Light pollution forces a change in dung beetle orientation behavior

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In brief
Light pollution illuminating the night sky can obscure the visual compass cues on which many animals rely. In simultaneous experiments at light-polluted and dark-sky sites, Foster et al. show that light pollution forces nocturnal dung beetles to abandon celestial cues, instead moving toward earthbound lights.

Highlights
- Visual compass cues are obscured by skyglow in light-polluted skies
- Starlight at a light-polluted site is insufficient for dung beetle orientation
- Light pollution led dung beetles to adopt a beaconing strategy
Light pollution forces a change in dung beetle orientation behavior

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SUMMARY

Increasing global light pollution1,2 threatens the night-time darkness to which most animals are adapted. Light pollution can have detrimental effects on behavior,3–5 including by disrupting the journeys of migratory birds,5,6 sand hoppers,7–9 and moths.10 This is particularly concerning, since many night-active species rely on compass information in the sky, including the moon,11,12 the skylight polarization pattern,13,14 and the stars,15 to hold their course. Even animals not directly exposed to streetlights and illuminated buildings may still experience indirect light pollution in the form of skyglow,3,4 which can extend far beyond urban areas.1,2 While some recent research used simulated light pollution to estimate how skyglow may affect orientation behavior,7–9 the consequences of authentic light pollution for celestial orientation have so far been neglected. Here, we present the results of behavioral experiments at light-polluted and dark-sky sites paired with photographic measurements of each environment. We find that light pollution obscures natural celestial cues and induces dramatic changes in dung beetle orientation behavior, forcing them to rely on bright earthbound beacons in place of their celestial compass. This change in behavior results in attraction toward artificial lights, thereby increasing inter-individual competition and reducing dispersal efficiency. For the many other species of insect, bird, and mammal that rely on the night sky for orientation and migration, these effects could dramatically hinder their vital night-time journeys.

RESULTS

Comparing orientation at light-polluted and dark-sky sites

Throughout evolutionary history, animals have escaped diurnal competitors, predators, parasites16 and the heat of the day17 by operating at night. In the modern age, human disturbances continue this trend by encouraging nocturnality in some previously diurnal species.18 To find their way, night-active animals rely on celestial compass cues, including the moon,11,12 the skylight polarization pattern,13,14 and the stars.15 But the nighttime darkness to which these animals are adapted is itself now threatened by encroaching light pollution.1,2 The effects of light projected upward into the sky, scattered or reflected downward in the form of “skyglow,” can extend far beyond urban areas1,2 and obscure celestial compass cues.

In this study, we investigated how light pollution, in combination with different celestial cues, affects orientation in the ball-rolling African dung beetle Scarabaeus satyrus Boheman. This nocturnal species performs a well-described orientation behavior19–24 typically relying on the Milky Way19,20,22 and the lunar polarization pattern15,21,22 to hold its course. We recorded orientation behavior at a light-polluted urban site and a dark-sky rural site under moonlit, starlit, and overcast skies. Available visual information in each scene was recorded using a calibrated camera system25 and processed to quantify potential compass cues.

Light pollution obscures natural celestial cues

At our urban site in central Johannesburg, widespread light pollution dramatically increased sky brightness. On the same overcast night, the sky was 10,000 times brighter than at our dark-sky site (Figures 1C and 1G). On clear nights, indirect light pollution obscured and degraded natural celestial-compass cues. This skyglow obscured the Milky Way, leaving only bright stars visible (Figures 1A and 1B). As reported in previous studies,24,26 on the moonlit night, skyglow reduced the degree of polarization of the lunar skylight polarization pattern, from 60%–70% (the typical range around the full moon24) to just 19% (Figure S1; more typical for a crescent moon24). Direct light pollution from nearby buildings was also present under all celestial conditions, either projected onto the observer or reflected from other buildings. As a result, the contrast of terrestrial cues at low elevations was amplified by artificial lights, while dim celestial compass cues at high elevations were replaced by skyglow.
To further quantify visual compass information, we calculated rotational root-mean-squared (RMS) image difference functions, comparing the initial and rotated views an animal would experience as it deviates from its intended heading (Figure S2). Dung beetles similarly record a "snapshot" of visual cues during a rotational "dance" performed before rolling their dung ball, which they are thought to compare with current visual input to steer straight. Image difference was calculated across the 360° range of possible view rotations to produce RMS image difference functions for each scene. These functions were calculated for the camera’s complete (hemispherical) field of view, and separately above (celestial cues: stars, lunar skylight, and skyglow) and below (terrestrial cues: trees, buildings, and security lights) 55° elevation. The large near-spherical bipartite eyes of this species likely provide an almost uninterrupted field of view from horizon to zenith during the dance, so both sets of cues could potentially be included in its snapshot. Finally, a "snapshot index" (Figures 1D and 1H) was derived from this function, scaled so that unstructured scenes produce an index of 1. Hence, values close to 1 indicate low reliability, and larger indices signify reliable compass cues.

