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Review

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How animals follow the stars

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Throughout history, the stars have provided humans with ever more information about our world, enabling increasingly accurate systems of navigation in addition to fuelling some of the greatest scientific controversies. What information animals have evolved to extract from a starry sky and how they do so, is a topic of study that combines the practical and theoretical challenges faced by both astronomers and field biologists. While a number of animal species have been demonstrated to use the stars as a source of directional information, the strategies that these animals use to convert this complex and variable pattern of dim-light points into a reliable 'stellar orientation' cue have been more difficult to ascertain. In this review, we assess the stars as a visual stimulus that conveys directional information, and compare the bodies of evidence available for the different stellar orientation strategies proposed to date. In this context, we also introduce new technologies that may aid in the study of stellar orientation, and suggest how field experiments may be used to characterize the mechanisms underlying stellar orientation.

1. Starlight as an orientation cue

At the beginning of astronomical night, as the last solar skylight drops below the horizon, the moon, lunar skylight and stars become the brightest celestial references. After the moon has set, night-active animals are soon left with only the stars. This array of bright points gradually moves across the sky as a function of latitude and date, following a schedule that is similar to that of the solar day. The movements of the planets vary more, so their influence is not usually considered in studies of night-sky orientation (although variability of position does not prevent the moon from being used to guide dispersal behaviour [1,2]). For the purposes of this review, we will mainly address the stars themselves as orientation references, but the quality and clarity of stellar orientation cues in nature are undoubtedly a combination of light from all visible celestial bodies, zodiacal light, *Gegenschein* and atmospheric effects (for Definitions of Terms, see the electronic supplementary material). As a result, the combined informational content of the night sky can be easier to measure than to predict under natural circumstances (see the Sky imaging section).

We may well question why animals should perform directed behaviours during the darkest period of the night. Generally, there is some evidence that night-active species benefit from reduced competition, and fewer predators and parasites [3]. For activities that require significant movement, such as foraging and migration, the drop in temperature at night may also help avoid heat exhaustion in warmer climates. In some species, activity under starlight could result from the synchronization of directed behaviour with the brighter, more robust orientation cues at dusk. For example, many night-migrating birds take-off with the setting sun [4], to which they calibrate their magnetic compass [5], and can then use their star compass to maintain this established heading. A similar strategy may be adopted by nocturnal central-place foragers that leave their nest at sunset, such as sweat bees, ground spiders and ants [3,6,7].

2. Seeing stars

On a moonless starry night, the scarcity of light becomes a limiting factor for celestial orientation. Because of this, the scale of stellar orientation cues determines both their detectability and robustness. Single stars viewed from the Earth subtend less than 0.1 arcsec (or 0.000025°), which is much smaller than the spatial sampling period of the retinal mosaic of any animal. Individual stars are, therefore, detected as point sources. It follows that groups of stars can be detected as a number of individual point sources, or, at lower spatial resolution, as a luminous object of a distinct brightness and shape. Broad-scale patterns of brightness can also be detected as luminous objects, but might instead be interpreted as a general feature of the sky as a whole, such as a gradient of intensity across it.

At typical starlight illumination levels, photon shot noise and receptor noise begin to obscure reliable photoreceptor signals. For tasks such as motion detection and object segmentation, spatial pooling can improve absolute sensitivity [8]. Such processes may also enhance the detection of broad-scale patterns of brightness and smaller groupings of stars, where they are detected as extended luminous objects and receptive field sizes remain smaller than the object itself. For detection of stars as point sources, spatial pooling cannot increase the signal, because all of the light from the point necessarily falls within a receptive field, whatever its size. The discrimination of individual stars in the night sky should thus be limited to animal species with sufficient visual resolution to discriminate the background between (bright) stars under low-light conditions. In particular, animals with camera eyes may be best suited to identifying individual stars, given the resolving power they afford, while those with compound eyes face a greater trade-off between photon catch and resolution, and are therefore more likely to orient using luminous patterns or intensity gradients.

3. Strategies for stellar orientation

In order to describe the different types of orientation cue that animals may extract from the starry sky, it is worth considering how humans have used the stars to navigate over the ages. Just as the rising and setting sun provides a reliable east–west axis wherever it can be sighted, so too do the stars near the celestial equator, and the most basic form of human star navigation may involve a combination of estimating the axis between the rising and setting points of stars such as *Altair* (declination +08°52′06″) and identifying stars near the centre of celestial rotation, such as *Polaris* (+89°15′50.8″). This necessitates learning to identify individual stars by their configuration. A combination of stars rising and setting at different points north and south of the celestial equator is thought to have made up the 'sidereal compass' of Arab sailors in the Indian Ocean, described as early as the tenth century [9] and used up to the present day in some islands of the South Pacific [10].

The position of a single star, sufficiently bright and distinguishable via its position within a specific asterism, can be used to set a vessel's bearing at a given point in time. Such a star is known as a 'lodestar'. The peoples of the South Pacific use 'star paths' ('*kaveinga*' in Anutan), consisting of a set of stars that fall approximately along the same line of declination (figure 1), to set bearings throughout the night [10], substituting stars at higher or lower elevations each time the chosen star sets or rises too high for its azimuth to be estimated reliably.

Star patterns can also be used to obtain a 'stellar map' that indicates the observer's location on the globe. Experienced

