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Report

Dung Beetles Use the Milky Way for Orientation

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Summary

When the moon is absent from the night sky, stars remain as celestial visual cues. Nonetheless, only birds [1, 2], seals [3], and humans [4] are known to use stars for orientation. African ball-rolling dung beetles exploit the sun, the moon, and the celestial polarization pattern to move along straight paths, away from the intense competition at the dung pile [5–9]. Even on clear moonless nights, many beetles still manage to orientate along straight paths [5]. This led us to hypothesize that dung beetles exploit the starry sky for orientation, a feat that has, to our knowledge, never been demonstrated in an insect. Here, we show that dung beetles transport their dung balls along straight paths under a starlit sky but lose this ability under overcast conditions. In a planetarium, the beetles orientate equally well when rolling under a full starlit sky as when only the Milky Way is present. The use of this bidirectional celestial cue for orientation has been proposed for vertebrates [10], spiders [11], and insects [5, 12], but never proven. This finding represents the first convincing demonstration for the use of the starry sky for orientation in insects and provides the first documented use of the Milky Way for orientation in the animal kingdom.

Results and Discussion

On a starlit night, beetles were released with their dung balls from the center of a circular arena of flattened and leveled sand, enclosed within a 1 m high, featureless circular wall. To determine how accurately dung beetles can orientate along straight paths when prevented from seeing *any* celestial cues, we obscured the dorsal visual fields of *Scarabaeus satyrus* with small cardboard caps (Figure 1C), whereas the ventral eyes were not impeded. The beetles were filmed from above, and rolling paths were reconstructed from these films and measured over a radial distance of 120 cm. The length of a perfectly straight path was thus 120 cm. Beetles prevented from seeing the sky had a mean path length of 476.7 ± 75.3 cm (n = 10) (Figure 1B). This is significantly longer than when the beetles could see the moonless night sky (207.9 ± 33.4 cm, n = 9; t test, $T_{27} = 3.3$, p = 0.003) (Figure 1A). To test for a possible effect of the cap, we also fitted beetles with a transparent plastic cap of the same shape as the cardboard version. The path lengths of beetles rolling with transparent caps (143.4 ± 11.8 cm, n = 9) were not significantly different from when they had an unimpeded view of the sky (t test, $T_{34} = 0.80$, p = 0.40). Thus, the straight-line orientation of *S. satyrus* is significantly impaired if they are prevented from seeing the starlit sky.

In the previous experiments, the beetles could possibly have used overhead landmarks (such as tree tops and the camera gantry) as an orientation cue. To remove all such visual cues, including the observer, we designed a second arena, with an elevated circular wooden floor (2 m diameter) enclosed by a circular black cloth wall (1 m in height) that obscured all terrestrial landmarks. From within this arena, the beetles could use only visual cues from the night sky to orientate. We released ball-rolling beetles from the center of the arena by placing them on a circular wooden platform (10 cm diameter) that was inserted from below into an equally sized hole in the arena floor. Beetles were then timed as they rolled from the center of the arena to its edge. The arena wall had a slightly larger diameter than the floor, leaving a 5 cm gap, large enough to allow beetles reaching the edge to fall from the floor into a collecting trough below (resulting in an audible "thump" used as a cue to stop timing rolling beetles). Since rolling speed did not change with celestial conditions [5], when beetles were wearing a cap (3.42 ± 0.33 m/s, n = 11), or even when beetles were rolling in complete darkness (3.83 ± 0.28 m/s, n = 14), (ANOVA, $F_{3/64} = 2.36$, p = 0.08), the time taken to roll from the center of the arena to its edge was therefore directly proportional to track straightness, i.e., shorter exit times indicated straighter tracks. Exit times under the natural sky are shown in Figure 2 (left panel).

Under a full moon, beetles took 21.4 ± 4.2 s (n = 10) to exit the arena. On a moonless, starry night, the straight-line orientation precision of the beetles was somewhat reduced, but not significantly so (40.1 ± 15.3 s, n = 13; t test, $T_{34} = 1.2$, p = 0.24). However, when the beetles were prevented from seeing the night sky by a cardboard cap, the time taken to reach the periphery of the arena became significantly longer (124.5 ± 30.76 s, n = 6; t test, $T_{34} = 5.4$, p < 0.0001). That a view of the clear starry sky is important for straight-line orientation is further supported by observations of beetles rolling under a completely overcast sky in the same arena. Under these conditions, when neither moonlight nor the stars were visible in the sky, the beetles took 117.4 ± 28.0 s (n = 6) to exit the arena. This is significantly longer than when the beetles rolled under the starry sky (t test, $T_{34} = 5.0$, p < 0.0001). These findings further support our hypothesis that dung beetles can use the starry sky to orientate.

