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Research

How dim is dim? Precision of the celestial compass in moonlight and sunlight

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Prominent in the sky, but not visible to humans, is a pattern of polarized skylight formed around both the Sun and the Moon. Dung beetles are, at present, the only animal group known to use the much dimmer polarization pattern formed around the Moon as a compass cue for maintaining travel direction. However, the Moon is not visible every night and the intensity of the celestial polarization pattern gradually declines as the Moon wanes. Therefore, for nocturnal orientation on all moonlit nights, the absolute sensitivity of the dung beetle's polarization detector may limit the precision of this behaviour. To test this, we studied the straight-line foraging behaviour of the nocturnal ball-rolling dung beetle *Scarabaeus satyrus* to establish when the Moon is too dim—and the polarization pattern too weak—to provide a reliable cue for orientation. Our results show that celestial orientation is as accurate during crescent Moon as it is during full Moon. Moreover, this orientation accuracy is equal to that measured for diurnal species that orient under the 100 million times brighter polarization pattern formed around the Sun. This indicates that, in nocturnal species, the sensitivity of the optical polarization compass can be greatly increased without any loss of precision.

Keywords: orientation; polarized light; dung beetle; vision; navigation

1. INTRODUCTION

At night, the Moon overwhelms all other sources of natural light in the sky and is used by many nocturnal navigators as an orientation cue [1–9]. However, instead of relying on the disc of the Moon for its orientation, dung beetles rely primarily on the celestial pattern of polarized light centred upon it [10,11]. After locating a dung pat, the dung beetle quickly forms a ball and rolls it away. To avoid competition, the beetle must move away from the dung pat as swiftly and efficiently as possible, i.e. along a straight-line path [10–13]. On nights with a full Moon, the crepuscular dung beetle *Scarabaeus zambesianus* prolongs its activity by switching from using the polarization pattern of the setting Sun as an orientation cue, to using the polarization pattern of the rising Moon [11]. When the Moon no longer rises within 30 minutes sunset, *S. zambesianus* ceases its activity after twilight. However, its more nocturnal relative, *Scarabaeus satyrus*—which becomes active 1 h after sunset—needs to forage without the benefit of any cues from the Sun. The pattern of polarization present around a full Moon is up to 1 million times dimmer than that which is present around the Sun during the day [14], and on nights with a small crescent Moon, the celestial polarization pattern is almost 100 times dimmer again [15,16]. How does the orientation precision of these crepuscular and nocturnal beetles compare to that of their diurnal relatives? At which phases of the Moon are the celestial polarization patterns still bright enough to support the straight-line orientation without any loss of precision?

2. MATERIAL AND METHODS

(a) *Animals and field site*

Dung beetles (Coleoptera: Scarabaeinae) were collected using dung-baited pit-fall traps. The rolling behaviours of *Garetta unicolor, Scarabaeus rugosus, Kheper lamarki, Pachylomerus femoralis* (all diurnal), *S. zambesianus* and *S. satyrus* (crepuscular and nocturnal, respectively) were studied within the game reserve 'Stonehenge', 70 km northwest of Vryburg in the Northwest Province of South Africa. All experiments were performed between February and March 2008 and 2009. During these periods, the Moon phase varied from full to almost new, and rose progressively later in the evening.

(b) *Precision of the diurnal and the nocturnal celestial compass*

(i) *Precision of straight-line orientation*

Beetles were observed rolling on a levelled circular arena measuring 3 m in diameter. The arena was enclosed within a 1 m high, featureless circular wall to shade the

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One contribution of 20 to a Theme Issue 'New directions in biological research on polarized light'.