Although skyglow obscured the Milky Way and lunar skylight at the light-polluted site, we found that snapshot indices were, in fact, significantly greater for light-polluted skies (Mann-Whitney Wilcoxon test, W = 0, p = 0.050). On the moonlit night, light pollution raised the snapshot index for the sky (above 55° elevation) significantly (Figure 1). For degree of polarization in (A), see Figure S1. For original root-mean-squared image difference curves, see Figure S2 (A–F).
Light pollution alters orientation behavior

We next compared orientation precision at the light-polluted and dark-sky sites, quantified as the mean vector lengths calculated from each beetle’s ten consecutive exit bearings. Beetles were generally better oriented at our light-polluted site (Figure 2; Pren- tice test, $\chi^2 = 8.249$, d.f. = 1, $p = 0.002$) with a median mean vector length of 0.953 (approaching 1, perfect orientation). It appears that, despite the loss of natural celestial cues to skylight, light pollution did not hinder orientation in these animals.

In particular, on an overcast night when clouds obscured celestial cues at both sites (Figures 1C and 1G), beetles tested simultaneously were better oriented at the light-polluted site (light polluted versus dark sky: $W = 89$, $p = 0.007$). On the starlit night, orientation precision was also higher at the light-polluted site, though not significantly so ($W = 136$, $p = 0.075$). On the moonlit night, there was no apparent difference in orientation precision between the two sites ($W = 34$, $p = 0.173$), despite the lower degree of polarization skylight observed at the light-polluted site. Consequently, the cloud-induced drop in orientation precision at the dark-sky site (overcast versus moonlit: $W = 79$, $p = 0.034$; overcast versus starlit: $W = 156$, $p = 0.022$)

was not observed at the light-polluted site (Figure 2; overcast versus moonlit: $W = 63$, $p = 0.206$; overcast versus starlit: $W = 78$, $p = 0.836$). Such persistently high performance when celestial cues were obscured by clouds suggests that light-polluted skies drove beetles to rely on different cues.

To better describe this light-pollution-induced change in behavior, we examined the headings followed by each beetle. We observed heading biases toward brightly lit buildings (Figures 1B and 1C) on both starlit and overcast nights, suggesting a reliance on terrestrial cues that were unaffected by cloud cover. This contrasted with the heading biases at the dark-sky site (Figures 1F and 1G), where they coincided with celestial cues on starlit nights (east toward the rising Milky Way; Moore’s Rayleigh test, $\alpha = 74^\circ$, $R^* = 1.587$, $p < 0.001$), but with terrestrial cues on the overcast night (aligned with the tallest tree to the south; significant clustering, Rao’s spacing test, $U = 185.6$, $p < 0.05$).

These differences in individual heading biases between light-polluted and dark-sky sites indicate a population-level change in orientation strategy. Typically, individual beetles have an equal probability of choosing any heading in the full 360° range available to them, but may show a weak collective bias aligned with the brightest part of the Milky Way. We observed this bias at the dark-sky site (Figure 1F, Milky Way to the southeast), but not at the light-polluted site (Figure 1B), where frequent biases toward buildings suggest reliance on terrestrial cues. On the moonlit night, beetles at both sites exhibited the same collective bias (Mardia-Watson-Wheeler test, $W = 1.575$, d.f. = 2, $p = 0.455$) toward the moon (Figures 1A and 1E). Intriguingly, the rising moon occupied the same elevation range as the bright buildings guiding beetles under other conditions (Figures 1B and 1C), so a common mechanism producing biases aligned with high-contrast objects at low elevations (moon: Figures 1A and 1E; Milky Way: Figure 1F; trees: Figure 1G; artificial lights: Figures 1B and 1C) would best explain the heading biases observed.

