Keep it rolling

Straight-line orientation in South African ball-rolling dung beetles

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Straight-line orientation in South African ball-rolling dung beetles

Lana Khaldy

DOCTORAL DISSERTATION

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Abstract

Representing a substantial range and variety in morphological and ecological niche, found on all continents of the globe (except for the Antarctic), *the ball-rolling dung beetles* provide an excellent model in which to study *the heading direction network* and the factors by which it is influenced.

As soon as a ball-rolling dung beetle has located a fresh dung pile to feed on, it immediately starts shaping a piece of dung into a ball, rolling it away from the dung pat in as straight of a trajectory as the terrain allows. This *straight-line orientation behaviour* is thought to be a strategy to escape the fierce competition of dung at the pile. By investigating how *size* (Paper I), *ecological niche, phylogeny* (Paper II and Paper III) and *visual conditions* (Paper IV) influence this relatively straightforward orientation behaviour, I explore the orientation challenges faced, and the solutions presented.

In the first paper (Paper I), I investigated the effect of directional error on straight-line orientation in two differently sized beetles, and concluded that the directional error that unavoidably accumulates over a given distance as the beetle travels, is inversely proportional to the step size of the animal.

Next (Paper II), I investigated straight-line orientation in a diurnal woodland-living ball-rolling species. In this study I demonstrated that the woodland-living species, present in habitats of densely packed trees and tall grass, relies predominantly on directional information from the celestial pattern of polarised light. This stands in contrast to all previous observations on diurnal ball-rolling beetles, where the sun has been demonstrated as the predominant source of directional information in their heading direction networks.

In the third paper (Paper III) I continued to explore the relative weighting of directional information in three species of ball-rolling South African dung beetles from three different tribes living within the same savanna biome, but in different habitat types. In this study I found that species *within* a tribe share the same orientation strategy, but that this strategy differs *across* tribes.

In my final paper (Paper IV), I further explored the weight relationship of directional information from the sun (simulated by a green LED) and the celestial polarisation pattern (simulated by an overhead band of polarisation) in the heading direction network of the beetle. I concluded that the directional information conveying the highest certainty at a given moment in time is afforded the greatest weight in the heading direction network of the animal.

With my work, I hope to provide an insight to the dynamic nature of the biological compass and its ability to change and adapt to different visual environments.

Key words: Ball-rolling dung beetle – Orientation – Heading direction network – Compass – Weighting – Celestial cues – Sun – Polarised light

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Table of Contents

Scientific Papers

I. **Khaldy L**, Peleg O, Tocco C, Mahadevan L, Byrne M, Dacke M. (2019). The effect of step size on straight-line orientation. *J R Soc Interface* **16**, 20190181. https://doi.org/10.1098/rsif.2019.0181

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III. **Khaldy L**, Tocco C, Byrne M, Dacke M. (2021). Compass cue integration and its relation to the visual ecology of three tribes of ball-rolling dung beetles. *Insects* **12**, 526. https://doi.org/10.3390/insects12060526

IV. **Khaldy L**, Foster JJ, Yilmaz A, Belušič G, Gagnon Y, Tocco C, Byrne M, Dacke M. The interplay of directional information provided by unpolarised and polarised light in the heading direction network of *Kheper lamarcki.* (*Manuscript submitted*).

Author Contributions

I. **L.K.**, O.P., C.T., M.B. and M.D. conducted experiments; **L.K.**, O.P., L.M. and M.D. designed experiments; **L.K.**, O.P. and M.D. analysed the data; **L.K.** drafted the manuscript; all authors revised the manuscript.

II. **L.K.** and C.T. conducted experiments; **L.K.** and M.D. designed experiments; **L.K.** analysed the data; **L.K.** drafted the manuscript; all authors revised the manuscript.

III. **L.K** and C.T. conducted experiments; **L.K.** designed experiments; **L.K.** analysed the data; **L.K.** drafted the manuscript; all authors revised the manuscript.