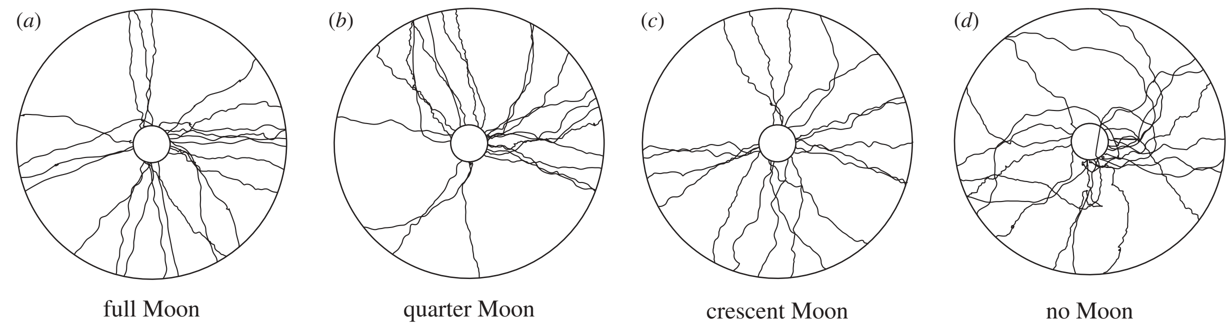

Figure 1. The different paths of the ball-rolling beetle *S. satyrus* rolling outwards from the centre of a circular arena (as seen from above) are reconstructed from video footage recorded under a sky lit by (*a*) full Moon (average length of the tracks, $L = 132.6 \pm 1.7$ cm; rolling speed, $V = 4.5 \pm 0.3$ cm^{-1}; $n = 25$), (*b*) quarter Moon ($L = 135.1 \pm 2.1$ cm; $V = 3.8 \pm 0.3$ cm^{-1}; $n = 26$), (*c*) crescent Moon ($L = 134.5 \pm 1.4$ cm; $V = 3.9 \pm 0.2$ cm^{-1}; $n = 20$) and (*d*) on a moonless night ($L = 185.1 \pm 12.2$ cm; $V = 3.8 \pm 0.3$ cm^{-1}; $n = 25$). The diameter of the arena was 3 m. A 1 m high wall around the arena prevented a direct view of the Moon or terrestrial landmarks. The tracking of the beetle began once it rolled out from the inner, 30 cm diameter circle. The tracks were analysed for speed and length. The orientation performance—as measured by these two parameters—remains consistent for as long as there is a Moon present in the sky (ANOVA, L: $p = 0.33$, V: $p = 0.14$). The tracks do, however, become significantly longer (more curved) if the beetles roll on a moonless night (ANOVA, $p < 0.001$). On these nights, there is no polarization pattern present in the sky to guide the beetles along a given route and their orientation along a straight line becomes significantly impaired. A moonless night is defined as a night when the Moon is lower than 18° below the horizon and the reflected light from this celestial body is no longer visible in the night sky.

Table 1. Details of experimental conditions for measurements of the precision of straight-line orientation of the ball-rolling beetle *S. satyrus* under different lunar phases.

lunar phase	date (2008)	days after new Moon (n)	time of day	light intensity (cd m^{-2})	lunar altitude (degrees)	sky condition
full Moon	19th Feb	12	21.40–22.30	4×10^{-2}	44–46	thin clouds
quarter Moon	29th Feb	22	00.10–02.00	3×10^{-3}	23–46	thin clouds
new Moon	4th Mar	26	03.50–04.40	4×10^{-4}	24–35	clear sky
no Moon	2nd Mar	24	22.10–23.05	7×10^{-5}	−26– −18	clear sky

beetle from the direct illumination of the Moon and to prevent orientation by terrestrial landmarks. Twenty to twenty-six dung beetles of the nocturnal species *S. satyrus* were released one by one with their dung balls from the centre of the arena. The arena was filmed from above using a Sony HDR-HC5E Handycam fitted with a 0.42× wide-angle lens suspended from a wooden gantry 3 m above the centre of the arena. Distortions in the image owing to the wide-angle optics were corrected by calibrating the camera image using a sheet of black-and-white checkerboard pattern with known check size that was placed at different locations on the arena and filmed from above. At night, the 'Night Shot' facility of the camera was used to illuminate and film the arena in infrared light. Rolling tracks were reconstructed from the films and their lengths and speeds were determined.

Details of experimental conditions for measurements of the precision of straight-line orientation under different Moon phases are summarized in table 1.

(ii) *Correction for falling off a ramp*

A Perspex ramp (12 cm wide × 20 cm long, 5 cm drop) was placed in the path of a ball-rolling beetle. The ramp surface was covered in a sandpaper to give the beetle traction during up-hill rolling. Beetles rolled up the ramp and fell off the end, losing control of their ball. This usually caused the beetle to climb on top of its ball and rotate around its own axis before resuming rolling. The absolute differences between the original and final angles of rolling were analysed to determine the fidelity to the original rolling direction. A difference of 0° indicated perfect fidelity.

(iii) *Correction for rotation*

Beetles rolling balls were placed at the edge of a sand-covered wooden disc (42 cm diameter) and allowed to roll towards the disc centre. As the beetle reached the centre of the disc, it was rotated through 90° in either a clockwise or anticlockwise direction. The absolute angular difference between the original path and the path following rotation was analysed to determine the ability of the beetle to correct for this rotation. A difference of 0° indicated perfect correction.