Artificial lights induce beaconing

While these results imply a link between the amplification of terrestrial-cue contrast by direct light pollution and high orientation performance, they do not rule out a role for indirect light pollution also present during these experiments. To distinguish between the effects of direct light pollution (glare and nearby reflected light from terrestrial sources) and indirect light pollution (scattered and distant light from skyglow) on orientation behavior, we performed a further set of experiments under clear skies, in which either direct or indirect light pollution dominated the scene.

We began with a single floodlight at a dark-sky site, recording two sets of headings for each individual beetle: one set with the floodlight switched on and one set with it switched off. When the floodlight was switched on, reflected light from the surrounding trees increased by a factor of 10,000–100,000, to levels otherwise observed on buildings at the light-polluted site (Figure 3A, red and pink image regions; 1010–1011 photons cm$^{-2}$ s$^{-1}$ sr$^{-1}$ nm$^{-1}$). This resulted in a substantial increase in the snapshot index for terrestrial cues (Figure 3C). With the floodlight switched on, the same individual beetles became significantly better oriented (Wilcoxon signed-rank test, $V = 45$, $p = 0.042$). Heading
Biases also changed markedly, concentrating toward the floodlight (south-southwest; Moore’s Rayleigh test, $\alpha = 210^\circ$, $R^* = 1.660$, $p < 0.001$; Figure 3A, radial lines) rather than dispersing more widely, as they did when the floodlight was turned off (Figure S3A).

We continued by exposing beetles to direct light pollution from multiple artificial lights: the veranda lights at our dark-sky site (Figure 3B, yellow regions) or large security lights at our light-polluted site (Figure 3C, white regions). Like the floodlight, the veranda lights also lit nearby trees, raising their radiance 10–100 times. This lowered their contrast with the starlit sky, in turn reducing the scene’s snapshot indices (Figure 3D). Each of the large security lights was as bright as the floodlight, but much wider, even blocking part of the sky and minimizing snapshot indices at high elevations (Figures 3C and 3D). Beetles exposed to multiple lights were nonetheless well oriented (median mean vector length = 0.863) and evenly dispersed (Rao’s spacing test, $p > 0.10$) at both sites. It hence appears that multiple lights eliminated the heading bias concentration observed with a single light source, inducing dispersal like that observed previously on the light-polluted starlit night (Figure 1B), perhaps because different individuals oriented toward different artificial lights.

Among ball-rolling dung beetles, individual headings spread across a 360° range allow each individual to avoid encounters with others while rapidly exiting the initial high-competition region.31 Such dispersal strategies have also been observed in other insects32 and may be a common approach to competition avoidance. Nonetheless, both dung beetles22,33 and Drosophila34 exhibit biases toward high-contrast cues under laboratory conditions.
was necessary for orientation. Dorsal eyes covered, confirmed that an unobstructed view of the starlit sky under dark, overcast skies, and under light-polluted conditions with beetles’ significantly reduced orientation precision. Further walled-arena experiments when darkened walls blocked low elevations from view, indirect light pollution and security lights at a light-polluted site) also elicited well-oriented behavior. Individuals were significantly better oriented than when it was switched off, leaving only starlight. Multiple artificial lights (veranda lights beneath a dark sky and security lights at a light-polluted site) also elicited well-oriented behavior. When darkened walls blocked low elevations from view, indirect light pollution significantly reduced orientation precision. Further walled-arena experiments under dark, overcast skies, and under light-polluted conditions with beetles’ dorsal eyes covered, confirmed that an unobstructed view of the starlit sky was necessary for orientation.

