

## Chapter 2

# Polarized Light Orientation in Ball-Rolling Dung Beetles

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**Abstract** Many dung beetles, unlike most insect navigators, do not need to locate a stationary nest at the end of their foraging journey. This makes the nature of their orientation task fundamentally different, and in the case of straight-line orientation, the beetles appear to rely single-handedly on celestial compass cues to move along straight paths. With a focus on the sky, diurnal dung beetles rely on the sun and the skylight cues that span the entire sky. These cues include the linear polarization pattern of skylight. As day turns to night, crepuscular and nocturnal dung beetles start to fly at around sunset. At this time, the full sky is polarized in one single direction, and the ball-rolling beetles can be observed to turn sharply when rolling under a linear polarizer placed with its E-vector oriented  $90^\circ$  to that of skylight. When the moon has risen, the beetles continue to orient along straight paths well after sunset, guided by the celestial polarization pattern created by the scattered moonlight. The intensity of this relatively dim polarization pattern will gradually decline as the moon wanes. Remarkably, even the extremely dim celestial polarization pattern formed around a crescent moon is sufficient to guide the nocturnal beetles along straight paths. Moreover, straight-line orientation on these dark nights is performed with the same precision and speed as in dung beetles orienting under the much brighter polarization pattern of the sun or full moon. So strong is their desire to roll their balls of dung that nocturnal beetles can be made to roll at day and diurnal beetles can be compelled to roll in the middle of the night. This incredible flexibility opens up the possibility to perform a new set of experiments directed towards an understanding of how celestial compasses have been adapted to the visual environment in which the insect is normally active.

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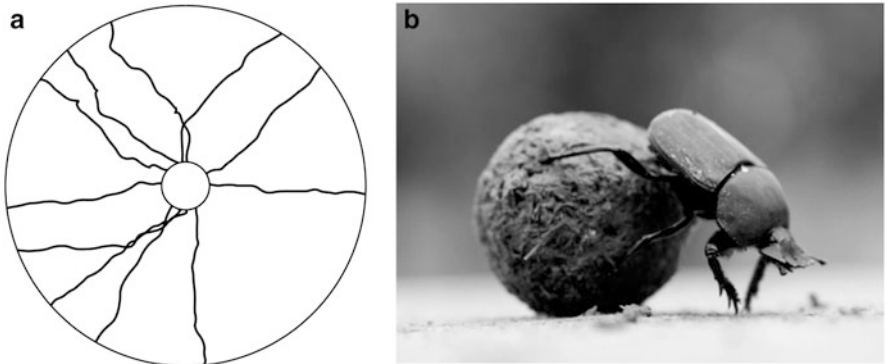
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## 2.1 Introduction

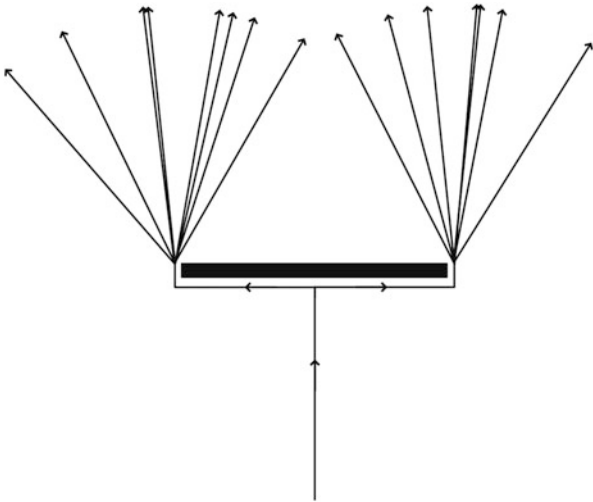
A freshly made dung pile on the African savannah attracts visitors from near and far. Ball-rolling dung beetles fly in from kilometres away and gather at this food source to feed and mate. Once the foraging beetles have climbed onto the dung pile, they begin to sculpt the dung into a transportable package of food. Using their flat heads and legs, they quickly form even the sloppiest excrement into a ball and start to push it away. The beetles exit the pile in different directions (Fig. 2.1a) (Dacke et al. 2003a, 2013a, b, 2014) in search of a suitable (but not predetermined) place to bury and consume their smelly meal. Newly arriving beetles are hot from flying (and therefore faster and stronger than colder beetles) and will try to steal a ready-made ball from the exiting beetles, rather than making one of their own (Bartholomew and Heinrich 1978). To protect its nutritional prize from these competitors at and around the dung pat, a beetle must roll its ball away as swiftly and efficiently as possible, that is, along a straight line.