The night sky is sprinkled with stars, seen from Earth as point sources of light varying in size and intensity, but the vast majority of these stars should be too dim for the tiny compound eyes of the beetle to discriminate [13]. To determine what orientation information *S. satyrus* extracts from the starry sky—despite the theoretical limitations of its visual system—we moved our wooden arena into the Johannesburg planetarium. Here, approximately 4,000 stars and the Milky Way (as a diffuse streak of light) can be projected onto the 18 m diameter domed ceiling. Experiments were performed under five different conditions: (1) complete starry sky, with more than 4,000 stars and the Milky Way, (2) Milky

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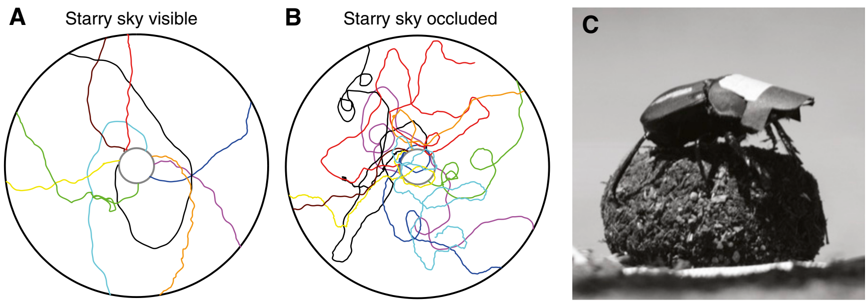

Figure 1. The Effect of Celestial Input on the Straight-Line Orientation of Dung Beetles

Paths of the dung beetle *S. satyrus* rolling outward from the center of a circular arena (3 m diameter, black circle) under an unobstructed (A) or an occluded (B) view of a moonless starry sky. So that the view of the sky could be blocked, small "caps" were attached to the thorax of the beetle (C). The tracking of the beetle began once it had rolled out from an inner, 30 cm diameter circle (gray circle).

Way only, (3), dim stars, with the brightest 18 stars excluded, (4) 18 brightest stars only, or (5) total darkness (Figure 2, right panel).

We found that beetles took the same amount of time to exit the arena, irrespective of whether they could see the full projection of the starry sky (including the Milky Way; 43.3 ± 6.9 s, n = 13) or only the Milky Way (53.3 ± 12.1 s, n = 10; t test, T_{48} = 0.60, p = 0.55). This indicates that on a moonless night, *S. satyrus* orientates using the bright band of light produced by the Milky Way. It is important to note that in the planetarium, the Milky Way is represented by a diffuse streak of light, projected on top of a high density of small point sources. To the dung beetle eye—which can at best discriminate only the brightest stars in the night sky—the greater density of dim stars in the Milky Way would be perceived as an intensity gradient similar to that presented in the planetarium. If this diffuse streak of light is removed from the full star projection, the higher density of stars in this region of the sky still defines the axis of the Milky Way. Under these conditions, beetles take somewhat longer to reach the edge of the arena (65.2 ± 12.1 s, n = 10), but this orientation is, once again, not significantly different from the performance under the full starry sky (t test, T_{48} = 0.87, p = 0.39). With only the 18 brightest stars available as an orientation cue, or in total darkness, the beetles take significantly longer to reach the edge of the arena: 81.3 ± 14.0 (n = 10; t test, T_{48} = 2.3, p = 0.03) and 120.7 ± 24.9 s (n = 6; t test, T_{48} = 3.9, p = 0.0003), respectively. This clearly shows that the beetles do not orientate to a single bright "lodestar," but rather to the band of light that represents the Milky Way.

A final test for the role of the Milky Way as an orientation cue for dung beetles would be to remove it completely from the real night sky. Fortunately, in October the Milky Way lies close to the horizon after sunset and is not visible for a beetle rolling within the walled arena. Previous experiments performed at this time of year show that the dung beetle *S. zambesianus* is unable to roll along straight tracks on moonless nights [7]. We are thus confident that when visible, dung beetles use the Milky Way for nocturnal orientation.

Since the moon is potentially visible for only half of all nights, the stars, and more importantly the Milky Way, can provide a more dependable celestial cue for orientation. This study shows that some insects can use the starry sky for orientation, even though they might not necessarily be able to discriminate the individual stars. In theory, insects could use any large and dense group of bright stars for orientation or nocturnal migration, a possibility that has been proposed but never demonstrated [5, 12, 14, 15]. The bidirectional orientation of cricket frogs on moonless nights [10] suggests that amphibians might also use the intensity gradient created by the Milky Way to orientate. Although this is the first description of an insect using the Milky Way for their orientation, this ability might turn out to be widespread in the animal kingdom.

Experimental Procedures

The orientation performance of the nocturnal dung beetle *Scarabaeus satyrus* was studied in South Africa both in the field (within the game reserve "Stonehenge"; 24°E, 26°S) and in the Johannesburg planetarium. All experiments were performed in February and March 2009.

Orientation Performance Measured from Path Length, in the Field

In this experiment, dung beetles were released with their dung balls from the center of a circular arena (3 m diameter) made of flattened and leveled sand, enclosed within a 1 m high circular wall constructed of cloth. As they rolled, beetles were filmed in infrared from above with a Sony HDR-HC5E Handycam fitted with a 0.42× wide-angle lens, suspended 3 m above the center of the arena from a wooden gantry.