**Skyglow forces reliance on terrestrial cues**
Finally, to isolate the effects of indirect light pollution, further experiments were performed in an arena surrounded by darkened walls. At the arena’s center, these walls blocked the surroundings from view below 60° of elevation, where direct light pollution would have otherwise been visible. This reduced spectral radiance at low elevations to $10^4$–$10^6$ photons cm$^{-2}$ s$^{-1}$ sr$^{-1}$ nm$^{-1}$ (Figure S4B), minimizing the influence of direct light pollution on orientation. At the light-polluted site, the observable sky region (Figure 3E, white circle) was 10–100 times brighter than at the dark-sky site (Figure 3F, white circle), with a larger snapshot index (Figure 3H), indicating increased navigational reliability. Despite this greater predicted reliability of the light-polluted starlit skies, beetles viewing them were worse oriented than those viewing an unpolluted starlit sky (W = 94, p = 0.038), performing similarly to beetles with their dorsal eyes completely covered tested at the same site (Figure 4). This failure to orient when celestial cues were obscured by skyglow confirms that skyglow itself did not act as a compass cue, and that beetles exposed to both direct and indirect light pollution in earlier experiments relied on terrestrial cues.

**DISCUSSION**
From this first simultaneous comparison of light pollution’s effects on both the visual environment and orientation performance of a nocturnal insect, we find that light pollution interfered with orientation behavior under most conditions. These effects may extend to the plethora of other night-active species, including arthropods, seals, and migratory birds, that rely on stars, the moon, and patterns of polarized skylight to orient. The sky measurements presented here (Figures 1 and 3) and in previous studies show how artificial skyglow can obscure all but the brightest stars and reduce the polarization of lunar skylight, decreasing the availability of natural celestial compass cues.

**Loss of celestial cues**
At our light-polluted site, we observed disorientation in beetles forced to rely on celestial cues (Figure 3E), suggesting that the skyglow dominating the celestial radiance distribution did not, itself, provide sufficient directional information. Although camera measurements revealed brightness gradients of the type used by this species at lower intensities, it appears that the beetles were not able to utilize these cues at this far-greater light intensity. Beetles with an unobstructed view of brightly lit buildings under similar conditions were well oriented (Figure 1B), indicating that they were able to compensate for the loss of celestial cues by relying on terrestrial ones. This represents a noteworthy change in strategy, since ball-rolling dung beetles typically rely more on celestial cues than terrestrial ones, failing to respond to changes in the landmark panorama, even when path integrating. In this study, the relatively poor performance observed under overcast conditions at the dark sky site as compared to the light-polluted site (Figure 2) suggests that S. satyrus are poorly adapted to exploit terrestrial cues for orientation, only doing so effectively when their contrast is amplified by direct light pollution.

Beetle behavior on the moonlit night was the one exception to this trend, appearing virtually unaltered by light pollution (Figures 1A and 1E). The most likely explanation may be that the presence of the moon, a natural, high-contrast low-elevation cue, precludes reliance on artificial lights. It should also be noted that, despite the decrease due to skyglow (Figure S1), at 19%, the degree of polarization of lunar skylight at the light-polluted site remained above the 11% threshold reported for this species. As a consequence, these beetles may have been able to utilize compass information from skylight polarization, in combination with the moon’s position, to achieve natural orientation behavior. Less-sensitive species may therefore be more strongly affected by the degradation of polarized skylight. Future work
focusing on different combinations of lunar elevation, phase, and skylight quality may help clarify how light pollution affects orientation behavior on moonlit nights.

Since individuals in our experiments under a dark starlit sky were well oriented (Figure 1F), the animals most threatened by the loss of natural celestial cues may be those that occupy the hinterland between city and true wilderness. Skyglow remains visible far beyond city boundaries, so in this region, animals would view light-polluted skies in which natural celestial cues are obscured alongside low-contrast natural terrestrial cues that are a poor substitute for celestial compass information. Reduced orientation accuracy results in more tortuous paths, which inflate the energetic cost of traveling a given straight-line distance.

Night-active species that rely more on terrestrial cues may also suffer reduced orientation performance when natural celestial cues are obscured. Nocturnal bull ants utilize compass information from both terrestrial and celestial cues under natural conditions, likely learning available terrestrial cues over repeated journeys and integrating compass information from multiple sources to achieve optimum orientation performance. This species alters the relative weighting of cues in a context-dependent manner, weighting celestial cues more strongly when returning to their nest. As a consequence, the loss of celestial cues could result in less-efficient foraging and less accurate homing, even when other directional cues are available. This effect may lead other species to change strategy in order to maintain orientation precision when celestial cues are lost, perhaps also by orienting toward terrestrial beacons.