Despite their peculiar style of food transport—rolling a large ball backwards while keeping their heads close to the ground (Fig. 2.1b)—the dung beetles manage to move along near-perfect straight paths whilst traversing over flat terrain. When analysed over a distance of 120 cm, the paths are on average no more than  $127 \pm 3$  cm long (mean  $\pm$  standard deviation,  $n = 11$ ), (Fig. 2.1a) (Dacke et al. 2013b). The extra distance of 7 cm is an unavoidable consequence of the slight side-to-side rocking motion made by the beetles as they push the ball along an overall constant rolling direction.

It is unclear what makes the beetles choose their departure bearings from the dung pat, but it appears as if the process of making a new ball provides the behavioural circumstance necessary for choosing an exit direction (Baird et al. 2010). Once the bearing has been selected, the beetle keeps steadfastly to it. Forcing a beetle off course by placing obstacles in its way, making it fall from a ramp or even spinning it around on a rotating platform will only temporarily deflect the beetle in a different direction (Byrne et al. 2003; Dacke et al. 2003b; Baird et al. 2012). When negotiating a barrier, the beetles are forced to move around it, but as soon they reach its edge, they take a course that is parallel to the desired direction of travel (Fig. 2.2). A similar manipulation on a homing animal would result in a new intermediate course to compensate for the sideways movement, but since a ball-rolling beetle does not navigate towards a particular location, it simply continues along its original direction of travel. This simplifies the task of orientation, while still effectively taking the beetle away from the busy dung pile.



**Fig. 2.1** (a) Paths of the ball-rolling beetle *Scarabaeus lamarcki* rolling outwards from the centre of a 3 m diameter circular arena (as seen from *above*) on a clear day. The tracking of the beetle began once it rolled out from the inner, 60 cm diameter circle. A perfectly straight track will thus be 120 cm long. The paths made by the 11 beetles in the figure are on average no more than  $127 \pm 3$  cm long (mean  $\pm$  standard deviation). (b) The diurnal dung beetle *Scarabaeus lamarcki* rolling its ball of dung [modified after Dacke et al. (2013b), photo: Emily Baird]



**Fig. 2.2** Schematic drawing of the orientation of 15 ball-rolling dung beetles (*Scarabaeus lamarcki*) before and after encountering a barrier. *Arrows* mark the direction of movement. The absolute mean angle of deviation from the original course is  $16.9^\circ$  [modified after Dacke (et al. 2003b)]

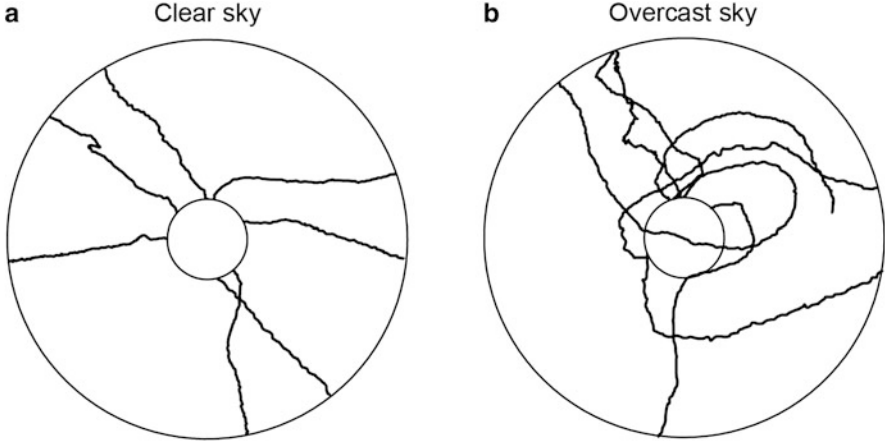
## 2.2 Polarized Light Orientation During the Day