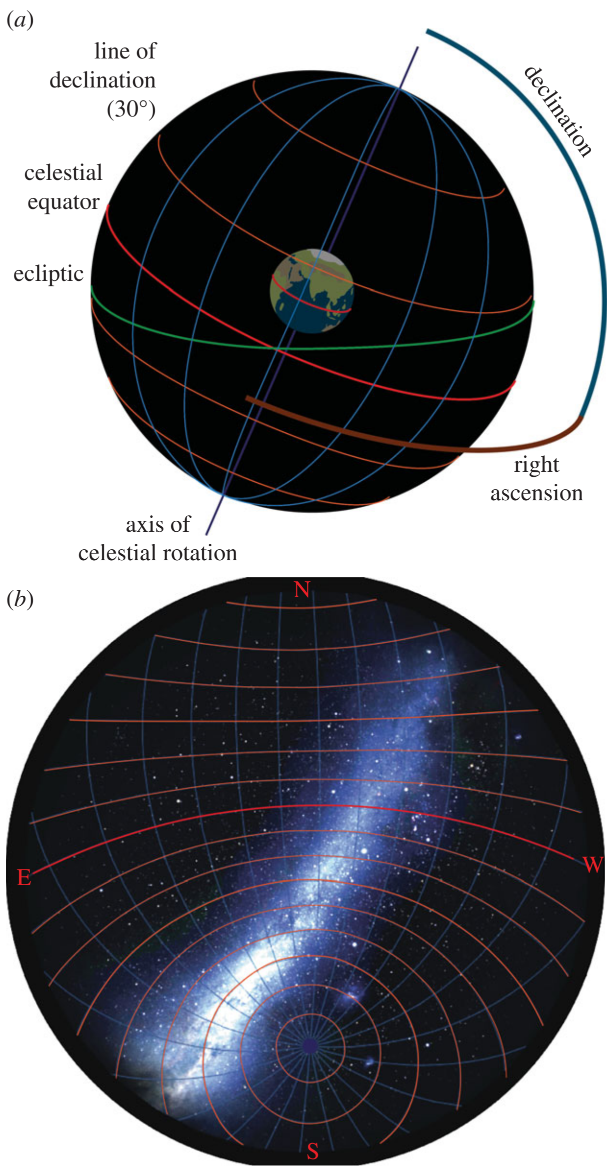

Figure 1. The celestial sphere. (*a*) To an earthbound observer, the stars appear to move on a sphere that completes one revolution westwards for each sidereal day. The position of a star on this sphere is given by its right ascension and declination (e.g. *Polaris*: $02^h31^m49.09^s$, +89°15′50.8″). Stars on the same line of declination rise and set at the same angle to the east–west axis, and those on the celestial equator rise at geographical east and set at geographical west. The ecliptic gives the position of the solar system's central plane, near which zodiacal light and the visible planets can be observed. (*b*) The starry sky, simulated in Stellarium 0.13.3 (Stellarium Developers, www.stellarium.org) for the planetarium conditions used by Dacke and co-workers [11], showing the celestial equator (red), lines of declination (orange) and convergence of the celestial equatorial coordinate grid on the southern centre of celestial rotation (blue). (Online version in colour.)

sailors can determine their latitude by observing which line of declination is closest to the zenith [10] or measuring the distance between the centre of celestial rotation and the horizon [9]. Assessing longitude from celestial cues is more challenging because the Earth's daily rotation changes the stars' positions in the same way as a change in longitude. Without a precise estimate of universal time (which allows the observer to compensate for the Earth's rotation), longitude can only be measured from the exact positions of the sun or moon relative to the stars. In the eighteenth century, before the development of marine chronometers, improved accuracy in astronomical predictions made it viable to use the angle between the moon and *Regulus*, or another bright star, to determine longitude (after [12]).

(a) Centre of celestial rotation: night-migrating birds

In birds, the best evidence suggests an orientation strategy based on identifying the starry sky's centre of rotation. Orientation using this reference does not require any time compensation because the orbital poles appear at the same azimuth at any given hour of any given night. The first species found to use this orientation reference was the indigo bunting, *Passerina cyanea* [13,14]. During their autumn migration, wild-caught birds were presented with an autumn starry sky in the Longway Planetarium (Flint, Michigan) while constrained within funnels of blotting paper that monitored the direction of their hops when they attempted to take-off. Their hops were consistently oriented southwards, as when presented with a real starry sky [13]. This behaviour persisted with the removal of successive constellations, and *P. cyanea* was only disoriented when all of the constellations within 35° of *Polaris* were blocked from view [14]. Birds attempting to migrate south in autumn, and those manipulated physiologically for early spring migration northwards, displayed season-appropriate orientation when presented with the same planetarium sky [15]. Various attempts to demonstrate stellar orientation in other migratory bird species [16–19] indicate that several other night-migrating species also use the centre of celestial rotation as their stellar orientation reference.

The interplay of other compass cues, such as magnetic cues and polarized light, with the star compass used by migratory birds is a field of active research [5,20] and their weighting and hierarchy in selecting flight direction is far from settled (reviewed in [5,18,21]). Several bird species can orient using the stars in the absence of magnetic cues [18,19,22,23], ignore conflicting magnetic cues when observing a clear starry sky [5,24,25] and some may even recalibrate their magnetic compass to agree with conflicting stellar cues [26]. Both planetarium [27] and laboratory experiments [16,17,20] have shown that the centre of rotation must be learned, and Emlen's initial study even suggested that *P. cyanea* can learn to identify *Betelgeuse*, rather than *Polaris*, as the centre of rotation [14] in a planetarium modified to rotate around that point.

Since the centre of celestial rotation does not provide information about longitude, it may not be sufficient on its own to permit accurate long-distance navigation. Indeed birds 'displaced' artificially along the east–west axis using a planetarium [18] do not react to a mismatch between the positions of the stars and the time at their true location.

(b) 'Lodestar' orientation in seals

Most species of pinniped are not migratory, but many conduct long foraging and dispersal journeys over the course of days and nights (e.g. [28]). In a series of studies involving the harbour seal *Phoca vitulina*, it was established that seals can detect simulated and real bright stars [29] and that they can learn to orient within a floating planetarium [30]. Since the two seals trained were directed to the rewarded azimuth with a laser pointer highlighting an individual star (*Sirius*) in the initial stages of training, the authors concluded that the seals had learnt to identify a lodestar indicating the correct azimuth of travel. Nevertheless, the planetarium paradigm employed, in which a stationary sky for the same location and sidereal time was displayed in each trial, does not rule out other orientation strategies using the same pattern of stars. It is also possible, because the seals were rewarded for touching the planetarium wall beneath the 'lodestar' (at which point parallax cues may have indicated the pattern's true proximity), that for the seals this was a landmark learning task rather than a celestial orientation one.

(c) Milky Way orientation in dung beetles

In contrast to the migratory birds and itinerant seals that we have discussed so far, ball-rolling dung beetles rarely undertake long, directed journeys over the course of multiple days. The best-studied orientation behaviour in dung beetles involves the construction and transport of a dung ball, which is buried and consumed several metres away from the dung pile to avoid competition from other beetles. These ball-rolling beetles use celestial cues to maintain their initial heading and prevent them from returning to their point of origin. For crepuscular and nocturnal beetles, the moon [2] and patterns of lunar skylight [31,32] form part of this celestial compass. One nocturnal species, *Scarabaeus satyrus*, remains oriented in the absence of lunar skylight, but not in the absence of starlight, indicating a capacity to use stellar cues [11,33].