**Reliance on terrestrial beacons**

In addition to the observed biases toward buildings at our light-polluted site, our experiment with a floodlight at a dark-sky site suggests that beetles exposed to direct light pollution orient by traveling toward artificial lights (Figure 3A), using them as beacons. While this strategy limits an animal to movement in the beacon’s direction, this also leads different individuals to disperse in the same direction, limiting their opportunities to avoid one another. For ball-rolling dung beetles, the spread of individual biases has direct fitness consequences, since competitive encounters, in which their dung ball may be hijacked, are energetically costly. The restriction of headings to a small distance dominates the radiance distribution of an unpolluted moonlit sky (Figure 1E). If flight-to-light behavior is indeed driven by a beaconing strategy similar to that observed in this study, then it might be averted through subtle changes to outdoor lighting that reduce either contrast or impact on ambient illumination.

Our results demonstrate that the effects of light pollution on orientation behavior vary in a context-dependent manner. These contrasting and somewhat counterintuitive effects of indirect and direct light pollution on compass orientation highlight the importance of mitigating both forms and the potential for unanticipated effects of encroaching light pollution on nocturnal animals. We propose that future efforts to mitigate the impact of light pollution should focus not only on preserving night-time darkness from a human perspective, but also on minimizing disturbance to the compass cues on which nocturnal species rely.

**STAR METHODS**

Detailed methods are provided in the online version of this paper and include the following:

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Author contributions

All authors conceptualized the study and edited the manuscript. J.J.F. drafted the manuscript and analyzed the behavioral data. J.S. and J.J.F. analyzed the sky-image data. J.J.F., C.T., L.K., E.B., M.J.B., and M.D. performed the behavioral experiments.

Declaration of interests

The authors declare no competing interests.

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STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Deposited data      |        |            |
| Exit headings from orientation experiments | This study | Github repository https://github.com/JJFosterLab/light-pollution |
| Image data from all experiments | This study | Figshare https://doi.org/10.6084/m9.figshare.14755299. |

| Experimental models: Organisms/strains |
|----------------------------------------|
| Nocturnal African dung beetles (Scarabaeus satyrus) | Wild-caught | NCBI Taxonomy ID: 205316 |

| Software and algorithms |
|-------------------------|
| MATLAB | Mathworks, Inc. | version R2020a |
| R | R Foundation for Statistical Computing | version 4.0.3 |

| Other |
|-------|
| Digital single-lens reflex camera | Nikon Corp., Japan | D810 |
| Fisheye lens | Sigma Corp., Japan | Sigma 8 mm F3.5 EX DG |
| IR-sensitive video camera | Sony, Japan | HDR-CX730 |
| Sky Quality Meter | Unihedron, Canada | SQM-L |

RESOURCE AVAILABILITY

Lead contact
Further information and requests for methods and materials may be directed to and will be fulfilled by the lead contact, James Foster (jjfoster86@gmail.com).

Materials availability
This study did not generate new unique reagents.

Data and code availability
All analysis and behavioral data are available at https://github.com/JJFosterLab/light-pollution. All image data is available on Figshare at https://doi.org/10.6084/m9.figshare.14755299.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethical statement
All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Animal care was in accordance with national/institutional guidelines (EU Directive 2010/63/EU; South African National Standard for The Care and Use of Animals for Scientific Purposes).

Animal collection and husbandry
Nocturnal dung beetles of the species Scarabaeus satyrus Boheman were collected in November of 2017, 2018 and 2019, and February 2020 at the game farm “Stonehenge,” in North-West Province, South Africa; 70 km North-West of Vryburg. All beetles were kept in sand filled boxes, in which they were transported to the test sites, and fed ad libitum with dung from cows and gnus.