Navigating insects use a number of compass cues to find their way to a food source and back home again. These include the sun, the pattern of polarized skylight and landmarks (for reviews see Wehner 1992; Wehner and Srinivasan 2003; Collett and Collett 2009). Dung beetles, however, seem to rely exclusively on celestial compass cues for orientation. The sudden removal of visual landmarks, such as bushes, trees or the centrally placed dung pile, has no effect on orientation precision (Dacke et al. 2013b). Under a heavily overcast sky when the sun is no longer visible and the degree of skylight polarization is greatly reduced (Pomozi et al. 2001; Hegedüs et al. 2007; see also Chap. 18), the skydome and the surrounding landmarks are the only sources of directional information. Nonetheless, ball-rolling dung beetles do not make use of this information, since the tracks of beetles rolling over 80 cm under a completely overcast sky become curved and significantly longer ( $116 \pm 4$  cm,  $n = 7$ ) than when rolling under a clear sky ( $84 \pm 0$  cm) (Dacke et al. 2013b) (Fig. 2.3). Thus, when the beetles can no longer see the celestial compass cues, their straight-line orientation performance is significantly impaired (Dacke et al. 2003a, 2011, 2013b).

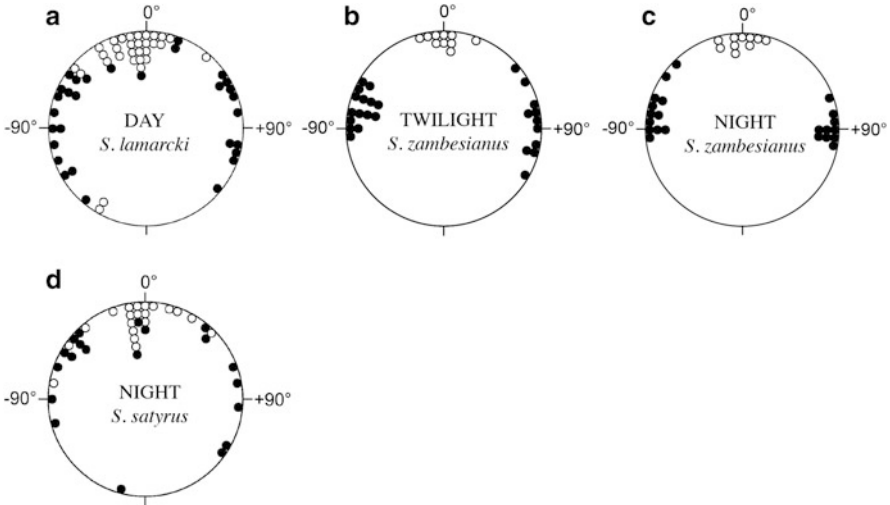
To our knowledge, ball-rolling dung beetles are the only animals with a visual compass system that ignore the extra orientation precision that landmarks can offer. These beetles, unlike most insect navigators, do not need to locate a stationary nest at the end of their foraging journey. This makes the nature of their orientation task fundamentally different, and in the case of the straight-line orientation, celestial compass cues appear to provide the precision these beetles need to ensure a safe exit from the dung pile. That is, for as long as the sky is not completely overcast, but this is a rare event in the life of the South African beetle.

