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Night sky orientation with diurnal and nocturnal eyes: dim-light adaptations are critical when the moon is out of sight

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The visual systems of many animals feature energetically costly specializations to enable them to function in dim light. It is often unclear, however, how large the behavioural benefit of these specializations is, because a direct comparison in a behaviourally relevant task between closely related day- and night-active species is not usually possible. Here we compared the orientation performance of diurnal and nocturnal species of dung beetles, *Scarabaeus* (*Kheper*) *lamarcki* and *Scarabaeus satyrus*, respectively, attempting to roll dung balls along straight paths both during the day and at night. Using video tracking, we quantified the straightness of paths and the repeatability of roll bearings as beetles exited a flat arena in their natural habitat or under controlled conditions indoors. Both species oriented equally well when either the moon or an artificial point light source was available, but when the view of the moon was blocked and only wide-field cues such as the lunar polarization pattern or the stars were available for orientation, nocturnal beetles were oriented substantially better. We found no evidence that ball-rolling speed changed with light level, which suggests little or no temporal summation in the visual system. Finally, we found that both diurnal and nocturnal beetles tended to choose bearings that led them towards a bright light source, but away from a dim one. Our results show that even diurnal insects, at least those with superposition eyes, could orient by the light of the moon, but that dim-light adaptations are needed for precise orientation when the moon is not visible.

Seeing at night is a challenging task. The skylight on a moonless night can be over one hundred million times dimmer than on a sunny day (Lythgoe, 1979). As light levels drop, fewer photons reach each photoreceptor, and the signal-to-noise ratio in the visual system eventually falls to a level where even objects or light sources that present a large relative contrast to the background can no longer be distinguished from it. Nevertheless, many animals, including small insects, are exclusively active at night and rely on vision to guide them in tasks such as locomotion, foraging, courtship and navigation (Warrant, 2008; Warrant & Dacke, 2011). To deal with extremely low light intensities, nocturnal animals have developed visual systems with a wide range of anatomical and physiological adaptations. Insects living in dim light, for example, generally have compound eyes whose ommatidia have larger facet lenses of shorter focal length, as well as longer and wider rhabdoms, in order to increase the photon capture of each photoreceptor (Greiner, Ribi, & Warrant, 2004; Greiner et al., 2007; Meyer-Rochow & Nilsson, 1999; Warrant, 2008; Warrant & Dacke, 2011; Warrant & McIntyre, 1991). Many night-active insects also possess superposition compound eyes, in which hundreds or thousands of facets contribute light to each photoreceptor instead of just one as in apposition eyes. Even in their sum, however, these optical adaptations rarely boost sensitivity by more than a factor of 1000, and they are therefore not sufficient to explain how some insects can deal with the eight orders of magnitude of light intensity variation between night and day. Various neural mechanisms, including a change in photoreceptor gain, as well as spatial and temporal summation of signals at different stages of the neural processing network, have been suggested as solutions to bridge this sensitivity gap (Frederiksen, Wcislo, & Warrant, 2008; Greiner, Ribi, Wcislo, & Warrant, 2004; Greiner, Ribi, & Warrant, 2005; van Hateren, 1993; Laughlin, 1981; Theobald, Greiner, Wcislo, & Warrant, 2006; Warrant, 1999). The fact that hornets, *Vespa crabro*, for example, can fly and forage at night without any obvious dim-light adaptations at the level of the optics of their compound eyes (Kelber et al., 2011) suggests that neural adaptations alone can

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provide a large enough sensitivity boost to allow an animal to extend its activity period to much dimmer light intensities.

Considering that large eyes are costly to develop and maintain, and that vision consumes a large proportion of an animal's energy budget (Laughlin, de Ruyter van Steveninck, & Anderson, 1998; Moran, Softley, & Warrant, 2015), the question arises as to how large an advantage neural and receptor adaptations confer on a nocturnal insect. And how many of the changes in neural processing could also be dynamically engaged in a nonspecialized, diurnal eye if it was forced to work at night? Ideally, these questions should be answered by observing an exclusively diurnal species perform its natural behaviour at night. This experiment is possible in ball-rolling dung beetles owing to their extremely robust straight-line orientation behaviour, which can be elicited under practically any circumstances, even at times when the species would never naturally be active on the soil surface, allowing us to get a direct comparison of a behaviourally relevant task in the animal's natural habitat.