3. PRECISION OF THE NOCTURNAL CELESTIAL COMPASS AT DIFFERENT PHASES OF THE MOON

Over a period of 3.5 weeks in the field—including nights with a full, quarter and crescent Moon—we recorded the tracks of *S. satyrus* rolling in a level, circular arena (figure 1: arena perimeter seen from

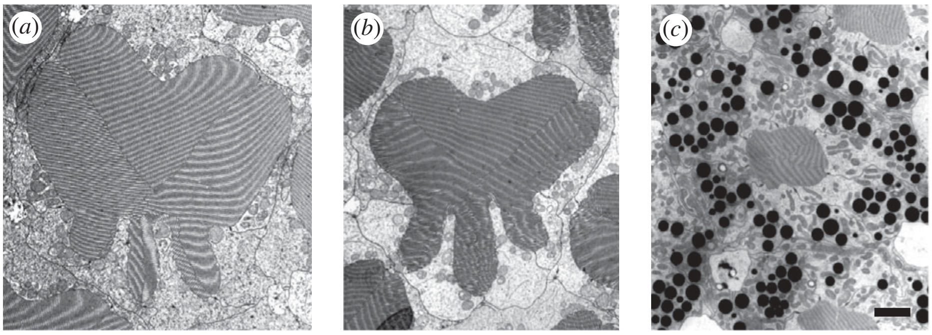

Figure 2. Cross sections of rhabdoms in the dorsal rim area of the eyes of (*a*) *S. satyrus* (nocturnal), (*b*) *S. zambesianus* (crepuscular) and (*c*) *Pachysoma striatum* (diurnal). The rhabdoms have microvilli in only two directions. This is an arrangement that allows for an analysis of the polarization direction of light. Also note the difference in the size of the rhabdoms and the amount of pigmentation between the three species, both morphological adaptations to the time of activity. Scale bar (applies to all panels), 2 μm.

above). A 1 m high wall around the arena prevented the beetles from seeing terrestrial landmarks or the disc of the Moon. The beetle and its ball were placed in the centre of the arena, from where it immediately rolled the ball away towards the edge of the arena. The rolling trajectories of the beetles were filmed by a camera mounted above the arena. Each individual track was analysed over a radial distance of 120 cm. The length of a perfectly straight track was thus exactly 120 cm. The mean lengths of the tracks measured were 132.6 ± 1.7 cm ($n = 25$) on a full Moon night (figure 1*a*), 135.1 ± 2.1 cm ($n = 26$) on a quarter Moon night (figure 1*b*) and 134.5 ± 1.4 cm ($n = 20$) on a crescent Moon night (figure 1*c*). Tracks longer than 120 cm indicate that the beetle has either wobbled from side to side while maintaining an overall constant rolling direction (caused by the side-to-side rocking motion of the beetle as it rolls the ball backwards, as evidenced in figure 1*a*–*c*) or has moved along a curved track (indicating orientation difficulties: figure 1*d*). However, the mean lengths of the tracks at full Moon and crescent Moon do not differ by more than 2 cm over a distance of 120 cm. No significant differences in the lengths of the tracks at different phases of the Moon were found (ANOVA, $p = 0.33$). It is not until we allow beetles to roll on nights without a Moon (i.e. when the Moon was further than 18° below the horizon) that the tracks become curved and significantly longer; 185.1 ± 12.2 cm ($n = 25$; ANOVA, $p < 0.001$; figure 1*d*). The orientation precision of the beetles along a straight line is thus maintained as long as there is a Moon—full or crescent—present in the sky. Even though the ball-rolling beetles are prevented from seeing the Moon itself, the dim polarization pattern centred on the disc of the Moon is still available as an orientation cue in the night sky. The faint light gradient in the sky, with its brightest part at the position of the Moon, could possibly serve as an additional directional cue. The use of this gradient for orientation has, however, been demonstrated only under the bright sun-lit sky [17,18]. Earlier studies of the orientation performance of the closely related *S. zambesianus* also show that the celestial pattern of polarized light is the primary cue used for orientation along a straight path on moon-lit nights [10,11]. The close phylogenetic relationship and resemblance in behaviour and eye structure (figure 2*a*,*b*) between the two beetles leads us to hypothesize that this is the main cue used for visual orientation by *S. satyrus* also.