With a focus on the sky, diurnal dung beetles can rely on the skylight cues that span the entire sky. These cues include the pattern of polarized skylight and gradients of colour and intensity (Edrich et al. 1979; Brines and Gould 1982; Rossel and Wehner 1984; Horváth and Varjú 2004; Ugolini et al. 2009). Beetles rolling under a linearly polarizing filter, placed with its E-vector (direction of polarization) oriented  $90^\circ$  to that of skylight, will turn by a mean angle of  $77 \pm 6^\circ$  ( $n = 30$ ) (el Jundi et al. 2014) (Fig. 2.4a, black circles). In these experiments, the sun was hidden from view and the  $90^\circ$  rotation of the E-vector direction did not allow the beetles to discriminate between an apparent left rotation or a right rotation of the polarization direction. As a result, 17 beetles turned to the left and 13 beetles turned to the right. Conversely, the beetles maintained their rolling direction under the polarizer, if it was instead placed with its E-vector parallel to that of skylight (mean change in bearing  $18 \pm 6^\circ$ ,  $n = 30$ , Fig. 2.4a, white circles). This clearly shows that dung beetles are able to orient by using the celestial polarization pattern as a compass cue, while the role of the other skylight cues remains to be tested.

Artificially changing the apparent position of the sun by  $180^\circ$ , in a classical experiment using a mirror while blocking the view of the sun with a board



**Fig. 2.3** Paths of the ball-rolling dung beetle, *Scarabaeus lamarcki*, rolling outwards from the centre of a 2 m diameter circular arena (as seen from *above*) under a clear (a) and an overcast sky (b). Tracking of the beetle began once it rolled out from the inner, 40 cm diameter circle. A perfectly straight track will thus be 80 cm long. The tracks are significantly longer when orienting under the overcast sky ( $116 \pm 4$  cm, mean  $\pm$  SD) than under the clear sky ( $84 \pm 0$  cm) (*t*-test,  $p < 0.01$ ). Thus, when the beetles can no longer see the celestial compass cues, their straight-line orientation performance is significantly impaired [modified after Dacke et al. (2013b)]



**Fig. 2.4** Circular diagram of turns made by ball-rolling dung beetles in response to a polarization pattern rotated by  $90^\circ$  (black circles) or  $0^\circ$  (white circles), during the day (a), at twilight (b) or during the night (c, d). In these experiments, the sun and the moon were hidden from view and the  $90^\circ$  change in the E-vector direction did not allow the beetles to discriminate between an apparent left rotation or a right rotation of the direction of polarization. As a result, some of the beetles turned to the left and some of others turned to the right. The data is binned in  $5^\circ$  intervals and the species tested in each condition is indicated in the *centre of the diagram* [modified after el Jundi et al. (2014): a; Dacke et al. 2003b: b; Dacke et al. 2003a: c]

(Santschi 1911), caused the beetles to change their bearing by  $128 \pm 6^\circ$  ( $n = 60$ ) (Dacke et al. 2014). This indicates that the primary cue for orientation is the sun, rather than the pattern of polarized skylight, which remains unaffected by this treatment. If the same experiment was repeated at solar elevations below  $30^\circ$ , rather than above  $75^\circ$  as in the first set of experiments, the beetles changed their bearing by no more than  $104 \pm 7^\circ$  ( $n = 60$ ). As the sun draws closer to the horizon, the degree of polarization in the zenith of the sky increases (Brines and Gould 1982), and it is likely that the observed decrease in the relative influence of the sun at low solar elevations is a consequence of the increased input to the polarized light compass.

### 2.3 Polarized Light Orientation During Twilight

As day turns to night, diurnal dung beetles cease their activity, while crepuscular dung beetles just start to wake up (Caveney et al. 1995). The beetle *Scarabaeus zambesianus* starts to fly at around sunset and can be seen in dim light at our experimental dung piles some 30 min after sunset. The setting of the sun, and the drastic decrease in surrounding light levels, is a phenomenon of twilight that is clearly perceptible to the human observer. At the same time, though invisible to us, the sunset also generates the simplest celestial polarization pattern—the full sky is polarized in one single direction. This is also the time of the day with the highest degree of polarization in the zenith of the sky (between 70 and 80 %; Brines and Gould 1982). This provides us with ideal conditions to manipulate the celestial polarization pattern as it appears to the ball-rolling dung beetles. Like their diurnal relatives, *S. zambesianus* can be made to turn by  $81 \pm 16^\circ$  when rolling under a linear polarizer placed with its E-vector oriented  $90^\circ$  to that of skylight (Fig. 2.4b) (Dacke et al. 2003b).

