi, W. A. and Zeil, J. (2007b). Eye structure correlates with distinct foraging-bout timing in primitive ants. *Curr. Biol.* **17**, R879-R880.

Heimonen, K., Salmela, I., Kontiokari, P. and Weckström, M. (2006). Large functional variability in cockroach photoreceptors: optimization to low light levels. *J. Neurosci.* **26**, 13454-13462.

Hölldobler, B. (1980). Canopy orientation: a new kind of orientation in ants. *Science* **210**, 86-88.

Hölldobler, B. and Taylor, R. W. (1983). A behavioral study of the primitive ant *Nothomyrmecia macrops* Clark. *Insectes Soc.* **30**, 384-401.

Hopkins, M. J. G., Hopkins, H. C. F. and Sothers, C. A. (2000). Nocturnal pollination of *Parkia velutina* by *Megalopta* bees in Amazonia and its possible significance in the evolution of chiropterophily. *J. Trop. Ecol.* **16**, 733-746.

Hunt, J. H., Jeanne, R. L. and Keeping, M. G. (1995). Observations on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Insectes Soc.* **42**, 223-236.

Jander, U. and Jander, R. (2002). Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct. Dev.* **30**, 179-193.

Janzen, D. H. (1968). Notes on nesting and foraging behavior of *Megalopta* (Hymenoptera: Halictidae) in Costa Rica. *J. Kansas Entomol. Soc.* **41**, 342-350.

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. (1967a). The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee. *Anim. Behav.* **15**, 479-486.

Kerfoot, W. B. (1967b). Correlation between ocellar size and the foraging activities of bees (Hymenoptera; Apoidea). *Am. Nat.* **101**, 65-70.

Kirchner, W. H. and Dreller, C. (1993). Acoustical signals in the dance language of the giant honeybee, *Apis dorsata*. *Behav. Ecol. Sociobiol.* **33**, 67-72.

Kirschfeld, K. (1974). The absolute sensitivity of lens and compound eyes. *Z. Naturforsch. C* **29**, 592-596.

Klotz, J. H. and Reid, B. L. (1993). Nocturnal orientation in the black carpenter ant *Camponotus pennsylvanicus* (DeGeer) (Hymenoptera: Formicidae). *Insectes Soc.* **40**, 95-106.

Kronfeld-Schor, N. and Dayan, T. (2003). Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* **34**, 153-181.

Land, M. F. (1981). Optics and vision in invertebrates. In *Handbook of Sensory Physiology.* Vol. VII 6B (ed. H. Autrum), pp. 471-592. Berlin: Springer.

Laughlin, S. B. (1981). Neural principles in the peripheral visual systems of invertebrates. In *Handbook of Sensory Physiology.* Vol. VII 6B (ed. H. Autrum), pp. 133-280. Berlin: Springer.

Laughlin, S. B. (1990). Invertebrate vision at low luminances. In *Night Vision* (ed. R. F. Hess, L. T. Sharpe and K. Nordby), pp. 223-250. Cambridge: Cambridge University Press.

Laughlin, S. B. (1996). Matched filtering by a photoreceptor membrane. *Vision Res.* **36**, 1529-1541.

Laughlin, S. B. (2001). Energy as a constraint on the coding and processing of sensory information. *Curr. Opin. Neurobiol.* **11**, 475-480.

Laughlin, S. B. and Weckström, M. (1993). Fast and slow photoreceptors – a comparative study of the functional diversity of coding and conductances in the Diptera. *J. Comp. Physiol. A* **172**, 593-609.

Laughlin, S. B., Blest, A. D. and Stowe, S. (1980). The sensitivity of receptors in the posterior median eye of the nocturnal spider *Dinopis*. *J. Comp. Physiol.* **141**, 53-65.

Laughlin, S. B., van Steveninck, R. R. D. and Anderson, J. C. (1998). The metabolic cost of neural information. *Nat. Neurosci.* **1**, 36-41.

Lehrer, M. (1996). Small-scale navigation in the honeybee: active acquisition of visual information about the goal. *J. Exp. Biol.* **199**, 253-261.

Lillywhite, P. G. and Laughlin, S. B. (1979). Transducer noise in a photoreceptor. *Nature* **277**, 569-572.

Linsley, E. G., MacSwain, J. W. and Smith, R. F. (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.

Martin, S. J. (1995). Hornets (Hymenoptera: Vespinae) of Malaysia. *Malayan Nat. J.* **49**, 71-82.