METHOD DETAILS

Orientation precision experiments
The orientation precision of beetles rolling dung balls was recorded under a range of sky conditions in November of 2017, 2018, 2019 and February 2020. Experiments were conducted at three sites in South Africa: two rural sites 50 km West of Bela-Bela (Waterberg district, Limpopo: Thornwood lodge, 24°46’08’’S, 28°00’52’’E; Bergsig Eco Estate, 24°43’46’’S, 27°57’08’’E) that lacked substantial...
light pollution (sky quality 21.16–21.86 mag arcsec⁻²), and an urban site 200 km to the South, just 1 km outside of Johannesburg’s central business district (University of the Witwatersrand: 26°11′28″S, 28°01′57″E), where much of the sky was obscured by skyglow (sky quality 17.77 mag arcsec⁻²).

**Experimental procedure**

Ten beetles were tested under each condition. Each beetle was allowed to roll its ball to the edge of a 1 m diameter arena. The exit bearing for each trial was noted and the beetle’s track was recorded by an IR-sensitive video camera (HDR-CX730: Sony, Tokyo, Japan), on a tripod 1.5 m above ground level at the arena’s southernmost edge. Prior to experiments, beetles were marked with a strip of high-gain reflective tape (ScotchliteTM 7610: 3M Company, Maplewood, USA) to aid in tracking of the beetle’s rolling path.

At the beginning and end of each experiment spectral radiance images of the whole sky were recorded using a digital camera (D810: Nikon Corp., Japan) equipped with a fisheye lens (Sigma 8 mm F3.5 EX DG: Sigma Corp., Japan). An exposure bracket was used to ensure that these images covered a broad dynamic range. This camera system was calibrated to provide absolute spectral radiance estimates for each pixel averaged across the camera’s three spectral channels. Sky quality meter measurements were also recorded for reference to the broader light pollution literature.

**Comparing light-polluted and dark-sky sites**

In a set of experiments comparing light-polluted urban skies and dark rural ones, beetles viewed skies with a range of celestial cues: a clear moonlit sky (Moonlit), a clear starlit sky (Starlit), and an overcast starlit sky (Overcast). Where possible, experiments were conducted under similar conditions at both sites, on the same night (Moonlit, Overcast), or within 24 h of one another (Starlit). Moonlit sky experiments were carried out in parallel in Limpopo and Johannesburg between 20:30 and 21:15 on the night of 22/11/2018, when the sky was clear at both sites, permitting a view of a waxing gibbous moon (98% illuminated).

The starlit sky experiments were carried out on nights when the moon was more than 18° below the horizon, and lunar daylight was not present, in parallel between 01:20 and 03:00 on 21/11/2017, and sequentially between 20:40 and 21:45 on 27/11/2018 in Limpopo and between 20:30 and 21:10 in Johannesburg the following night. Overcast sky experiments were carried out on nights when the moon was more than 18° below the horizon, and cloud cover was above 7/8, simultaneously in Limpopo and Johannesburg between 21:15 and 23:00 on the night of 21/11/2017.

**Effects of direct and indirect light pollution**

A further set of experiments compared the effects of direct and indirect light pollution. Direct light pollution was provided at the two rural sites by a single floodlight or a set of smaller lights on the verandas of two buildings, and at the Oppenheimer Life Sciences entrance to the University of the Witwatersrand’s Braamfontein Campus in Johannesburg by a set of large security lights. In the indirect light pollution tests, terrestrial cues were shielded from view by walls, constructed from steel wire lined with theatrical blackout curtain. These restricted a beetle’s field of view to elevations above 60° from the arena’s center (Figure S4), leaving only the light-polluted sky. A parasol was used to prevent the brightest electric lights from producing reflections on the surfaces of the walls. To test how well the beetles were guided by ventral optic flow and idiothetic cues under these conditions, a further set of animals was tested at the urban site with an opaque putty (White Tack, UHU GmbH; Buhl, Germany) covering each beetle’s dorsal eyes (Eyes Covered) and blocking the animal’s entire field of view above the horizon. To compare the effects of sky quality, walled-arena experiments were also carried out at a rural dark-sky site under clear starlit and completely overcast skies. In all walled-arena experiments, the beetle failed to exit the arena within 60 s (50% longer than the mean time to exit an arena double the size under a dark starlit sky) the beetle’s bearing relative to the arena’s center was recorded at its current position.