The degree of polarization in the zenith of the sky decreases to 50 % when the sun is between  $8^\circ$  and  $12^\circ$  below the horizon, and from 15 % to near zero when the sun is between  $+16^\circ$  and  $-18^\circ$  (Dave and Ramanathan 1955; Rozenberg 1966). When the sun is more than  $18^\circ$  below the horizon, sunlight no longer influences the night sky and the celestial polarization pattern vanishes. Since night has now succeeded day, *S. zambesianus* beetles behave as if the sky were overcast; unable to extract any relevant compass input from the sky they start to roll in circles (Dacke et al. 2003a). This is true, however, only for nights when the moon has not yet risen.

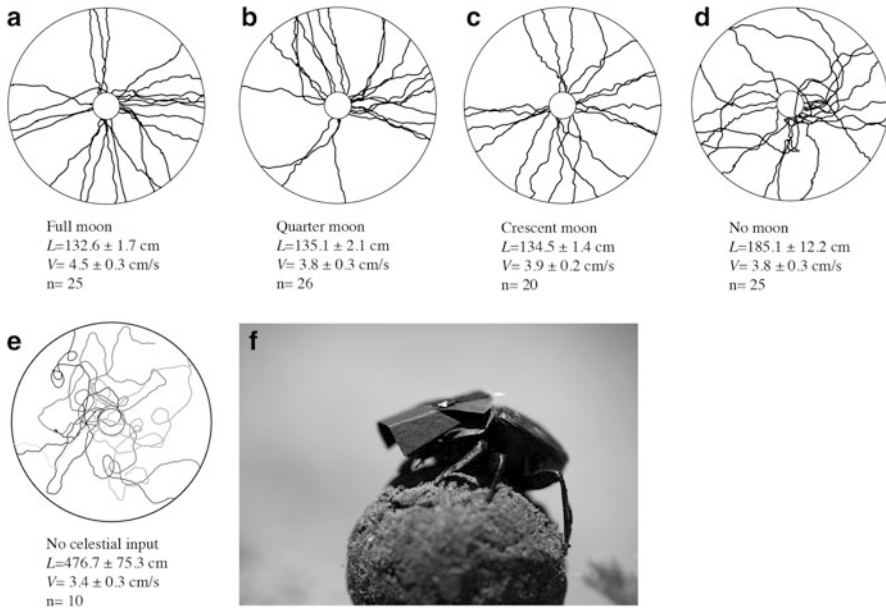
## 2.4 Polarized Light Orientation at Night

As a celestial body reflecting sunlight, the moon emits roughly the same spectrum of light as direct sunlight, but obviously with a much lower luminance (Lythgoe 1979). Moonlight, like sunlight, scatters in the earth's atmosphere, and a celestial pattern of polarized light is also present around the moon. On a full moon night, this pattern shows no significant difference in its structure from that of the pattern of polarized light formed around the sun, although it is at least a million times dimmer (Gál et al. 2001).

When the moon has risen, *S. zambesianus* can continue to orient along straight paths well after sunset. If the rising moon is hidden from view, and a linear polarizer is placed with its transmission axis perpendicular to the dominant E-vector in the sky, the beetles can again be observed to change their direction of rolling by close to  $90^\circ$  ( $80 \pm 3^\circ$ ,  $n = 22$ ) (Dacke et al. 2003a) (Fig. 2.4c). For almost 10 years, *S. zambesianus* was the only animal that had been observed to orient using the dim polarization pattern of the moonlit sky. Recently, we demonstrated that the nocturnal dung beetle *Scarabaeus satyrus* also uses this cue to orient (el Jundi et al. 2014) (Fig. 2.4d). The main difference between the dim light activity of these two species is that *S. zambesianus* will only remain active on nights when the moon has risen in conjunction with the setting sun, while *S. satyrus* can function on every night of the lunar month.