Maschwitz, U. and Hänel, H. (1988). Biology of the southeast Asian nocturnal wasp *Provespa anomala* (Hymenoptera, Vespidae). *Entomol. Gen.* **14**, 47-52.

Matsuura, M. (1999). Size and composition of swarming colonies in *Provespa anomala* (Hymenoptera, Vespidae), a nocturnal social wasp. *Insectes Soc.* **46**, 219-223.

McIntyre, P. D. and Caveney, S. (1998). Superposition optics and the time of flight in onitine dung beetles. *J. Comp. Physiol. A* **183**, 45-60.

Menzel, R. (1981). Achromatic vision in the honeybee at low light intensities. *J. Comp. Physiol.* **141**, 389-393.

Menzi, U. (1987). Visual adaptation in nocturnal and diurnal ants. *J. Comp. Physiol.* **160**, 11-21.

Meyer-Rochow, V. B. and Nilsson, H. L. (1998). Compound eyes in polar regions, caves and the deep-sea. In *Atlas of Arthropod Sensory Receptors* (ed. E. Eguchi and Y. Tominaga), pp. 134-155. Berlin, Heidelberg, New York: Springer.

Moser, J. C., Reeve, J. D., Bento, J. M. S., Della Lucia, T. M. C., Cameron, R. S. and Heck, N. M. (2004). Eye size and behaviour of day- and night-flying leafcutting ant alates. *J. Zool. Lond.* **264**, 69-75.

Nascimento, F. S. and Tannure-Nascimento, I. C. (2005). Foraging patterns in a nocturnal swarm-founding wasp, *Apoica flavissima* van der vecht (Hymenoptera: Vespidae). *Neotrop. Entomol.* **34**, 177-181.

Niven, J. E., Anderson, J. C. and Laughlin, S. B. (2007). Fly photoreceptors demonstrate energy-information trade-offs in neural coding. *PLoS Biol.* **5**, 828-840.

Ohly, K. P. (1975). The neurons of the first synaptic regions of the optic neuropil of the firefly, *Phausius splendidula* L. (Coleoptera). *Cell Tissue Res.* **158**, 89-109.

Pirhofer-Walzl, K., Warrant, E. J. and Barth, F. G. (2007). Adaptations for vision in dim light: impulse responses and bumps in nocturnal spider photoreceptor cells (*Cupiennius salei* Keys). *J. Comp. Physiol. A* **193**, 1081-1087.

Ribi, W. A. (1975). The first optic ganglion of the bee I. Correlation between visual cell types and their terminals in the lamina and medulla. *Cell Tissue Res.* **165**, 103-111.

Ribi, W. A. (1977). Fine structure of the first optic ganglion (lamina) of the cockroach *Periplaneta americana*. *Tissue Cell* **9**, 57-72.

Ribi, W. A. (1981). The first optic ganglion of the bee. IV. Synaptic fine structures and connectivity patterns of receptor cell axons and first order interneurones. *Cell Tissue Res.* **215**, 443-464.

Roberts, R. B. (1971). Biology of the crepuscular bee *Ptiloglossa guinnae* n. sp. with notes on associated bees, mites and yeasts. *J. Kansas Entomol. Soc.* **44**, 283-294.

Rose, A. (1942). The relative sensitivities of television pickup tubes, photographic film and the human eye. *Proc. Inst. Radio Eng.* **30**, 293-300.

Rose, R. and Menzel, R. (1981). Luminance dependence of pigment colour discrimination in bees. *J. Comp. Physiol.* **141**, 379-388.

Roubik, D. W. (1992). *Ecology and Natural History of Tropical Bees.* Cambridge: Cambridge University Press.

Skorupski, P., Spaethe, J. and Chittka, L. (2006). Visual search and decision making in bees: time, speed and accuracy. *Int. J. Comp. Psychol.* **19**, 342-357.

Smith, A. R., Wcislo, W. T. and O'Donnell, S. (2003). Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **54**, 22-29.

Snyder, A. W. (1977). Acuity of compound eyes, physical limitations and design. *J. Comp. Physiol.* **116**, 161-182.

Snyder, A. W., Stavenga, D. G. and Laughlin, S. B. (1977a). Spatial information capacity of compound eyes. *J. Comp. Physiol.* **116**, 183-207.

Snyder, A. W., Laughlin, S. B. and Stavenga, D. G. (1977b). Information capacity of eyes. *Vision Res.* **17**, 1163-1175.