So that all visual cues from the dorsal eyes of the beetles could be obscured, small cardboard "caps" were cut from thin black card. When attached to the dorsal thorax of the dung beetle with masking tape, the cap extended over the head and covered the dorsal visual field and part of the lateral visual fields of the two dorsal eyes (Figure 1). Identical caps were also constructed from overhead transparencies and taped to the dorsal thorax of the beetles. Rolling tracks were reconstructed from the films, and their straightness was determined over a radial distance of 120 cm. Distortions in the image due to the wide-angle optics were corrected for.

Orientation Performance Measured from Rolling Time, in the Field

In the second series of experiments in the field, beetles were released with their dung balls from the center of an elevated circular arena with a flat wooden floor (2 m diameter, 1 m off the ground), enclosed within a 1 m high black circular wall (2.1 m diameter) that prevented a view of any surrounding landmarks. The wall was constructed from heavy black cloth attached to a leveled, circular wall of metal mesh leaving a gap of 5 cm between the arena floor and the bottom edge of the wall. Beetles were released, on their dung balls, by placement on a circular wooden platform (diameter 10 cm) inserted from below into an equally sized circular hole at the center of the arena floor. The beetles rolled from the center of the arena, reached the periphery of the arena, and fell off the edge into a collecting trough 5 cm below the arena floor. Beetles were timed from the moment they started to roll from the center of the arena until they fell from its edge. Both of these events could be clearly distinguished by their audible profile. If a beetle took more than 5 min to reach the periphery of the arena, it was assigned a rolling time of 300 s and removed from the arena. Each beetle was run in the arena three times. Its average individual performance was calculated and used in the analyses. Experiments were performed under three different sky conditions: (1) moonlit sky, (2) clear moonless sky (with and without caps), and (3) overcast sky. 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. A different set of beetles was used for each experimental condition.

Orientation Performance Measured from Rolling Time, in the Planetarium

For further investigation of star orientation in dung beetles, the wooden arena described above was moved into the Johannesburg planetarium,

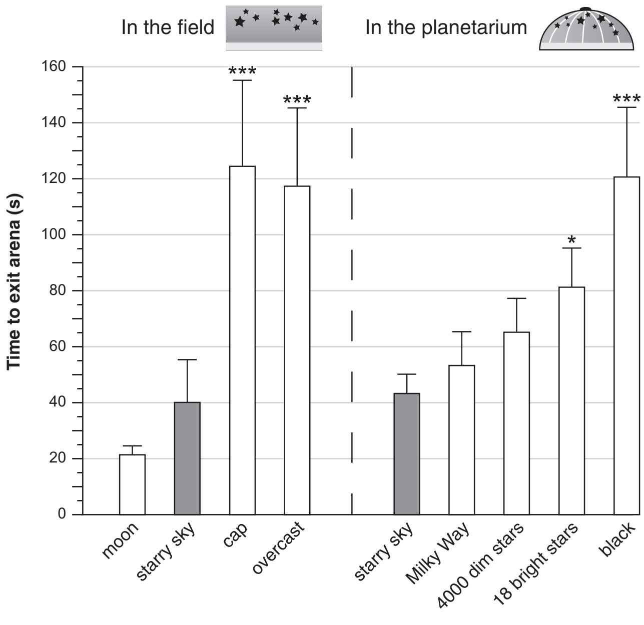

Figure 2. The Effect of Stars on the Orientation Performance of Ball-Rolling Dung Beetles

The time taken for beetles to roll from the center of a circular arena (2 m diameter) to its edge was recorded as a measure of orientation performance in the field and in a planetarium. In the field (left panel), times were recorded on a moonlit night (moon), a moonless starlit night (starry sky), a moonless starlit night with the sky occluded by a cap (cap), and an overcast night (overcast). In the planetarium, times were recorded under four ceiling projection conditions: a complete starry sky (starry sky), a diffuse streak of light that imitates the Milky Way (Milky Way), 4,000 dim stars excluding the Milky Way (4000 dim stars), 18 brightest stars excluding the Milky Way (18 bright stars), or complete darkness (black). Asterisks indicate the results of a comparison between the orientation performance under a full starry sky (gray bars) and the other experimental conditions, either in the field or in the planetarium (*$p < 0.05$, ***$p < 0.001$). Error bars indicate the SEM.

and the same general experimental procedure was followed. The Johannesburg planetarium has an 18 m diameter dome. A Zeiss MK 3 star projector projects approximately 4,000 stars and the Milky Way onto the 13 m high, domed ceiling. The Milky Way is represented by a diffuse band of light projected across the dome. The star projection was set at a local sidereal time of 7 hr 40 min, which created a night sky as seen from the field site at 9:30 p.m. on February 23, 2009. Experiments were performed at night, as described above, under four different ceiling projection conditions: (1) complete starry sky (with more than 4,000 stars and the Milky Way), (2) dim stars only (4,000 small stars) with the Milky Way and the brightest 18 stars excluded, (3) Milky Way only (the diffuse streak of light that defines the Milky Way), (4) 18 brightest stars only, and (5) total darkness. A different set of beetles was used for each experimental condition.

Generalized linear models (using the "glm" function in R, release GUI 1.26, the R Foundation for Statistical Computing) were used for assessment of the effect of caps, skylight condition, and star projection on the path length and rolling time of beetles.

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