For *S. satyrus* it is the Milky Way, as opposed to any individual star or asterism, that appears to act as the primary stellar orientation cue. When transferred to a planetarium displaying only the streak of the Milky Way, beetles rolled their dung balls to the edge of a circular arena in a similar time to that needed when viewing the real starry sky, or indeed when all stars were displayed in the planetarium [11]. These beetles took longer when the Milky Way streak was absent from the sky, the result of less-oriented, and hence more circuitous, paths. They also performed poorly when viewing only the 18 brightest stars in the sky, indicating that, unlike birds and seals, dung beetles do not use learned asterisms to orient. A recent study used an artificial 'Milky Way' band consisting of LED lights to test how different cues within the Milky Way could affect orientation [34]. Beetles were not able to orient using brightness patterns within this light band, but required a difference in brightness between the two halves of the band, at a Michelson contrast of greater than 13%. This suggests that an intensity comparison across the sky is responsible for Milky Way orientation in *S. satyrus*; the authors suggested that the beetles may identify the azimuth of a bright sky region or the direction of a broad-field brightness gradient. Given the trade-off between resolution and sensitivity in the visual systems of many nocturnal insects [8,35], such a broad-field intensity comparison may be better suited to the visual systems of nocturnal insects than a strategy that relies on precise visual matches to learned patterns of stars.

The Milky Way's galactic plane is at approximately 60° to the ecliptic, and at different times of night and year the Milky Way may bisect the sky or form a low arch close to the horizon (figure 2*a–f*). At times when the Milky Way comes close to the zenith, the band arches overhead in a near straight line, forming a roughly symmetrical configuration. At the field site in South Africa where the outdoor experiments with *S. satyrus*

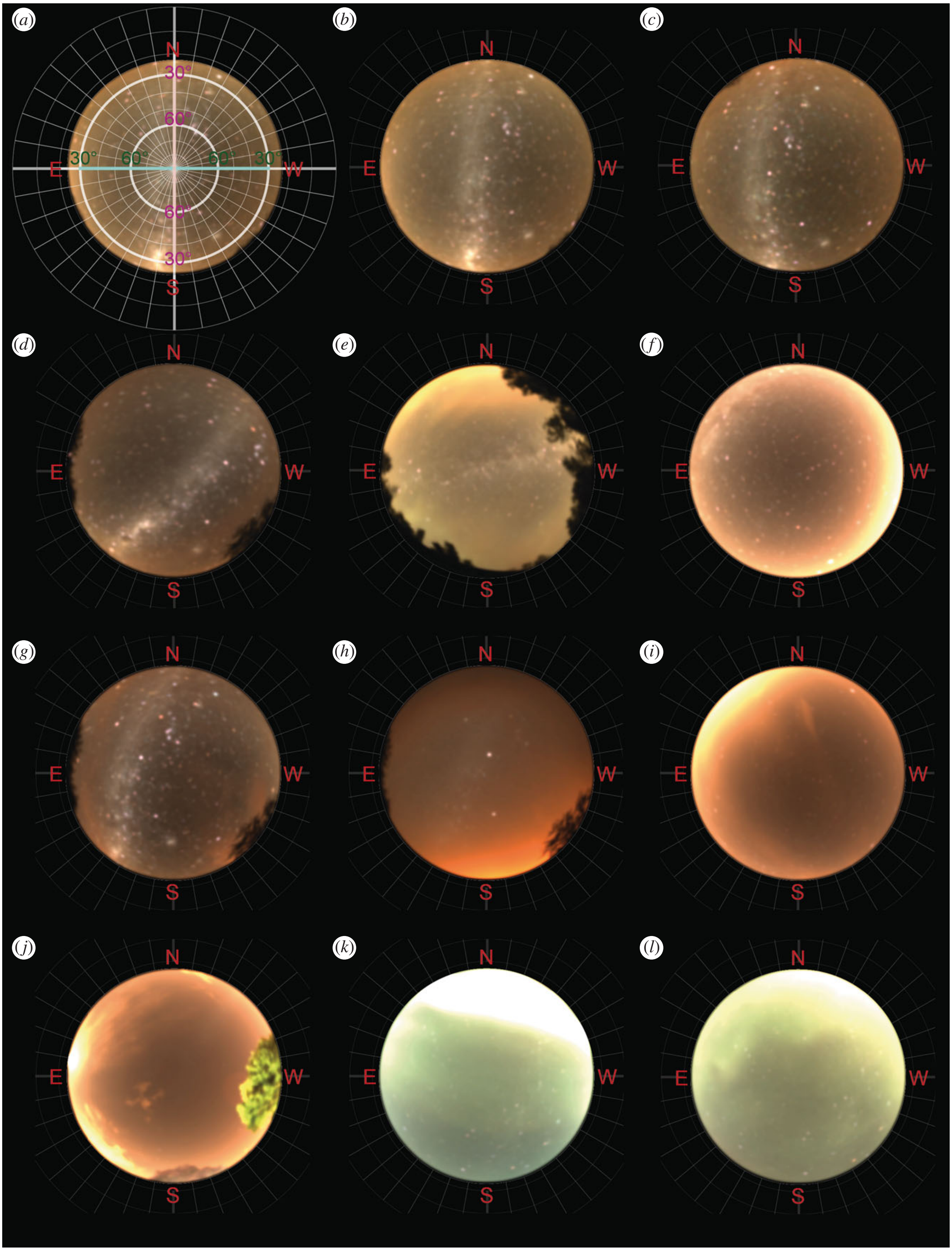

Figure 2. (*Caption opposite.*)

took place, a bright spot in the Milky Way within the constellation *Crux* was visible when the Milky Way crossed close to the zenith. This brightness difference across the Milky Way streak presumably prevents the band from appearing symmetrical to the beetles. In one study of cricket frogs (*Acris gryllus*) escaping towards their home shore under a starry sky, escape directions followed a bimodal orientation pattern [36], with frogs escaping in both the correct direction and its opposite. Since the Milky Way was at a high elevation during this study, it may well have appeared symmetrically ambiguous to these frogs. At the test site in Mississippi, as in much of the northern hemisphere, the galactic centre and adjacent bright sections of the Milky Way remain below the horizon throughout the night. As a consequence, brightness