Somanathan, H. and Borges, R. (2001). Nocturnal pollination by the carpenter bee *Xylocopa tenuiscapa* (Apidae) and the effect of floral display on fruit set of *Heterophragma quadriloculare* (Bignoniaceae) in India. *Biotropica* **33**, 78-89.

Somanathan, H., Borges, R. M., Warrant, E. J. and Kelber, A. (2008). Visual ecology of Indian carpenter bees. I. Light intensities and flight activity. *J. Comp. Physiol. A* **194**, 97-107.

Spiewok, S. and Schmolz, E. (2006). Changes in temperature and light alter the flight speed of hornets (*Vespa crabro* L.). *Physiol. Biochem. Zool.* **79**, 188-193.

Srinivasan, M. V., Zhang, S. and Reinhard, J. (2006). Small brains, smart minds: vision, peception, navigation and "cognition" in insects. In *Invertebrate Vision* (ed. E. J. Warrant and D.-E. Nilsson), pp. 462-493. Cambridge: Cambridge University Press.

Strausfeld, N. J. and Blest, A. D. (1970). Golgi studies on insects. I. The optic lobes of Lepidoptera. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **258**, 81-134.

Stürzl, W. and Zeil, J. (2007). Depth, contrast and view-based homing in outdoor scenes. *Biol. Cybern.* **96**, 519-531.

Taylor, R. W. (2007). Bloody funny wasps! Speculations on the evolution of eusociality in ants. In *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E. O. Wilson – 50 Years of Contributions* (*Memoirs of the American Entomological Institute, Vol. 80*) (ed. R. R. Snelling, B. L. Fisher and P. S. Ward), pp. 580-609. Gainesville, FL: American Entomological Institute.

Theobald, J. C., Greiner, B., Wcislo, W. T. and Warrant, E. J. (2006). Visual summation in night-flying sweat bees: a theoretical study. *Vision Res.* **46**, 2298-2309.

Theobald, J. C., Coates, M. M., Wcislo, W. T. and Warrant, E. J. (2007). Flight performance in night-flying sweat bees suffers at low light levels. *J. Exp. Biol.* **210**, 4034-4042.

van Hateren, J. H. (1993). Spatiotemporal contrast sensitivity of early vision. *Vision Res.* **33**, 257-267.

von Schremmer, F. (1972). Beobachtungen zur Biologie von *Apoica pallida* (Olivier, 1791), einer neotropischen sozialen Faltenwespe (Hymenoptera: Vespidae). *Insectes Soc.* **19**, 343-357.

Warrant, E. J. (1999). Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.* **39**, 1611-1630.

Warrant, E. J. (2004). Vision in the dimmest habitats on earth. *J. Comp. Physiol. A* **190**, 765-789.

Warrant, E. J. (2006). Invertebrate vision in dim light. In *Invertebrate Vision* (ed. E. J. Warrant and D.-E. Nilsson), pp. 83-126. Cambridge: Cambridge University Press.

Warrant, E. J. (2007). Nocturnal bees. *Curr. Biol.* **17**, R991-R992.

Warrant, E. J. (2008). Nocturnal vision. In *The Senses: A Comprehensive Reference*, vol. 2, *Vision II* (ed. T. Albright and R. H. Masland; series ed., A. I. Basbaum, A. Kaneko, G. M. Shepherd and G. Westheimer), pp. 53-86. Oxford; Academic Press.

Warrant, E. J. and Locket, N. A. (2004). Vision in the deep sea. *Biol. Rev.* **79**, 671-712.

Warrant, E. J. and Nilsson, D.-E. (1998). Absorption of white light in photoreceptors. *Vision Res.* **38**, 195-207.

Warrant, E. J., Porombka, T. and Kirchner, W. H. (1996). Neural image enhancement allows honey bees to see at night. *Proc. R. Soc. Lond. B Biol. Sci.* **263**, 1521-1526.

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.

Warrant, E. J., Kelber, A., Wallén, R. and Wcislo, W. (2006). The physiological optics of ocelli in nocturnal and diurnal bees and wasps. *Arthropod Struct. Dev.* **35**, 293-305.

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. Linn. Soc. Lond.* **83**, 377-387.

Wehner, R. and Labhart, T. (2006). Polarisation vision. In *Invertebrate Vision* (ed. E. J. Warrant and D.-E. Nilsson), pp. 291-348. Cambridge: Cambridge University Press.

Zeil, J., Kelber, A. and Voss, R. (1996). Structure and function of learning flights in bees and wasps. *J. Exp. Biol.* **199**, 245-252.