The intensity of the relatively dim celestial polarization pattern will gradually decline as the moon wanes. On nights with a crescent moon, the intensity of the polarization pattern is almost 100 times dimmer than on a full moon night (Land 1981; Lynch and Livingston 2001). Remarkably, even the extremely dim celestial polarization pattern formed by a crescent moon is sufficient to guide the nocturnal ball-rolling dung beetles along a straight path. Moreover, straight-line orientation on these dark nights is performed with the same precision and speed as in beetles orienting under the much brighter polarization pattern of the sun or full moon (Dacke et al. 2011) (Fig. 2.5a–c).

When the moon leaves the sky, the tracks made by the ball-rolling dung beetles become curved and significantly longer than on moonlit nights (Fig. 2.5d). However, beetles pushing their balls on these dark nights are not lost, and many of them still travel along relatively straight paths. To investigate the importance of celestial cues on the nocturnal orientation behaviour of these beetles, we occluded the dorsal visual field (and therefore all celestial input) using an opaque cap taped to the dorsal thorax (Fig. 2.5f). Tracks made by beetles wearing a cap are curved and significantly longer than when they have a full view of the sky (Fig. 2.5e) (Dacke et al. 2013a). Experiments in the field and in the planetarium reveal that on these moonless nights the nocturnal beetles still have one more ace to play: celestial orientation to the Milky Way (Dacke et al. 2013a). Since the moon is potentially visible for only half of all nights, the stars and more importantly the Milky Way, provide an additional celestial cue for orientation to keep the beetles on track. An



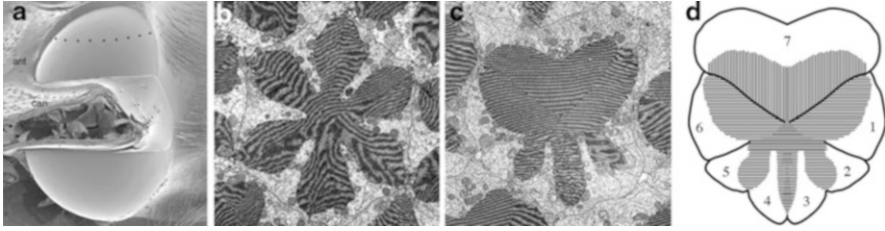
**Fig. 2.5** Paths of the ball-rolling beetle, *Scarabaeus satyrus*, rolling outwards from the centre of a 3 m diameter circular arena (as seen from above) under a sky lit by the full moon (a), quarter moon (b), new moon (c), on a moonless night (d) or with an occluded view of a moonless starry sky (e). To block the view of the sky, small “caps” were attached to the thorax of the beetle (f). The tracking of the beetle began once it rolled out from the inner, 60 cm diameter circle. The average length of the tracks ( $L \pm$  standard deviation) and rolling speed ( $V \pm$  standard deviation) under each condition are given next to each figure. The orientation performance—as measured by these two parameters—remained consistent for as long as there was a moon present in the sky (ANOVA,  $L: p = 0.33$ ,  $V: p = 0.14$ ). The tracks did, however, become significantly longer (more curved), if the beetles rolled on a moonless night (ANOVA,  $p < 0.001$ ). On these nights there was no polarization pattern present in the sky to guide the beetles along a given route and their orientation along a straight line became significantly impaired. If the night sky was occluded from view by the use of a cap, the tracks became significantly longer again ( $t$ -test,  $p > 0.001$ ). Thus, the straight-line orientation of *S. satyrus* was significantly impaired if they were prevented from seeing the starlit sky [modified after Dacke et al. (2011: a–d, 2013a: e); photo: Emily Baird]

orientation to the Milky Way for straight-line travel is another “first” for the celestially fixated South African dung beetles.