Figure 2. (*Opposite.*) The appearance of the starry sky. Images of the night sky were recorded to raw format by a digital camera with a fisheye lens, pointed up towards the zenith. The images displayed here have been linearized and a 2° half-width Gaussian filter applied (see the Sky imaging section) to reduce the influence of sensor noise and fine details not resolvable to most animals. All images are displayed on a radial azimuth-elevation grid (*a*), so that increments in elevation are evenly spaced and azimuths appear at their true bearing relative to local magnetic north. Images normalized to a maximum spectral radiance: 3×10^6 photons $cm^{-2}\ s^{-1}\ sr^{-1}\ nm^{-1}$ for (*a*)–(*h*), 1×10^7 photons $cm^{-2}\ s^{-1}\ sr^{-1}\ nm^{-1}$ for (*i*), (*k*) and (*l*), and 1×10^8 photons $cm^{-2}\ s^{-1}\ sr^{-1}\ nm^{-1}$ for (*j*). Elevations less than 20° from the horizon have been removed, because they are mostly occupied by vegetation and other terrestrial cues. (*b*) The Milky Way crossing the zenith [34], recorded near Vryburg in South Africa (26°23′55.82″ S, 24°19′37.38″E). Followed by images of the Milky Way arching east (*c*) and southwest (*d*), observed at the same location. The 'bright spot' appears at 30°–40° elevation in the south and southeast, respectively. (*e*) The Milky Way crossing east–west, recorded near at Tvärminne Zoological Station in Finland (59°50′40.00″ S, 23°14′57.10″ E). (*f*) The Milky Way at a low elevation to the northeast, recorded near Silvåkra, Sweden (55°41′16.8″ N, 13°30′48.3″ E). (*g*–*h*) A partly cloudy sky, for which star configuration and the sky's intensity profile are largely uninterrupted; and an overcast sky with thin clouds, for which brighter stars and planets are still detectable, but upwelling light scattered by the clouds masks most details to the south. Both observed at the same location as (*a*)–(*d*). (*i*) A rural sky with moderate skyglow (light pollution) and light cloud cover, recorded near Lund in Sweden (55°44′51.4″ N, 13°17′26.2″ E). (*j*) A city sky with strong skyglow and sparse cloud cover, recorded in Johannesburg, South Africa (26°10′40.0″ S, 28°03′28.0″ E). (*k*) *Aurora borealis* masking stars from view near Sodankylä, Finland (67°21′58.5″ N, 26°37′21.2″ E). In this case, the *Aurora* is concentrated on the edge of the auroral oval, centred on the northern magnetic pole, so that the northern sky is consistently orders of magnitude brighter. (*l*) A more diffuse *Aurora* recorded at the same location, masking stars from view but providing a weaker directional cue. (Online version in colour.)

differences across the Milky Way may have been weaker than those observed in the southern hemisphere.

Two limitations of a brightness-comparison based strategy for stellar orientation, driven by differences in brightness across the Milky Way or relative star density across the sky as a whole, are changes in atmospheric conditions (figure 2*g*–*l*) and the rotation of the celestial sphere. For brief journeys, such as the dung-ball-rolling behaviour of beetles and escape behaviour of frogs, atmospheric conditions may remain stable and star motion minimal. On a succession of clear nights, however, celestial motion could drastically affect the capacity of a brightness-orienting animal to maintain a straight heading over greater distances. To adjust for celestial rotation, the animal might employ a time-compensated compass, or recalibrate its star compass relative to other references, such as the direction of sunset [4], wind [37], landmarks or magnetic cues [5].

(d) 'Uncompensated' night-sky orientation in moths

Much like birds and seals, several species of lepidopteran direct their dispersive or migratory journeys using a time-compensated sun compass [18,38–40]. While the best-studied examples are butterflies that roost overnight during these journeys, their well-developed celestial compass may be shared by night-flying Lepidoptera. In an early study of heading fidelity in night-dispersive behaviour, tethered yellow underwing moths (*Noctua pronuba*) were found to orient to both the moon and the stars [41]. In both cases, the authors noted a tendency for the moths to drift over time, interpreting this drift as an indication that the moths do not time-compensate for celestial rotation or identify the centre of celestial rotation (although the size of the drift was unfortunately too small to test statistically). The recorded drift of $\approx 16°\ h^{-1}$ (50° between 22.00 and 01.00) could indicate that the moths fixated a point around 95° from the centre of celestial rotation (i.e. at −5° declination). This line of declination would include the bright region of the Milky Way in the constellations of *Sagittarius* and *Scorpio*, although because both field sites were near to human habitation it is doubtful that the Milky Way itself would have been visible to a human observer ([42]; figure 2*i*).

Since Sotthibandhu & Baker [41], no further work has been published identifying the strategy for star orientation used by night-flying moths. Work is currently underway to investigate the role of stars in nocturnal migration in *N. pronuba* and red underwing *Catocala nupta* in Europe (D Dreyer 2017, personal communication) as well as the bogong moth, *Agrotis infusa*, an Australian noctuid that has been proposed to use celestial cues to orient during their annual migration [43]. Which, if any, of the strategies described above are used by *A. infusa* for stellar orientation, and how celestial cues interact with magnetic compass information [44] remains to be determined.

4. Testing orientation strategies

(a) *In situ* experiments

The first step in any study of animal orientation is to observe how oriented behaviour varies under natural conditions. In general, stellar orientation can be identified by observing orientation behaviour in the animal's natural habitat (at locations with minimal light pollution, and times of night when solar and lunar skylight are absent) and then screening local landmarks from view (e.g. [11,45]). If animals are oriented under these circumstances, but disoriented when the stars are obscured, while factors such as wind and overall light levels remain similar (e.g. on an overcast night), this can be taken as a first indication that the animals orient using the starry sky. Further testing conditions are then required to confirm this, and to identify the underlying orientation strategy. Nights can be chosen so that different features of the starry sky are visible, for example, so that the Milky Way crosses the zenith, or so that a particular asterism or bright star is visible or absent. Differences in weather conditions, such as overcast or partly cloudy skies, can act as a proxy for the availability of stellar cues by limiting the animal's view to fewer stars or obscuring them completely ([11,33,45]; figure 2*g*–*h*). Further, stellar cues available from natural skies on clear nights can be manipulated by selective screening or optical adjustment of different sky regions. Figure S1, in the electronic supplementary material, shows the reorientation patterns of dung beetles (*S. satyrus*) observing the Milky Way when the lowest 45° of the streak was blocked from view by black fabric screens raised at the arena's edge, demonstrating that the configurational information contained within these regions was not vital for the beetles to maintain their headings. The reduction by contrast between them may, however, have affected orientation precision, a feature of their orientation strategy later demonstrated using artificial stimuli [34].