IV. **L.K** conducted behavioural experiments; A.Y. and G.B. collected physiology data; C.T. and M.B. collected and transported animals; **L.K.**, J.F., Y.G. and M.D. designed behavioural experiments; **L.K.** analysed the behavioural data; A.Y. and G.B. analysed the physiology data; **L.K.** drafted the manuscript; all authors have revised the current draft of the manuscript.

Scientific Papers not included in this Thesis

- 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**, 11395-11400. https://doi.org/10.1073/pnas.1501272112.

- el Jundi B, Foster J, **Khaldy L**, Byrne MJ, Dacke M, Baird E. (2016). A snapshot-based mechanism for celestial orientation. *Curr Biol* **26**, 1456–62. https://doi.org/10.1016/j.cub.2016.03.030.

- 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 Lond B Biol Sci* **372**, 20160079. https://doi.org/10.1098/rstb.2016.0079.

- Foster JJ, Kirwan JD, el Jundi B, Smolka J, **Khaldy L**, Baird E, Byrne MJ, Nilsson D-E. (2019). Orienting to polarized light at night – Matching lunar skylight to performance in a nocturnal beetle. *J Exp Biol* **222**, 1–10. https://doi.org/10.1242/jeb.188532.

- Foster JJ, Tocco C, Smolka J, **Khaldy L**, Baird E, Byrne M, Nilsson D-E, Dacke M (2021). Light pollution forces a change in dung beetle orientation behaviour. *Curr Biol* **31**, 1-8. https://doi.org/10.1016/j.cub.2021.06.038

Popular summary

Although unpleasant to our senses, fresh dung is the best part of the day to many insects. Among these are the *South African ball-rolling dung beetles*. When it is time to feed, these insects emerge from the ground and fly to the nearest suitable dung pat. Once it has (crash)landed on or nearby the dung pile (the landing of a dung beetle is not a particularly graceful one), it quickly shapes a portion of the dung into a ball. There can be hundreds of beetles on the dung pat, all trying to get their share of the food. Some of these do not bother forming balls of their own but will rather try to hijack those of others. Thus, once the ball has been shaped, it is crucial to quickly get away from the chaos at the pile. One way to do this is to roll your ball away along a path as straight as the terrain allows, maximising the distance gained to your competitors with every step taken. To steer straight across the savanna, the beetles integrate directional information from different celestial cues, such as the position of the sun or the orientation of the skylight polarisation pattern (a light pattern in the sky created by the scattering of sunlight) into their *internal compass*.

As a dung beetle researcher, it is not uncommon to find yourself in the scorching heat of the savanna, staring at a pile of dung. After many hours of doing this myself, I started to pay attention to the wide variation in size of ball-rolling dung beetles, feeding from the same dung pat. When a beetle is moving its limbs, mechanical and sensory noise is generated, producing overall fluctuations in the forward motion of the beetle, causing it to deviate from its straight path. As beetles of different size have different step lengths, this made me wonder how the size of a beetle affects its ability to steer straight. In **Paper I**, I answered this by comparing the *straight-line orientation strategy* of two species of ball-rolling dung beetles that differ greatly in size. I found that the noise generated over a given distance is inversely proportional to the step size of the animal. This means that over the same distance, smaller sized beetles –that take many more steps than the larger ones– end up having a more tortuous roll path. Interestingly, in their natural setting on the savanna, both beetles take an equal number of steps before burying down, but because of the noise generated, smaller beetles end up radially closer to the dung pile compared to larger beetles.

Many of the ball-rolling beetles on the savanna will primarily steer by the sun, but what about beetles living in more cluttered environments? In **Paper II** I explored the straight-line orientation behaviours of a dung beetle species living in regions where the sun is frequently hidden behind clouds or the overhead canopy. I found that beetles inhabiting this environment primarily rely on the polarised skylight pattern to guide their paths. This could suggest that the visual environment of dung beetles plays a role in the design of the neuronal compass. However, my results were only demonstrated in one species. Therefore, following my findings from Paper II, I set out to explore the role of directional information from the sun and the skylight polarisation pattern in the *heading direction network* of beetles across different tribes, living within the same region. In **Paper III** I found that each of the three tribes tested presented a different strategy; the first tribe relied predominantly on the sun for directional guidance, the second tribe relied on the pattern of polarised skylight, while the third tribe did not appear to favour either of these two cues. This suggests that in these three tribes of beetles, the different weights given to these two sources of directional information is dictated by their phylogeny, rather than their visual ecology.

