The role of the sun in the celestial compass of dung beetles

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Recent research has focused on the different types of compass cues available to ball-rolling beetles for orientation, but little is known about the relative precision of each of these cues and how they interact. In this study, we find that the absolute orientation error of the celestial compass of the day-active dung beetle Scarabaeus lamarcki doubles from 16° at solar elevations below 60° to an error of 29° at solar elevations above 75°. As ball-rolling dung beetles rely solely on celestial compass cues for their orientation, these insects experience a large decrease in orientation precision towards the middle of the day. We also find that in the compass system of dung beetles, the solar cues and the skylight cues are used together and share the control of orientation behaviour. Finally, we demonstrate that the relative influence of the azimuthal position of the sun for straight-line orientation decreases as the sun draws closer to the horizon. In conclusion, ball-rolling dung beetles possess a dynamic celestial compass system in which the orientation precision and the relative influence of the solar compass cues change over the course of the day.

1. Introduction

Foraging dung beetles use a keen sense of smell to locate their food of preference [1]. Once a suitable pile of dung has been located, some species quickly sculpt a piece into a ball and start to roll it away along a straight path [2–6]. The end destination for the ball is, at this point, unknown [7]. The straight-line departure helps to minimize the time that the dung beetle spends near the dung pat, where foraging conspecifics congregate and frequently try to steal a ready-made ball. After some distance, the beetle finds a suitable patch of ground and buries itself together with its ball of dung. The ball is then slowly consumed in the safety of the ground [1].

Leaving a defined place might at first glance seem simple but is, as it turns out, impossible without an external directional reference—i.e. some form of compass [8]. This is true even for ensuring progress away from a dung pile. Foraging dung beetles use a number of celestial compass cues to guide them along their straight tracks: the sun, the moon, the pattern of polarized light and even the Milky Way [3,4,6,9–12].

Under thick clouds, however, the position of the sun or the moon can no longer be recognized, the stars are no longer visible and the degree of polarization in the sky decreases dramatically [13,14]. This renders the celestial compass system of the dung beetles effectively useless to the point that, on these rare, overcast days, the beetles roll their food in circles [2]. A similar problem occurs on a more regular basis: as the sun/moon draws closer to the zenith, the accuracy of the celestial compass decreases [15]. To compensate for this loss in accuracy around noon, navigating ants rely instead on the direction of the wind [15], whereas sandhoppers rather rely on their magnetic compass [16,17]. Neither of these seems to be an option for the celestially fixated beetles, which rely on a single compass system for orientation [2]. In the first part of this study, we test how the reliability of a purely celestial compass system changes over the course of the day.

In many of the diurnal dung beetle species tested so far, the primary cue for straight-line orientation appears to be the sun [12]. Consequently, if the
The aim of this experiment was to determine the precision of the celestial compass. This was tested under different conditions: (1) with a full view of the sky, (2) with the sun hidden from view by a square board (100 cm × 100 cm, placed approx. 1.5 m away from the beetle) and (3) with the sun hidden from view only during the second exit. This last condition was designed to test the effect of the removal of the sun once the beetle had set a bearing in its presence.

To test for a possible effect of heat stress on orientation performance, the temperature of the surface of the arena was recorded over an 8 cm diameter circle (non-contact infrared thermometer, CIR 350) at the centre of the board just after the beetle commenced rolling the second time with a full view of the sky (condition 1). As can be expected, the temperature of the arena varies with the elevation of the sun (high: 45.5 ± 0.7°C; medium: 41.4 ± 0.4°C; low: 38.7 ± 0.4°C; ANOVA, $F_{2,87} = 49.53, p < 0.001$), with a 10°C difference between midday and the late afternoon. At surface temperatures above 50°C, S. lamarcki climb on their dung balls more frequently and use them as a thermal refuge to cool down while rolling across hot soil [24]. In these experiments, the temperature of the arena never passed 50°C, and we did not observe any of the known behaviours related to heat stress. Furthermore, we find no significant positive association between the temperature of the arena and the orientation errors of the beetles (Spearman’s rank-order correlation, $r = 0.004$, d.f. = 87, $p = 0.97$). Thus, we consider it unlikely that the rise in temperature at higher sun elevations influenced the outcome of the experiments.