Rabøl [46] used prisms to displace the centre of celestial rotation, to test whether migratory birds interpreted a decrease in its elevation as a southward displacement, and hence an overshoot of their goal destination. Unfortunately, the prisms also altered the sky's intensity profile, causing the birds to reorient when the stars were occluded, but a variation of this arrangement might be used to simulate latitudinal displacement under a natural sky. In general, the main drawback of using natural skies as a stimulus is the lack of control over stimuli. In addition to changing weather conditions, the influences of light pollution, wind and magnetic cues can be difficult to compensate for and should ideally be both measured (see Sky imaging section) and checked by testing for disorientation when celestial cues are obscured.

(b) Geographical displacement

In addition to 'artificial' displacements in planetaria [18,47] and via optical manipulation [46], true geographical displacements allow experimenters to test the capacity of a study animal to read both directional and positional information from stellar cues. Where natural skies are used as the stimulus, geographical displacements can be used to test at least three different aspects of stellar orientation. Firstly, a displacement in any direction can address concerns about the influence of local cues, such as landmarks and wind, because accurate orientation at this new location should require the study animal to disregard changes in these cues. Secondly, where stellar orientation allows the animal to navigate to a specific location, north–south displacements beyond that location can be used to test for a capacity to judge latitude [46]. Thirdly, rapid east–west displacements test for time compensation of stellar cues, because stars appear at a different time of day relative to the animal's (jetlagged) internal clock.

Given that these tests indicate whether the study animal can gauge its geographical position from the sky, this technique has its most straightforward application in testing for a time-compensated star compass, which would allow the animal to compensate for such displacements. In the absence of such a compass, orientation behaviour can also indicate other strategies. If the study animal compensates for latitudinal but not longitudinal displacements, then it may use the elevation of the centre of celestial rotation [9] or a specific line of declination [10] to judge latitude. If the study animal does not compensate for displacement, but remains oriented in the same direction as prior to displacement, it may use the centre of celestial rotation's azimuth [14] or another consistent feature of the sky's intensity profile [33,34] as a reference without compensating for the elevations of these features. If the study animal is only well oriented on one side of the geographical equator, it may rely on sky features specific to that hemisphere. While displacement experiments have been performed on migratory birds [25,45], with somewhat inconsistent results, this technique is, to our knowledge, yet to be applied to any other star-orienting species. In all cases, other geographical cues, such as day length and magnetic direction and inclination, need to be accounted for, but, as for all orientation experiments, an appropriate negative control can check for these effects to some extent. We predict that the application of this method to a more diverse range of species, alongside manipulations and controls at the sight of capture, would help inform future studies into the functionality of star orientation within the animal kingdom.

(c) Sky imaging

One significant challenge that faces outdoor behavioural experiments is the accurate recording of celestial conditions. Recent advances in the technology available for sky imaging can be applied to this problem. While star-charts and GPS can provide information about what celestial bodies should be visible at a given time, date and location, it can be difficult to determine the effects of atmospheric conditions and light pollution by eye. Differences between the visual systems of humans and other animals necessitate a spatial light measurement system to characterize the sky as a visual stimulus. A calibrated digital single-lens reflex (DSLR) camera [48] can act as such a system. A clear starlit sky produces conditions 6–8 orders of magnitude dimmer than daylight, at approximately 2×10^{-5} cd m^{-2} [33] or 4.2×10^{6} photons cm^{-2} s^{-1} nm^{-1} across the visible spectrum [34,49], at which point the measured signal for portable spectrophotometry equipment [49] can be close to the dark noise level. Nevertheless, thanks to improvements in the photosensitive components in digital cameras, it is now possible to record the visual environment on moonless nights [34,50] and, via calibration, to use these images to estimate spectral photon radiance throughout an animal's full sphere of potential viewing angles [51].

Before a calibrated photograph can be recorded, several parameters and nonlinearities related to camera function need to be measured and accounted for [51]. Generally speaking, these include: ISO speed (signal gain) settings, exposure time, aperture size, vignetting [52,53] and the spectral sensitivity of the camera sensor, as a combination of the sensor itself and the transmission spectrum of the Bayer mask [48,53,54]. Once the camera has been calibrated, raw images can be converted to estimated spectral radiance, with spatial and spectral resolution set by the camera's components and lens. For most species studied to date, dim-light vision is mediated by a single photoreceptor class (with a few notable exceptions [55]) so it may be sufficient to use one colour channel, or the sum of all colour channels, to obtain an indication of the potential radiance distribution available to an animal's visual system (figure 3). In order to account for the optics of the animal's eye, and any later neural pooling, this radiance distribution must then be filtered to a lower spatial resolution, estimating the level of visual detail available to the animal's internal compass. If the absorption spectrum of the visual pigments, the photoreceptor morphology and anatomy are known, it may also be possible to estimate how many photons are received by each photoreceptor [8,56–59] and distinguish above- and below-threshold image features given the known qualities of the visual system's optics, physiology and neuronal processing [60].

In terms of stellar orientation, calibrated imaging systems allow us to describe the different features of the starry sky that are available at a given point in time. As noted above, orientation using the centre of celestial rotation, lodestars and lines of declination all require the recognition of asterisms (helping the observer to distinguish one star from