It is important to note, that a beetle relying predominantly on the sun, does not suddenly start to roll in circles as soon as passing clouds or branches of a tree shades the sun. Instead, these beetles rather rely on the 'second most popular' cue for directional guidance: the pattern of polarised skylight. But what is it that dictates when this change in directional guidance should be made? In **Paper IV** I built a setup presenting a simulated sun together with a simulated skylight polarisation pattern. By changing the properties of these two cues (for instance by changing their relative intensity) and analysing the beetle's response, I found that the more unreliable a cue appears to the beetle, the less weight is given to it in its heading direction network.

Through my four papers I hope to have demonstrated the dynamic nature of the heading direction network of the ball-rolling dung beetles that allow these incredible animals to steer straight across most continents and vegetation types of the world.

Populär Sammanfattning

En ordentlig hög dynga är den absoluta höjdpunkten på dagen för många insekter, inte minst för de *sydafrikanska boll-rullande dyngbaggarna*. När det är matdags, gräver sig dessa stora insekter upp ur marken, fäller ut sina vingar och flyger till en lämplig dynghög. Efter att ha (krasch)landat på eller vid denna tillfälliga uteservering (en dyngbagges landning är inte den mest graciösa), börjar skalbaggen snart skulptera sig en boll. Ofta finns det upp till hundra dyngbaggar på en dynghög, alla med det gemensamma målet att äta sig mätta. Några av dessa formar inte nödvändigtvis sina egna bollar, utan provar att stjäla andras. Så snart en dyngbagge färdigställt sin boll gäller det därför att få iväg den från kaoset runt dynghögen så snabbt som möjligt. Genom att hålla en stabil kurs med sin runda matlåda maximerar bollägaren det avstånd den kan lägga mellan sig och konkurrenterna med vart fotsteg den tar. För att styra rakt använder sig dyngbaggen av information från olika riktnings-signaler, såsom solens position eller himmelns polarisationsmönster (ett ljusmönster skapat från spridningen av solljus). Dessa integreras alla i dyngbaggens *interna kompass*.

Som dyngbaggeforskare händer det ofta att man finner sig stirrandes på en dynghög mitt på savannen. Efter att själv ha gjort detta ett par gånger började jag så småningom fundera på hur storleken på dyngbaggen påverkar dess förmåga att hålla en rak kurs. När en bagge rör sig framåt, skapas mekaniska störningar i lederna, vilka kan bidra till fluktuationer i dess rörelse framåt, vilket i sin tur kan leda till att dyngbaggen avviker från sin kurs. Hur påverkar då steglängden, som är kortare hos de mindre arterna, skalbaggens förmåga att rulla rakt? I **Artikel I**, tittade jag närmare på denna fråga genom att jämföra *orienteringsstrategin* hos två närbesläktade dyngbaggearter av olika storlek. Jag fann att störningen som genereras över ett visst avstånd är omvänt proportionell mot steglängden. Detta betyder att över samma avstånd kommer mindre baggar, som tar fler steg än större individer, ha en mer slingrig rullsträcka. Intressant nog, i deras naturliga miljö tar båda dyngbaggar ungefär lika många steg innan de gräver ner sin boll, men på grund av störningen som genereras, kommer mindre baggar hamna radiellt närmare dynghögen än större baggar.

För de flesta savann-levande dyngbaggar är solen en dominant riktingsgivare. Men gäller detta även för dyngbaggar som vill styra rakt genom miljöer med tätare vegetation? I **Artikel II** fokuserade jag på orienteringsstrategin hos en dyngbaggeart som lever i miljöer där solen ofta är skymd av moln eller trädtoppar och fann att dessa dyngbaggar främst förlitar sig på himmelns polarisationsmönster för att styra rakt. Detta tyder på att den visuella miljön inom vilken arten är aktiv kan spela en roll för hur olika riktningsgivare vägs samman för orientering. Att systemen är mer komplexa än så blev tydligt då jag utökade mina jämförande studier till tre olika släkten av dyngbaggar som lever inom samma miljö. I **Artikel III** fann jag att varje släkt av de tre jag testade, hade sin egen strategi: en förlitade sig främst på solen för att styra sin väg, en annan förlitade sig på polarisationsmönstret och en tredje tycktes inte främst förlita sig på någon av dessa två riktningsgivare. Inte oväntat spelar även dyngbaggens fylogeni en viktig roll för dess orienterings-strategi.