In the second set of experiments, the orientation errors at different elevations of the sun were analysed from the bearings taken before and after a 5 cm drop from the edge of an arena. A 1 m diameter, 5 cm high raised circular arena was positioned in the centre of a second, larger arena (2 m diameter). The beetles were individually placed alongside their balls at the centre of the raised arena and allowed to roll out, first to the edge of the inner

2. Material and methods

(a) Animals and field site

Individuals of the diurnal dung beetle *S. lamarcki* were collected within the game farm ‘Stonehenge’, 70 km northwest of Vryburg, North West province, South Africa (24°3'E, 26°4'S) in February and November 2012, and in February 2013. The experiments were conducted at the same location in February 2012 and 2013, and the animals were tested in the same year as they were caught.

(b) Precision of the celestial compass

The aim of this experiment was to determine the precision of the celestial compass at different solar elevations: 75–78° (high elevations), 45–60° (medium elevations) and 20–30° (low elevations). A circular wooden board (1 m diameter) with sand glued to its top surface was levelled to create a perfectly flat ball-rolling arena. Individual beetles were placed alongside their balls in the centre of the arena. Each beetle then climbed on top of its ball, performed an ‘orientation dance’ [18] and began to roll its ball towards the edge of the arena along the chosen direction. The beetle was then placed back alongside its ball in the centre of the arena and allowed to roll out a second time. The compass bearings of the two consecutive rolls were recorded as the beetle crossed the edge of the arena, and the absolute angular difference was calculated to determine the orientation error of the celestial compass system (figure 1a). An orientation error of 0° indicates the highest precision possible. The precision of the beetles’ celestial compass was tested under three conditions: (1) with a full view of the sky, (2) with the sun hidden from view by a square board (100 × 75 cm, placed approx. 1.5 m away from the beetle) and (3) with the sun hidden from view only during the second exit. This last condition was designed to test the effect of the removal of the sun once the beetle had set a bearing in its presence.

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The precision of the dung beetle celestial compass at different elevations of the sun. The orientation error of the dung beetle celestial compass was determined by letting 60 beetles roll out twice from the centre to the edge of the arena at different elevations of the sun: (a) 75–78° (high elevations), (b) 45–60° (medium elevations) and (c) 15–30° (low elevations). The angular difference between the two bearings was calculated (black arrows) and used to define the absolute orientation errors at the three different ranges of solar elevations (a–c). Numbers in text and figure show mean ± s.e.m.

![Diagram](http://rstb.royalsocietypublishing.org/)
the exact azimuth of the sun. In other words, the higher the elevation of the sun, the lower the accuracy with which its azimuthal position can be determined. High sun elevations also result in low degrees of polarization in the zenith of the sky [22]. This reduces the input to the skylight compass, while at the same time the accuracy of the solar compass is low.

A decrease in the performance of a celestial compass at high solar elevations has also been observed in the homing desert ant *Cataglyphis fortis* [15] and in beach-dwelling sandhoppers [16,19]. In nature, however, these animals continue to navigate with high precision in the middle of the day by extracting additional directional information from terrestrial landmarks, wind direction or the magnetic field [15,16,23]. These options do not seem to be available to dung beetles, which demonstrate a drastic decrease in orientation performance even when given full access to all of these cues. This finding supports the results from a recent study, which suggests that dung beetles rely exclusively on their celestial compass to orient [2]. However, the orientation precision that this single system offers, with a drastic decrease in precision around noon, will only temporarily impair the foraging efficiency of a ball-rolling beetle that can bury itself in the ground at any time. For a homing insect, the same error could instead be fatal. In the field, we rarely see *S. lamarcki* active in the middle of the day, and a similar bimodal activity pattern has been described for many other dung beetle species [25]. A break around midday not only serves to minimize the effective orientation errors of a purely sky-based compass system, but also spares the beetles from being active during some of the hottest hours of the day. In the field, high elevations of the sun always correspond with this midday drop in activity, and while we cannot exclude that the orientation precision of the ball-rolling beetles varies with the time of day we consider it very unlikely.

In conclusion, during the greater part of the day, the compass system of *S. lamarcki* offers an orientation precision of 16°. Orientation errors of less than 7° have been recorded for other diurnal dung beetle species in similar experiments [12], but whether these differences in precision can be accounted for by optical differences (i.e. divergence angle), variations in the size of the dorsal rim area used for polarized light detection, additional compass cues, small differences in the ball-rolling techniques or experimental set-ups remains to be investigated.