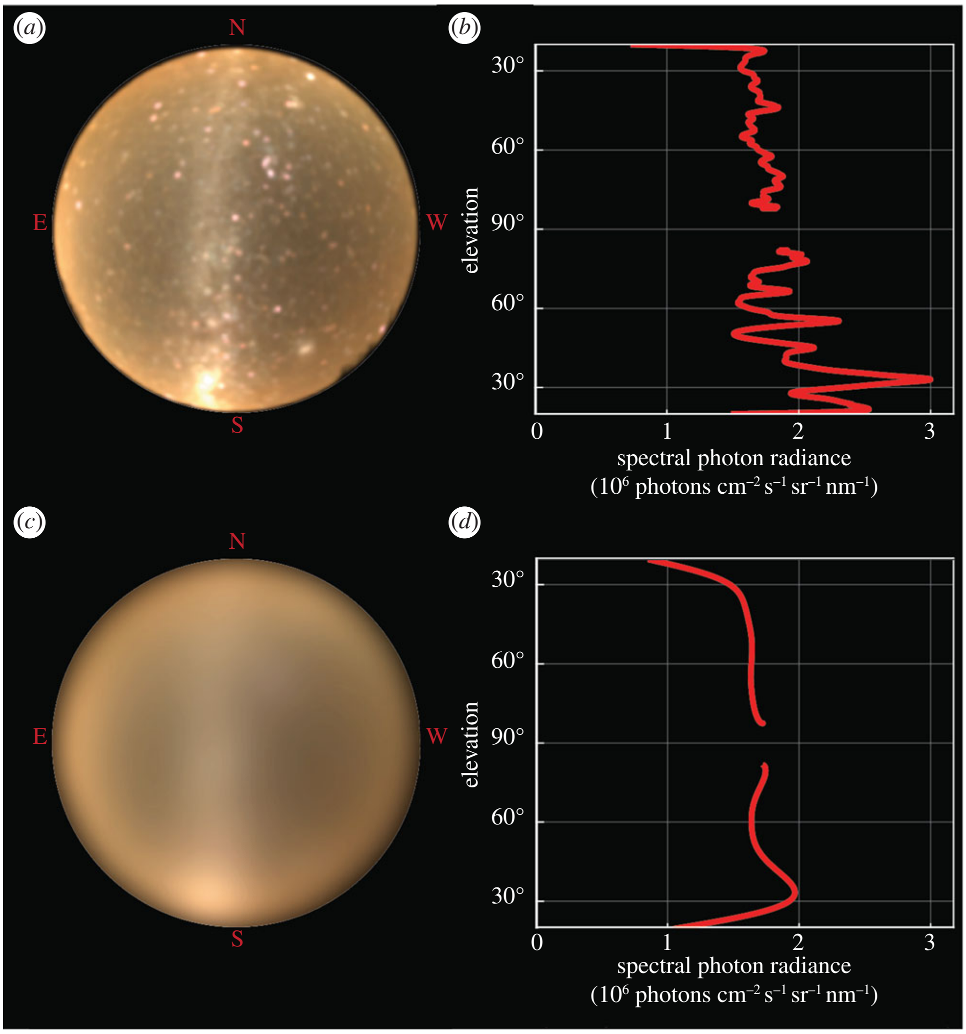

Figure 3. Spectral radiance across the night sky. (*a*) A calibrated image of the night sky [34] corrected so that the relationship between radiance and pixel byte value is linear for each colour channel. A Gaussian filter with a 2° half-width has been applied, to approximate an insect's visual resolution, and elevations below 20° excluded. (*b*) The estimated radiance profile across the Milky Way streak. The clear quantitative differences in brightness between its northern (top) and southern (bottom) halves may form the basis of an orientation cue. (*c*) The same data, filtered with a 16° half-width Gaussian to demonstrate the loss of visual detail and image contrast with increasing spatial pooling. At this resolution, individual asterisms may no longer be discernible, but larger features, such as the Milky Way streak, remain clear. (*d*) The radiance profile across the Milky Way streak in (*c*) (same pixels as in *b*). (Online version in colour.)

another). Where the combination of an animal's spatial resolution and contrast sensitivity is insufficient to discern the spaces between stars that define their configuration (figure 3*c*), the reliability of such a strategy would depend on the stability and contrast of any broader pattern of brightness across the sky, which could be measured by recording multiple images of the sky over the course of a night. Such a system might also be used to detect sky features that can be difficult for the human eye to detect, such as airglow, skyglow, zodiacal light and lunar skylight [61]. In addition, it could be used to compare an artificial sky (electronic supplementary material, figure S2) to a natural one, to ensure that experimental stimuli accurately replicate the features of the starry sky for the animal's visual system.

(d) Testing orientation with artificial stimuli

Since the pioneering studies of Sauer [62] and Emlen [13,14], the need to manipulate stellar cues has led experimenters to use artificial stars, in the form of planetaria [11,13,14,18,23,27,30,47,62,63] or purpose-built stimuli [16,17,20,34], to elicit and probe stellar orientation. The requirements of such stimuli are that they have appropriate intensity, contrast and spatial arrangement to elicit the mechanisms responsible for star orientation, ideally by appearing identical to the starry sky from the study animal's point of view. Both well-established methods and newer innovations offer means of achieving this to different degrees of accuracy. Our descriptions of types of artificial stimuli and recommendations for their use in testing stellar orientation can be found in the electronic supplementary material.

5. Future directions for star compass research

Although many animal species travel at night when the stars make up the most prominent celestial cue, we still know very little about how these animals integrate and interpret celestial cues to obtain directional, and perhaps location information. The best-studied star compasses, the centre of celestial rotation compass of migratory birds and the brightness comparison strategy of nocturnal dung beetles, are subject to vastly different constraints and apply to very different forms of directed behaviour. Given these examples, we might predict that a combination of visual resolution and the duration of oriented behaviour would shape the strategy used by a given species, but, as with the lodestar-based system proposed for seals, these strategies need not necessarily resemble those of birds or beetles.

Stellar orientation may also prove to be more versatile than has been demonstrated so far. Many migratory birds follow paths that cross the equator, at which point the centre of celestial rotation observed earlier in the journey disappears below the horizon. To date, no animal has been demonstrated to switch between different stellar cues with a change in location or season. Furthermore, it is not currently known whether any animal can use the elevation of the centre of celestial rotation, or asterisms that lie along a line of declination, to gauge their latitude. Similarly, no animal has been demonstrated to possess a time-compensated star compass. Such time compensation would allow the possessor to gauge their longitude, a capacity gained by human sailors only relatively recently.

We propose that new sky imaging technologies, combined with more explicit statements of the predicted features of different stellar orientation strategies, will allow star compasses to be discovered, confirmed and characterized in more species, and help to answer fundamental questions of how animals guide their darkest journeys.

Authors' contributions. All authors conceptualized the review and edited the manuscript. J.J.F. drafted the manuscript and analysed the behavioural data. J.S. and D.-E.N. designed the sky-imaging protocol, and J.S. and J.J.F. analysed the sky image data.