Det är viktigt att notera att en dyngbagge som förlitar sig främst på solen, kommer inte plötsligt att rulla i cirklar så snart denna riktnings-signal försvinner bakom ett moln eller om skalbaggen rullar in under skuggan av ett träd. Istället förlitar sig dyngbaggen på sin näst mest populära riktningsgivare: himmelns polarisationsmönster. I **Artikel IV** byggde jag en uppställning där jag introducerade en simulerad sol tillsammans med ett simulerat polarisationsmönster. Genom att ändra egenskaperna av dessa två riktnings-signaler (till exempel genom att ändra den relativa ljusintensiteten) och analysera dyngbaggens respons, fann jag att ju mer opålitlig en riktnings-signal är, desto mindre vikt läggs på denna signal i dyngbaggens kompass. Detta avslöjar en av de grundläggande principerna bakom dyngbaggekompassens förmåga att anpassa sig till olika visuella miljöer.

Jag hoppas att mina fyra artiklar bidragit till en större förståelse för vilka utmaningar en styrande insekt stöter på och hur den löser dessa. Oavsett väder, terräng eller stirrande forskare, kommer dyngbaggen att fortsätta sin färd framåt.

Paper overview

This thesis is primarily based on my four main studies regarding the heading direction network and straight-line orientation behaviour of South African ball-rolling dung beetles. However, where relevant, I will also refer to the five additional studies that I have co-authored. These five papers will be denoted with an asterisk (*) when appearing in the text. Below, I list the principal question addressed in each of my four main studies with a brief summary of what was achieved. Throughout the thesis, I will refer to these four papers by their roman numerals as given below.

Paper I

Khaldy L, Peleg O, Tocco C, Mahadevan L, Byrne M, Dacke M. (2019). The effect of step size on straight-line orientation. *J R Soc Interface* **16**, 20190181. https://doi.org/10.1098/rsif.2019.0181

What influence does the step size of the agent have on its's ability to maintain a straight bearing? What is the weight relationship of internal and external compass cues in the heading direction network of the dung beetle?

If an animal relies exclusively on internal sensory information while travelling along a trajectory, the directional error that is generated with each ensuing step will accumulate and effectively cause the animal to spiral. Only when the animal is allowed to use directional information from external compass cues can it correct for errors in its bearing. In this study, I investigated the effect of directional error on straight-line orientation in two closely related, but differently sized, species of dung beetles; *Scarabaeus ambiguus* Boheman and *Kheper lamarcki* (Mac Leay) [Scarabaeini]. For each species, I characterised the size of the directional error generated with each step, in the presence and absence of external compass cues, and investigated the influence of this error on the tortuosity of the travelled path. Next, we modelled the weight given to external compass cues over internal proprioceptive cues in the heading direction network of the beetle. From our results we concluded that the directional error that unavoidably accumulates as the beetle travels, is relative to the step size of the animal and that both species weight the two sources of directional information in a similar fashion. Furthermore, and perhaps not surprisingly, the dung beetles attribute significantly greater weight to external directional cues over internal directional information while performing straight-line orientation.

Paper II

Khaldy L, Tocco C, Byrne M, Baird E, Dacke M. (2019). Straight-line orientation in the woodland-living beetle *Sisyphus fasciculatus. J Comp Physiol A* **206**, 327-335. https://doi.org/10.1007/s00359-019-01331-7

Are all ball-rolling dung beetle species guided by a common weighting of directional cue information in their heading direction network?