## 2.5 The Morphology and Physiology of Polarized Light Analysis

As the previous sections indicate, ball-rolling dung beetles can be observed to push their spherical treasures of dung along straight paths on bright sunny days, under the reddish sunset sky as well as on dark moonless nights. The ability to successfully range across almost the complete range of light intensity habitats is made possible



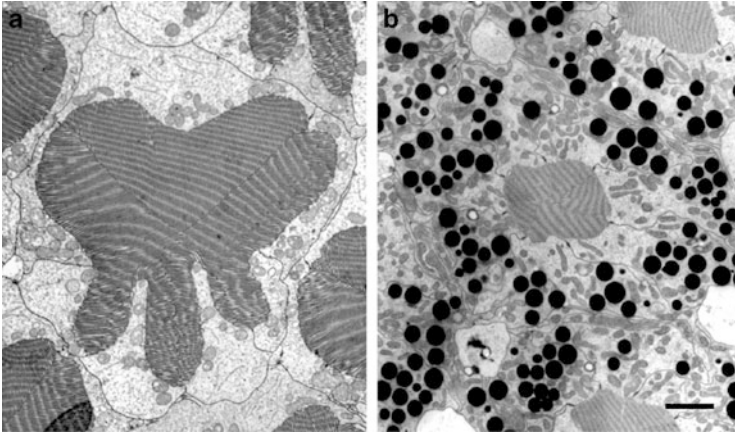


**Fig. 2.6** (a) Scanning electron micrograph of the dorsal and ventral eye of *Scarabaeus zambesianus*. A lateral view of the head of the beetle shows the canthus (*can*) that completely separates the eye into a dorsal and a ventral part. The stars mark the border of the dorsal rim area (DRA). (b, c) Electron micrographs of the rhabdoms in the ventral eye (b) and in the DRA (c). (d) Schematic drawing of a rhabdom in DRA. The rhabdoms are all formed by seven receptor cells (1–7), but differ in their shape and microvillar orientation. The rhabdoms of the DRA are *heart-shaped* with orthogonal microvilli, while the rhabdoms in the rest of the dorsal eye and in the ventral eye are *flower-shaped* with a variety of microvillar orientations [modified after Dacke et al. (2003b)]

through differences in the morphology of the eyes of nocturnal and diurnal dung beetles (Dacke et al. 2002, 2003b; Byrne and Dacke 2010). Here, we will focus on differences in the parts of the dung beetle eyes devoted to the analysis of celestial polarization.

In dung beetles, as in most other polarization-sensitive insects (Labhart and Meyer 1999), the photoreceptors for celestial polarization analysis are restricted to the dorsal rim area (DRA) of the eye. The location of this area is revealed by the structure of its rhabdoms, in which two sets of receptors with parallel microvilli are oriented  $90^\circ$  to each other (Fig. 2.6d). With a maximum sensitivity to light polarized parallel to the direction of the microvilli (Israelachvili and Wilson 1976; Goldsmith and Wehner 1977; Hardie 1984), this arrangement tunes the two groups of receptors to orthogonal planes of polarization. The straighter and better aligned the microvilli are, the greater the cell's sensitivity to light that is polarized parallel to the main microvillar direction (Wehner et al. 1975; Nilsson et al. 1987). Polarization contrast can be enhanced by a comparison between receptors tuned to different directions of polarization (Labhart 1988; Nilsson and Warrant 1999), and an orthogonal arrangement of the two sets of receptors thus meet the requirement for a polarization-opponent analyser.