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References

1. Papi F, Pardi L. 1963 On the lunar orientation of sandhoppers (*Amphipoda talitridae*). *Biol. Bull.* **124**, 97–105. (doi:10.2307/1539571)
2. Dacke M, Byrne MJ, Scholtz CH, Warrant EJ. 2004 Lunar orientation in a beetle. *Proc. R. Soc. Lond. B* **271**, 361–365. (doi:10.1098/rspb.2003.2594)
3. Wcislo WT, Arneson L, Roesch K, Gonzalez V, Smith A, Fernández H. 2004 The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biol. J. Linn. Soc.* **83**, 377–387. (doi:10.1111/j.1095-8312.2004.00399.x)
4. Moore FR. 1987 Sunset and the orientation behaviour of migrating birds. *Biol. Rev.* **62**, 65–86. (doi:10.1111/j.1469-185X.1987.tb00626.x)
5. Sjöberg S, Muheim R. 2016 A new view on an old debate: type of cue-conflict manipulation and availability of stars can explain the discrepancies between cue-calibration experiments with migratory songbirds. *Front. Behav. Neurosci.* **10**, 29. (doi:10.3389/fnbeh.2016.00029)
6. Dacke M, Nilsson D-E, Warrant EJ, Blest AD, Land MF, O'Carroll DC. 1999 Built-in polarizers form part of a compass organ in spiders. *Nature* **401**, 470–473. (doi:10.1038/46773)
7. Greiner B, Narendra A, Reid SF, Dacke M, Ribi WA, Zeil J. 2007 Eye structure correlates with distinct foraging-bout timing in primitive ants. *Curr. Biol.* **17**, R879–R880. (doi:10.1016/j.cub.2007.08.015)
8. Warrant EJ. 1999 Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.* **39**, 1611–1630. (doi:10.1016/S0042-6989(98)00262-4)
9. Tolmacheva M. 1980 On the Arab system of nautical orientation. *Arabica* **27**, 180–192. (doi:10.1163/157005880X00051)
10. Feinberg R. 1988 *Polynesian seafaring and navigation: ocean travel in Anutan culture and society*. Kent, Ohio: Kent State University Press.
11. Dacke M, Baird E, Byrne M, Scholtz CH, Warrant EJ. 2013 Dung beetles use the Milky Way for orientation. *Curr. Biol.* **23**, 298–300. (doi:j.cub.2012.12.034)
12. Commissioners of Longitude. 1766 *The nautical almanac and astronomical ephemeris for the year*. London, UK: Richardson and Clark.
13. Emlen S. 1967 Migratory orientation in the Indigo Bunting, *Passerina cyanea* I evidence for the use of celestial cues. *Auk* **84**, 309–342. (doi:10.2307/4083084)
14. Emlen S. 1967 Migratory orientation in the Indigo Bunting, *Passerina cyanea* II mechanism of celestial orientation. *Auk* **84**, 463–489. (doi:10.2307/4083330)
15. Emlen ST. 1969 Bird migration: influence of physiological state upon celestial orientation. *Science* **165**, 716–718. (doi:10.1126/science.165.3894.716)
16. Wiltschko W, Daum P, Ferngenbauer-Kimmel A, Wiltschko R. 1987 The development of the star compass in Garden Warblers, Sylvia borin. *Ethology* **74**, 285–292. (doi:10.1111/j.1439-0310.1987.tb00939.x)
17. Able KP, Able MA. 1990 Calibration of the magnetic compass of a migratory bird by celestial rotation. *Nature* **347**, 378–380. (doi:10.1038/347378a0)
18. Mouritsen H, Larsen ON. 2001 Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. *J. Exp. Biol.* **204**, 3855–3865.
19. Pakhomov A, Anashina A, Chernetsov N. 2017 Further evidence of a time-independent stellar compass in a night-migrating songbird. *Behav. Ecol. Sociobiol.* **71**, 2–7. (doi:10.1007/s00265-017-2279-3)
20. Michalik A, Alert B, Engels S, Lefeldt N, Mouritsen H. 2014 Star compass learning: how long does it take? *J. Ornithol.* **155**, 225–234. (doi:10.1007/s10336-013-1004-x)
21. Chernetsov N. 2015 Avian compass systems: do all migratory species possess all three? *J. Avian Biol.* **46**, 342–343. (doi:10.1111/jav.00593)
22. Bingman VP. 1984 Night sky orientation of migratory pied flycatchers raised in different magnetic fields. *Behav. Ecol. Sociobiol.* **15**, 77–80. (doi:10.1007/BF00310220)
23. Zapka M *et al.* 2009 Visual but not trigeminal mediation of magnetic compass information in a migratory bird. *Nature* **461**, 1274–1277. (doi:10.1038/nature08528)
24. Wiltschko W, Wiltschko R. 1975 The interaction of stars and magnetic field in the orientation system of night migrating birds. II. spring experiments with European robins (*Erithacus rubecula*). *Z. Tierpsychol.* **37**, 337–355. (doi:10.1111/j.1439-0310.1975.tb00885.x)
25. Rabøl J. 2010 Orientation by passerine birds under conflicting magnetic and stellar conditions: no calibration in relation to the magnetic field. *Dansk Ornithologisk Forenings Tidsskrift* **104**, 85–102.
26. Prinz K, Wiltschko W. 1992 Migratory orientation of pied flycatchers: interaction of stellar and magnetic information during ontogeny. *Anim. Behav.* **44**, 539–545. (doi:10.1016/0003-3472(92)90063-F)
27. Emlen ST. 1970 Celestial rotation: its importance in the development of migratory orientation. *Science* **170**, 1198–1201. (doi:10.1126/science.170.3963.1198)