**QUANTIFICATION AND STATISTICAL ANALYSIS**

**Non-parametric statistical analysis**

To compare orientation precision across sky conditions, mean vector lengths were calculated by averaging the unit vectors derived from each exit heading for the 10 trials performed by each beetle in each experiment. This measure indicates orientation precision on a scale of 0–1, where a mean vector of 0 would result from headings spaced evenly around the circle (perfectly disoriented) and a mean vector of 1 would result when all 10 exits were at the same bearing (perfectly oriented). Kruskal-Wallis tests compared mean vector length between different conditions in each experiment. A Prentice test was used to determine the overall effect of light pollution on orientation precision between light-polluted and dark-sky sites, treating sky condition (Moonlit, Starlit or Overcast) as a grouping factor. Mann-Whitney Wilcoxon rank sum post hoc tests were then used to check for specific differences between conditions. Correction for multiple testing was performed using the Benjamini-Hochberg method.

**Circular statistics**

To compare the distributions of heading biases in each experiment, the mean heading for each individual was calculated. Rao’s spacing test was used to test for irregular spacing, and hence clustering, of these headings, indicating subpopulations with similar heading biases. Where these were evident, Moore’s modified Rayleigh test was used to test for a collective bias across the
population of different individuals, accounting for both the mean heading and the mean vector length for each animal. Where heading bias patterns appeared similar between two conditions, the Mardia-Watson-Wheeler test 53 was used to compare the distributions of heading biases non-parametrically.

Sky measurements
An exposure bracket of three images was recorded directly prior to and following each experiment, using a digital camera fitted with a fisheye lens. Exposure times were chosen to best match the prevailing sky conditions. This camera had been calibrated in order to correct for exposure time, ISO settings, aperture size and effects of vignetting23,25 to provide estimates of absolute spectral radiance for each pixel. Images were recorded with the camera facing directly upward, toward the zenith, from the northernmost edge of the arena at 1.8 m above ground level (excluding local vegetation and the experimenters from the camera’s field of view). In rural areas, where space permitted, the camera and its tripod were removed to 4.5 m from the arena during the experiment, to avoid blocking the beetle’s view of the sky. General sky brightness was also recorded using a Sky Quality Meter (SQM-L: Unihedron, Grimsby ON, Canada) in units of magnitudes per square arcsecond, for comparison with the standard natural brightness2,54 of 22 mag arcsec–2. On starlit nights, SQM-L readings at dark-sky sites ranged between 21.16 and 21.86 mag arcsec–2, while at the light-polluted site they were stable around 17.77 mag arcsec–2.

Image analysis
Images were corrected to estimates of absolute spectral radiance per pixel, as averaged across the >400–700 nm sensitivity range of the camera. These images were filtered with 4° full-width at half maximum Gaussian filters to approximate the level of spatial detail available to S. satyrus.23 As an estimate of the orientation value of the scene imaged, we calculated the rotational image difference function27 with the entire scene (1°–90° elevation, excluding the image edge to avoiding imperfect interpolation), to 55° of elevation (height of the tallest building in any image) and above 55° elevation (only sky in all images). Image rotation was performed in steps of 0.1°, across the range from –180° to 180°, using bicubic interpolation. Since images were in units of photons cm–2 s–1 sr–1 nm–1, these units were also used to calculate image differences. Following previous work, these pixel-wise image differences were summarized as root-mean-squared (RMS) image difference27 at each angle. Assuming that the beetles record some form of snapshot of the available compass cues before starting to roll their dung ball,29 this function could indicate the extent of mismatch between the intensity cues recorded in the snapshot and the current view when the beetle is misaligned by a specific angle. A spline fitted to the values calculated between –180° and 180° permitted further estimation of RMS image difference at any arbitrary rotation angle, in the form of an RMS image difference function. Snapshot indices were calculated from the function’s minimum width at half maximum (MWHM) projected either side of 0° (perfect alignment). This was rescaled to an inverse proportion of one half-rotation,

\[
\text{snapshot index} = \frac{180°}{\text{MWHM}}
\]

generating a measure with a magnitude proportional to the reliability of compass information.