4. ANALYSIS OF DIM POLARIZED LIGHT PATTERNS

The problem of orienting by the dim polarization pattern of the crescent Moon—rather than by the bright polarization pattern that spans the sky during the day—is that many fewer photons are available to analyse the polarization direction of light. Signal reliability can be improved with an eye design of high optical sensitivity, but this often comes at the cost of either spatial or temporal resolution [19–21]. A gradual loss of spatial resolution in a compass system should induce a growing navigational error that would finally make it impossible to move along a straight path [22]. However, the consistency of the beetles' roll-path length at different phases of the Moon clearly shows that the optical compass of *S. satyrus* has overcome the constraints of decreasing light intensity.

One adaptation to increase the sensitivity of the polarized light detector in *S. satyrus* becomes obvious upon comparison of the rhabdoms in the dorsal rim area with those of a crepuscular and a diurnal dung beetle (figure 2). The wider rhabdoms in *S. satyrus* allow the receptors to collect more light, and thus increase their sensitivity [15]. A second strategy that *S. satyrus* may use to improve visual reliability as light intensity decreases is to sum photons over a longer period of time. The accuracy of straight-line orientation could then be maintained at the cost of moving progressively more slowly as light levels fall [23]. Analysis of the tracks in figure 1*a* reveals that the average rolling speed at full Moon is 4.5 ± 0.3 cm s^{-1}. The beetles do roll somewhat more slowly at quarter Moon (3.8 ± 0.3 cm s^{-1}), crescent Moon (3.9 ± 0.2 cm s^{-1}) and on moonless nights (3.8 ± 0.4 cm s^{-1}), but not significantly so (ANOVA, $p = 0.14$). The consistency in rolling speeds at light intensities that differ by 2 log units (full Moon to crescent Moon) implies that the temporal resolution of the dung beetle compass does not limit their ability to analyse the celestial polarization pattern at these light intensities.

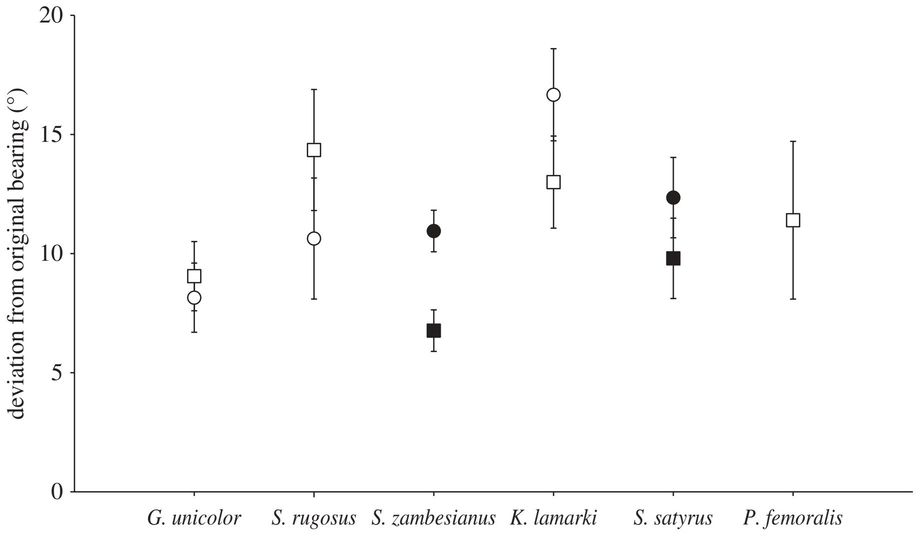

Figure 3. Beetles were forced off course by either a fall from a ramp or by an induced 90° rotation. When continuing to roll, the beetles attempted to reorient back to their original direction of travel. The deviation from the original bearing was measured after reorientation in six different species of beetles, four diurnal species (*G. unicolor*, *S. rugosus, K. lamarki* and *P. femoralis*) orienting to the solar polarization pattern during the day (open symbols) and two crepuscular/nocturnal species (*S. zambesianus* and *S. satyrus*) orienting to the million times dimmer celestial pattern created around the full Moon (closed symbols). The mean and standard error of the angle of deviation after a fall from the ramp (squares) or a 90° rotation (circles) are displayed on the *y*-axis for each species, ranked in order of size from small to large. A deviation of 0° indicates perfect fidelity to the original rolling direction. The large diurnal beetle *P. femoralis* had not fully compensated for the induced rotation when reaching the perimeter of the small wooden disc and was consequently excluded from this experiment. The different species do not vary in their precision of reorientation after a fall from either the ramp (ANOVA, $p = 0.14$) or after passive rotation (ANOVA, $p = 0.08$). The consistent orientation performance of the beetles under these rolling conditions shows that the use of a celestial polarization compass at night allows the same fidelity to the original direction of rolling as during the day.