28. Lowry LF, Frost KJ, Hoep JM, Delong RA. 2001 Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Mar. Mamm. Sci.* **17**, 835–861. (doi:10.1111/j.1748-7692.2001.tb01301.x)
29. Mauck B, Brown D, Schlosser W, Schaeffel F, Dehnhardt G. 2005 How a harbor seal sees the night sky. *Mar. Mamm. Sci.* **21**, 646–656. (doi:10.1111/j.1748-7692.2005.tb01257.x)
30. Mauck B, Gläser N, Schlosser W, Dehnhardt G. 2008 Harbour seals (*Phoca vitulina*) can steer by the stars. *Anim. Cogn.* **11**, 715–718. (doi:10.1007/s10071-008-0156-1)
31. Dacke M, Nordström P, Scholtz CH. 2003 Twilight orientation to polarised light in the crepuscular dung beetle *Scarabaeus zambesianus*. *J. Exp. Biol.* **206**, 1535–1543. (doi:10.1242/jeb.00289)
32. el Jundi B, Warrant EJ, Byrne MJ, Khaldy L, Baird E, Smolka J, Dacke M. 2015 Neural coding underlying the cue preference for celestial orientation. *Proc. Natl Acad. Sci. USA* **112**, 11 395–11 400. (doi:10.1073/pnas.1501272112)
33. Smolka J, Baird E, el Jundi B, Reber T, Byrne MJ, Dacke M. 2016 Night sky orientation with diurnal and nocturnal eyes: dim-light adaptations are critical when the moon is out of sight. *Anim. Behav.* **111**, 127–146. (doi:10.1016/j.anbehav.2015.10.005)
34. Foster JJ, el Jundi B, Smolka J, Khaldy L, Nilsson D-E, Byrne MJ, Dacke M. 2017 Stellar performance: mechanisms underlying Milky Way orientation in dung beetles. *Phil. Trans. R. Soc. B* **372**, 20160079. (doi:10.1098/rstb.2016.0079)
35. Warrant EJ, McIntyre PD. 1990 Limitations to resolution in superposition eyes. *J. Comp. Physiol. A* **167**, 785–803. (doi:10.1007/BF00189768)
36. Ferguson DE, Landreth HF, Turnipseed MR. 1965 Astronomical orientation of the southern cricket Frog, *Acris gryllus*. *Coepia* **1965**, 58–66. (doi:10.2307/1441240)
37. Wystrach A, Schwarz S. 2013 Ants use a predictive mechanism to compensate for passive displacements by wind. *Curr. Biol.* **23**, R1083–R1085. (doi:10.1016/j.cub.2013.10.072)
38. Mouritsen H, Frost BJ. 2002 Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proc. Natl Acad. Sci. USA* **99**, 10 162–10 166. (doi:10.1073/pnas.152137299)
39. Oliveira EG, Srygley RB, Dudley R. 1998 Do neotropical migrant butterflies navigate using a solar compass? *J. Exp. Biol.* **201**, 3317–3331.
40. Heinze S, Reppert SM. 2011 Sun compass integration of skylight cues in migratory monarch butterflies. *Neuron* **69**, 345–358. (doi:10.1016/j.neuron.2010.12.025)
41. Sotthibandhu S, Baker RR. 1979 Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. *Anim. Behav.* **27**, 786–800. (doi:10.1016/0003-3472(79)90015-0)
42. Falchi F, Cinzano P, Duriscoe D, Kyba CCM, Elvidge CD, Baugh K, Portnov BA, Rybnikova NA, Furgoni R. 2016 The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, e1600377. (doi:10.1126/sciadv.1600377)
43. Warrant E, Frost B, Green K, Mouritsen H, Dreyer D, Adden A, Brauburger K, Heinze S. 2016 The Australian bogong moth *Agrotis infusa*: a long-distance nocturnal navigator. *Front. Behav. Neurosci.* **10**, 77. (doi:10.3389/fnbeh.2016.00077)
44. Dreyer D, Frost B, Mouritsen H, Günther A, Green K, Whitehouse M, Johnsen S, Heinze S, Warrant E. In preparation. The Earth's magnetic field and visual landmarks steer migration in a nocturnal moth.
45. Rabøl J. 1975 The orientation of night-migrating passerines without the directional influence of the starry sky and/or the Earth magnetic field. *Z. Tierpsychol.* **38**, 251–266. (doi:10.1111/j.1439-0310.1975.tb02003.x)
46. Rabøl J, Rabol J. 1978 One-direction orientation versus goal area navigation in migratory birds. *Oikos* **30**, 216–223. (doi:10.2307/3543481)
47. Rabøl J. 1998 Star navigation in pied flycatchers *Ficedula hypoleuca* and redstarts *Phoenicurus phoenicurus*. *Dansk Ornitologisk Forenings Tidsskrift* **92**, 283–289.
48. Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko TS. 2007 Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211–237. (doi:10.1111/j.1095-8312.2007.00725.x)
49. Johnsen S, Kelber A, Warrant E, Sweeney AM, Widder EA, Lee RL, Hernández-Andrés J. 2006 Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. *J. Exp. Biol.* **209**, 789–800. (doi:10.1242/jeb.02053)
50. Hänel A *et al.* 2017 Measuring night sky brightness: methods and challenges. *J. Quant. Spectrosc. Radiat. Transf.* **205**, 278–290. (doi:10.1016/j.jqsrt.2017.09.008)
51. Nilsson D-E, Smolka J. In preparation. Environmental light field analysis—a new tool for characterising light in habitats.
52. Hong G, Luo MR, Rhodes PA. 2001 A study of digital camera colorimetric characterization based on polynomial modeling. *Color. Res. Appl.* **26**, 76–84. (doi:10.1002/1520-6378(200102)26:1<76::AID-COL8>3.0.CO;2-3)
53. Barnard K, Funt B. 2002 Camera characterization for color research. *Color. Res. Appl.* **27**, 152–163. (doi:10.1002/col.10050)
54. Lauziére YB, Gingras D, Ferrie FP. 1999 Color camera characterization with an application to detection under daylight. In *Trois-Rivières: Vision Interface*, Quebec, Canada, 19–21 May, pp. 280–287.
55. Kelber A, Yovanovich C, Olsson P. 2017 Thresholds and noise limitations of colour vision in dim light. *Phil. Trans. R. Soc. B* **372**, 20160065. (doi:10.1098/rstb.2016.0065)
56. Donner K. 1992 Noise and the absolute thresholds of cone and rod vision. *Vision. Res.* **32**, 853–866. (doi:10.1016/0042-6989(92)90028-H)
57. Warrant EJ, Nilsson DE. 1998 Absorption of white light in photoreceptors. *Vision. Res.* **38**, 195–207. (doi:10.1016/S0042-6989(97)00151-X)
58. Stavenga DG. 2003 Angular and spectral sensitivity of fly photoreceptors. I. integrated facet lens and rhabdomere optics. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **189**, 1–17. (doi:10.1007/s00359-002-0370-2)
59. Frederiksen R, Warrant EJ. 2008 The optical sensitivity of compound eyes: theory and experiment compared. *Biol. Lett.* **4**, 745–747. (doi:10.1098/rsbl.2008.0467)
60. O'Carroll DC, Wiederman SD. 2014 Contrast sensitivity and the detection of moving patterns and features. *Phil. Trans. R. Soc. B* **369**, 20130043. (doi:10.1098/rstb.2013.0043)
61. Gál J, Horváth G, Barta A, Wehner R. 2001 Polarization of the moonlit clear night sky measured by full-sky imaging polarimetry at full moon: comparison of the polarization of moonlit and sunlit skies. *J. Geophys. Res.* **106**, 22 647–22 653. (doi.org/10.1029/2000JD000085)
62. Sauer F. 1956 Zugorientierung einer Mönchsgrasmücke (*Sylvia a. atricapilla, L.*) unter künstlichem Sternenhimmel. *Naturwissenschaften* **43**, 231–232. (doi.org/10.1007/BF00600790)
63. Beason RC. 1987 Interaction of visual and non-visual cues during migratory orientation by the bobolink (*Dolichonyx oryzivorus*). *J. Orn.* **128**, 317–324. (doi:10.1007/BF01640301)