After landing at a fresh dung pile, ball-rolling dung beetles separate a piece of dung and shape it into a ball. They then select a seemingly random bearing (Baird, Byrne, Scholtz, Warrant, & Dacke, 2010), and, with their head down, walking backwards, roll the ball away with their hind legs until they have found an expedient spot to bury themselves together with the ball, and consume it in solitude or lay an egg in it. To escape from the dung pile as quickly as possible, to avoid competition from other newly arrived beetles keen to steal a ball rather than make one themselves, the ball-rolling beetles move away in straight lines. Simple as this may sound, keeping a straight line is impossible without external ‘compass’ cues (Cheung, Zhang, Stricker, & Srinivasan, 2007), even for humans (Souman, Frissen, Sreenivasa, & Ernst, 2009). For this compass, dung beetles use celestial cues exclusively. Ignoring even obvious landmarks, beetles lose their way when the sky is overcast or experimentally occluded (Dacke, Byrne, Smolka, Warrant, & Baird, 2013). Within the sky, however, they use a large range of directional cues, including the azimuthal position of the sun or moon (Byrne, Dacke, Nordström, Scholtz, & Warrant, 2003; Dacke, Byrne, Scholtz, & Warrant, 2004; Dacke, el Jundi, Smolka, Byrne & Baird, 2014), the pattern of polarized light formed around these celestial bodies (Byrne et al., 2003; Dacke, Nilsson, Scholtz, Byrne, & Warrant, 2003; Dacke, Nordström, & Scholtz, 2003; el Jundi, Smolka, Baird, Byrne, & Dacke, 2014; el Jundi et al., 2015), the gradient of skylight intensity that stretches from the solar to the antisolar hemisphere (el Jundi et al., 2014), and even the Milky Way (Dacke, Baird, Byrne, Scholtz, & Warrant, 2013). Astonishingly, the precision with which beetles orient to their familiar cues does not change over a very large range of light intensities (Dacke, Byrne, Baird, Scholtz, & Warrant, 2011). Like other dim-light active insects, nocturnal dung beetles have a range of visual specializations, which allow them to be active at night. Their superposition compound eyes (which all dung beetles possess) are enlarged compared to those of their diurnal cousins in all the expected parameters (Fig. 1; Byrne & Dacke, 2011; Caveney & McIntyre, 1981; Dacke, Nordström, et al., 2003; Frederiksen & Warrant, 2008; McIntyre & Caveney, 1998; Warrant & Mcintyre, 1990), including an enlargement of the dorsal rim area (the region analysing polarized skylight; Dacke, Nordström, et al., 2003; Dacke, Smolka, & Ribi, n.d.), and often feature a tracheal tapetum, which reflects light back onto the photoreceptor and effectively doubles the light path (Warrant & McIntyre, 1991). These optical specializations can increase the sensitivity of a nocturnal beetle's eye by up to 85 times compared to that of a diurnal beetle (Frederiksen & Warrant, 2008; McIntyre & Caveney, 1998). Physiologically, some nocturnal dung beetles adapt their photoreceptors to dim light with a slower frequency response and higher gain (Frederiksen, 2008; Warrant & Mcintyre, 1990). Taken together, these specializations should give nocturnal beetles vastly superior light sensitivity than diurnal beetles.

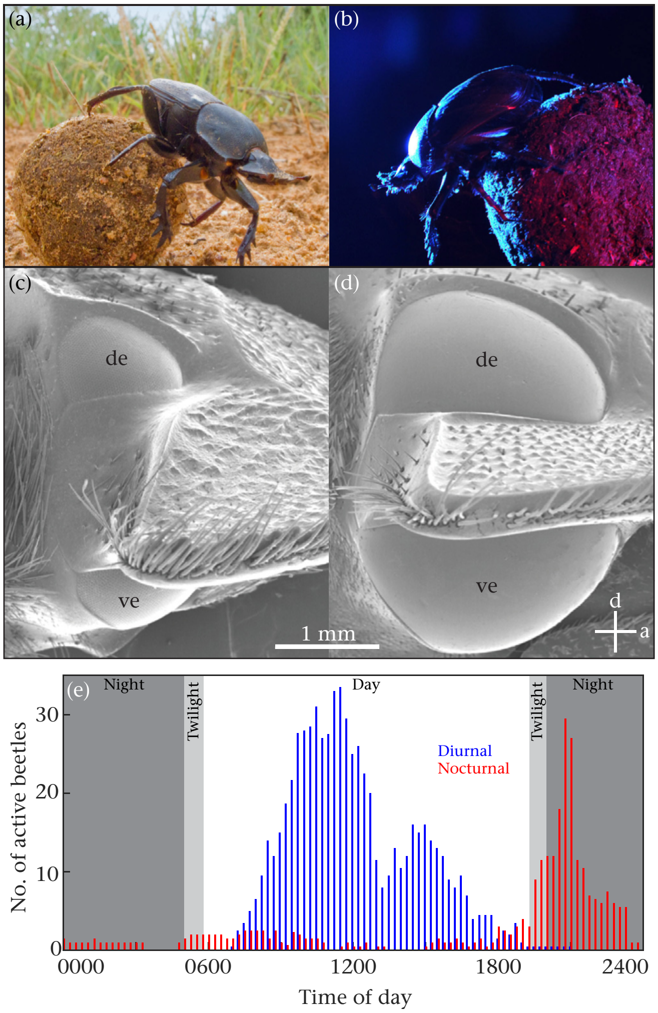

Figure 1. Comparison between study species. (a) The diurnal dung beetle *Scarabaeus lamarcki* and (b) the closely related nocturnal species *Scarabaeus satyrus*. (c, d) Lateral view of the head in scanning electron micrographs of (c) the diurnal and (d) the nocturnal species, showing that the eyes of the latter are substantially larger. The eyes of these two dung beetle species are split into a dorsal eye (de), which perceives most of the signals relevant for skylight orientation, and a ventral eye (ve), which is most likely involved in general visual processing and flight control. (e) Mean activity of 60 diurnal (blue) and 60 nocturnal (red) beetles over two 24 h periods in sand-filled bins in their natural habitat. Beetles were observed every 15 min, and any beetle present at the surface was counted as active.

In this study, we compared the straight-line orientation behaviour of a diurnal and a closely related nocturnal species of South African ball-rolling dung beetle across a large range of light intensities.

METHODS

Animals

All experiments were performed with the diurnal dung beetle species *Scarabaeus (Kheper) lamarcki* (Coleoptera, Scarabaeidae) and the nocturnal species *Scarabaeus satyrus*. We captured the beetles using pit-fall traps in their natural habitat on the game farm ‘Stonehenge’ in South Africa (24.3°E, 26.4°S). After collection, beetles were kept in plastic boxes (30 × 22 cm and 22 cm high) in the shade, where they were provided with soil and fresh cow dung. Field experiments were performed in January and February 2010 and 2013 and January 2014. Laboratory experiments were performed at Lund