The best described polarization analyser of dung beetles is that of *S. zambesianus* (Dacke et al. 2003b). The eyes of this crepuscular species, as in most other ball-rolling beetles, are divided into dorsal and ventral eyes by a cuticular ridge, the canthus (Fig. 2.6a). In the ventral eye, and the ventral half of the dorsal eye, the microvilli form a flower-shaped rhabdom (Fig. 2.6b). In these rhabdoms, the microvilli of the seven receptor cells run in different directions, making these parts of the eye unsuitable for the detection of light polarization. In the dorsal region of the eye (the area above the stars in Fig. 2.6a), the microvilli run in only two directions, forming miniature heart-shaped rhabdoms in cross section (Fig. 2.6c, d). This, together with the finding that these rhabdoms do not twist along



**Fig. 2.7** Cross sections of DRA-rhabdoms in the crepuscular dung beetle *Scarabaeus zambesianus* (a) and the diurnal beetle *Pachysoma striatum* (b). Note the difference in the size of the rhabdom and amount of pigmentation, both morphological adaptations to the time of activity. Scale bar: 2  $\mu\text{m}$  [modified after Dacke et al. (2003b)]

their length, makes them well suited for detection and analysis of polarization. Intracellular recordings show that the receptor cell in the DRA of *S. zambesianus* is at least ten times more sensitive to light polarized parallel to the microvilli than perpendicular to them (Dacke et al. 2004). In other words, they have a polarization sensitivity of at least 10, which is similar to that recorded for other insects (Labhart 1980, 1986; Blum and Labhart 2000; Dacke et al. 2002).

The ability of all visual systems to reliably detect visual information, such as the polarization of light, decreases with falling light intensities. This is because of the random variance of photon arrival on the retina: a photoreceptor that absorbs  $N$  photons will experience an uncertainty of  $(N)^{1/2}$  associated with this sample (Land 1981; Warrant and McIntyre 1993). This uncertainty, or noise, will reduce the reliability of any visual measurement as light intensity decreases. The photoreceptors themselves also add to this noise by producing spontaneous electrical events that cannot be distinguished from the response to a photon. This means that the darker it gets, the increasing relative noise levels will gradually make it more difficult for the crepuscular and nocturnal dung beetles to reliably detect the direction of skylight polarization.

One possible way for an eye to improve vision in low light levels is to catch more of the available photons. Compared to the diurnal dung beetle *Pachysoma striatum*, the rhabdom in *S. zambesianus* is much longer and three times as wide (Fig. 2.7). This allows the receptors to catch more light and, thus, makes them more sensitive in dim light. In addition, a tracheal *tapetum lucidum* (biological multi-layer mirror) at the base of the retina of *S. zambesianus* reflects light back through the rhabdom, giving it a second opportunity to collect light and effectively doubling its length. Photon catch can also be improved neurally by summing photons in time and space

(Warrant 1999), but this very likely possibility remains to be investigated among the ball-rolling dung beetles.

The nocturnal dung beetles *Scarabaeus deludens* and *Scarabaeus goryi* also have an orthogonal microvilli arrangement of the large photoreceptors in the dorsal part of their eyes. Combined with a need to roll in straight lines, it is more than likely that these beetles, like all their nocturnal relatives, orient to the polarization pattern of the night sky. Laboratory experiments strongly suggest that crickets and tenebroid beetles can also make use of the celestial polarization pattern formed by scattered moonlight (Herzmann and Labhart 1989; Bisch 1999), but behavioural studies in the field at night are inherently difficult in these species. Thus, 10 years after the first demonstration of the use of a nocturnal polarization compass, ball-rolling dung beetles are still the only animals described to possess this ability.

## 2.6 Conclusions

Few insects, perhaps with the exception of ants, are so ideally suited for the study of celestial orientation as the dung beetles. Their purely celestially based orientation system helps us to avoid confounding orientation effects of landmarks, and when given a ball of dung (or even a golf ball!), these insects will immediately start to roll it along a set compass direction. So strong is their desire to roll that nocturnal beetles can be made to roll at day and diurnal beetles can be compelled to roll in the middle of the night. This incredible flexibility opens up the possibility to perform a new set of experiments directed towards understanding how the celestial compasses can be adapted to the environment in which the insect is normally active. The ball-rolling dung beetles are thus predicted to retain their crown as the best experimental model for nocturnal polarized light orientation for many years to come.

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