4. Relative importance of the sun for orientation at different elevations

(a) The effect of a mirrored sun at different sun elevations

To investigate the influence of the solar compass on straight-line orientation, we recorded the bearings of beetles rolling first with a view of the real sun and then with a view of a mirrored sun. While the sun’s apparent azimuthal position is changed by 180° in this treatment, the directional information from the skylight will remain unaffected. We expect beetles that use the sun as their primary orientation cue to change their rolling direction by 180° ± the error of the compass (grey sectors with sun symbol), while beetles orienting preferentially to the skylight cues should not change their rolling direction by more than the error of the compass (grey sectors marked with S). At high solar elevations, 77% of the dung beetles chose a direction consistent with a 180° turn (a), and at medium and low solar elevations, 52 and 37% of the population showed a similar response (b,c).

![Figure 3](http://rstb.royalsocietypublishing.org/Downloaded from http://rstb.royalsocietypublishing.org/)
from those recorded when the beetles had a full view of the sky (two-way ANOVA, $F_{1/134} = 0.56, p = 0.46$). This indicates that, even if the sun is used as the primary cue for straight-line orientation, the precision of the compass system is not significantly affected by its absence. This finding supports the results from previous studies of re-orientation in ball-rolling dung beetles in the sun and in the shade after induced falls or passive rotations [12].

While we find that the dung beetle’s compass is equally precise when orienting in the sun or in the shade, we also wanted to test how robust the dung-beetle celestial compass system is to the removal of the sun after the initial bearing has been set in its presence. In this part of the experiment, the sun was shaded only during the second exit of the beetle. In line with our previous results, we find that the mean orientation error at high elevations ($38 \pm 7.2^\circ, n = 15$) is almost twice as large as that at medium ($19.3 \pm 3.3^\circ, n = 15$) or low elevations ($17.3 \pm 2.4^\circ, n = 15$; ANOVA, $F_{2/42} = 5.67, p < 0.01$; figure 4, white/grey bars). Even though the orientation errors in this experimental condition are consistently larger compared with repeated rolls in the sun, they do not differ significantly (two-way ANOVA, $F_{1/179} = 3.24, p = 0.07$). Thus, even if the sun serves as one of the main orientation cues, the magnitude of the orientation error of the beetle is not significantly affected by a sudden removal of this cue or by its absence. Or, in more functional terms, the orientation performance of the dung beetle’s celestial compass does not vary between the shady and the sun-lit parts of its path (figure 4).

5. Conclusion

The orientation system of ball-rolling dung beetles relies exclusively on celestial information. Consequently, they experience an unavoidable loss in orientation precision in the middle of the day, when celestial cues give less precise directional information. From morning to midday (with solar elevations above $75^\circ$) the error given by the celestial compass of the beetles nearly doubles from $16^\circ$ to $29^\circ$. During these hours of the day, the beetles will either have to stay underground or forage with decreased orientation precision.

In the ball-rolling dung beetles S. lamarcki, the skylight compass and the solar compass are active together and share the control of behaviour. The solar compass dominates the skylight compass at all elevations of the sun, but the relative influence of the sun in the celestial compass system is flexible and changes with sun elevation. A recent model of navigational control suggests that a guidance system that produces a sharp activation pattern will have a stronger influence on the behavioural output than a system that produces a weaker activation pattern [23]. Our observations of the different compass cues within the dung beetle compass support this idea. In the beetles, the influence of the sun decreases at lower elevations. We suggest that this is because the polarized light in the zenith of the sky creates a stronger activation pattern the closer the sun moves to the horizon.

Within the observed population of dung beetles, we find large individual differences in the relative influence of the solar compass. At all elevations of the sun, we find instances in which the solar compass dominates over the skylight compass and vice versa. Whether there are separate ‘solar individuals’, who will repeatedly follow the direction of the sun, and ‘skylight’ individuals, who follow the direction of
polarized light or other celestial cues, remains to be investigated. In nature, of course, celestial orientation cues are never set in conflict with each other. Thus, the pooling of information from multiple cues would help to reduce errors in a directional decision, irrespective of the nature of the main orientation cue. Individual differences between the relative influence of different cues in the celestial compass system of beetles will thus not necessarily be reflected in orientation precision at the individual level.

While the sun is a local point-source that occupies only one ommatidium and can easily be obscured by clouds, the skylight cues span the entire sky. Despite these differences in reliability, S. lamarcki and many other ball-rolling dung beetles [12] preferentially follow the direction given by the sun. The homing dung beetle Pachysoma, which needs to navigate back to a tiny nest entrance among the sand dunes, seems to follow the direction given by its skylight compass instead [32]. This raises interesting questions regarding the evolution and precision of different types of compass systems. Is the celestial compass of Pachysoma more precise than that of ball-rolling beetles, and do they complement their celestial compass with landmark cues to increase their orientation precision? These questions will be the focus of our future studies.

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References