5. PRECISION OF CELESTIAL ORIENTATION AT NIGHT AND DAY

The near-straight rolling paths of *S. satyrus*—as reconstructed in figure 1—leaves little room for improvement, suggesting that the precision of a compass that reads the polarization pattern from the Moon is as precise as one that reads the much brighter polarization pattern from the Sun. Dung beetles, however, do not normally roll over completely flat, level ground—like that of our experimental arena. Instead, they are constantly forced to deviate from their original course when negotiating obstacles or falling into ruts or hollows, disturbances that require frequent reorientation to the original rolling direction. These corrections potentially pose a larger challenge to an orientation system than rolling on flat, level ground. In our second set of experiments, such challenges were investigated by exposing diurnal and nocturnal ball-rolling beetles to either an induced fall from a ramp, or a passive 90° rotation on a disc. The smaller the deviation between the original and the new direction of rolling, the better the orientation along a straight path.

After falling from the ramp, the beetles continued to roll in a direction that, on average, differed between 7° and 14° from their original direction of rolling (figure 3). Although there is no significant difference between the performances of the different species (ANOVA, $p = 0.14$), it is worth noting that the crepuscular *S. zambesianus* shows the highest fidelity to its original rolling direction (deviation angle = 7°). *Scarabaeus zambesianus* is also one of the better navigators after a passive rotation of 90° but again the diurnal and the nocturnal beetles do not differ significantly in the precision of their reorientation (ANOVA, $p = 0.08$). The consistent orientation performance of different beetle species under these challenging rolling conditions clearly shows that the nocturnal celestial compass allows the same directional rolling fidelity as its diurnal counterpart. Even though trials with the nocturnal species were limited to the four bright nights following full Moon, the consistency in orientation demonstrated by *S. satyrus* throughout the lunar month (figure 1) strongly suggests that polarized light orientation in dung beetles is as precise in bright sunlight as it is on a dimly lit night with just the crescent Moon.

6. CONCLUSIONS

Here, we report that even the extremely dim celestial polarization pattern formed around a crescent Moon is sufficient to guide a ball-rolling beetle along a straight route. Moreover, the straight-line orientation on these dark nights is performed with the same precision and speed as beetles orienting under the much brighter sky lit by the Sun or full Moon. Even when challenged with major disturbances along their chosen route, such as a 90° rotation or a 5 cm fall, the compass systems of nocturnal and diurnal beetles show no difference in performance. These results strongly indicate that the light-sensitive optical compass sacrifices neither spatial nor temporal resolution when supporting the straight-line orientation in dim light.

In the laboratory, crickets have been shown to detect the direction of highly polarized light at light intensities that are even lower than that of a clear, moonless night sky [24]. Dung beetles may do the same, but at such light levels the Moon, and its pattern of polarized light, are no longer present to guide beetles and their balls along a straight path. A polarization detection system with greater sensitivity than that demonstrated here would have no biological relevance for straight-line orientation in beetles, unless they can use polarized starlight [25]. It is, however, hard to see how the combined polarized light patterns formed around thousands of stars would provide a navigator with directional guidance. On the other hand, an orientation to stars themselves could possibly explain why some of the beetles are able to orient along straight paths even when the Moon is well below the horizon (figure 1*d*). It is interesting to note that the Milky Way was clearly visible during the experimental nights without a Moon, and ran like a bright streak across the sky, providing a potential orientation cue. In earlier investigations into the orientation performance of *S. zambesianus*, the beetles rolled their balls of dung along spiralling tracks after the Moon and its pattern of polarized light had vanished from the sky [11]. However, in these experiments, the Milky Way was positioned much closer to the horizon and was not visible from the arena. It remains to be tested whether dung beetles can use the Milky Way as an orientation cue for straight-line orientation.

With a precision equal to that found in the diurnal celestial compass, the nocturnal celestial compass displays a robustness throughout the lunar month that suggests it might be widely used by animals that need to find their way at night. Nocturnal bees [26], crickets [24,27], spiders [28], tenebrionid beetles [29] and possibly also birds [30–32] are possible candidates that might benefit from the ability to orient using the dim polarization pattern formed around the ever-changing disc of the Moon.

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