Prior to this study, nearly all behavioural work regarding straight-line orientation in dung beetles had been performed on ball-rolling dung beetle species present in vast, open habitats, and had concluded that the sun is given the greatest relative weight in the heading direction network. Here, I investigated straight-line orientation in the South African woodland-living beetle *Sisyphus fasciculatus* Boheman [Sisyphini], present in habitats with densely packed trees and tall grass. I concluded that, contrary to all previous observations on diurnal ball-rolling beetles, *S. fasciculatus* relies predominantly on directional information from the celestial pattern of polarised light.

Paper III

Khaldy L, Tocco C, Byrne M, Dacke M. (2021). Compass cue integration and its relation to the visual ecology of three tribes of ball-rolling dung beetles. *Insects* **12**, 526. https://doi.org/10.3390/insects12060526

What role does ecological niche and/or tribe play in the weighting of directional cue information in the heading direction network of the beetle?

In this study, I continued to explore the relative weighting of directional information in three species of ball-rolling South African dung beetles, from three different tribes living within the same savanna biome, but in different habitat types. I found that species within a tribe share the same orientation strategy, but that this strategy differs across tribes. Inter-tribal differences in body size, eye size, and overall morphology, most likely influence how species within each tribe weight the sources of directional information available to them. Nevertheless, dung beetles manage to solve the challenge of straight-line orientation via a weighted combination of visual cues that are particular to the habitat in which they are found. However, this system is dynamic, allowing the beetles to operate equally well, even in the absence of the cue they typically assign the greatest relative weight.

Paper IV

Khaldy L, Foster J, Yilmaz A, Belušič G, Gagnon Y, Tocco C, Byrne M, Dacke M.
The interplay of directional information provided by unpolarised and polarised light in
the heading direction network of *Kheper lamarcki* (*Manuscript submitted*)

How does the relative reliability of different directional cues influence the weight relationship in the heading direction network of the beetle?

The sun is the most prominent directional compass cue in the heading direction network of the diurnal ball-rolling dung beetle *Kheper lamarcki*. If this celestial body is occluded from the beetle's field of view, which can occur by passing clouds or when rolling in the shade of a tree, the distribution of the relative weight between the directional cues that remain shifts in favour of the celestial pattern of polarised light. In this lab-based study, I investigated the weight relationship of directional information from the sun (simulated by a green LED) and the celestial polarisation pattern (simulated by an overhead band of polarisation) in the heading direction network of the beetle. By altering the intensity, degree and direction of polarisation of the overhead light, this allowed me to determine how the weight relationship of the two sources of light is influenced by their relative reliability. From my results, I can conclude that the heading direction network of *K. lamarcki* relies on directional information in a Bayesian manner; directional information conveying the highest certainty at any moment in time is afforded the greatest weight in the heading direction network of the animal.

Background

The purpose of my work

To travel along a given direction, towards or away from a fixed point in space, oftentimes requires the possession of a great navigational toolkit; *a biological compass* or *a heading indicator* (see *Box 1*). To maintain a desired heading, the navigator (or more accurately its compass) must be able to sift through and extract relevant directional information from the vast range of external cues presented. As it is moving, directional information generated by the navigator itself, such as body rotations or leg movements, might also be considered and integrated into the compass. This means that, to maintain a desired direction, the compass must not only be able to extract the correct directional information, but also continuously compare the current heading to the desired one and reorient the navigator in reference to the stable cues provided. Although an extensive number of studies within insect navigation have provided excellent insight into the directional information utilised by and integrated into the heading direction networks of insects, understanding exactly how insect are able to steer with respect to multiple orientation cues, remains to be answered. It is here my thesis begins.

Because of its relatively straightforward orientation behaviour, the ball-rolling dung beetle provides an excellent model in which to study *the heading direction network* and the factors by which it is influenced. Found on all continents of the globe (except for the Antarctic), differing in shape, colour and size, these animals have one distinct behaviour in common; the ability to gather and shape a piece of dung into a ball and roll it away from the dung pat in as straight of a trajectory as the terrain allows (**Paper I**; **Paper II**; **Paper III**; Baird et al., 2010; Byrne et al., 2003; Dacke et al., 2013a; Dacke et al., 2013b; Dacke et al., 2014; Dacke et al., 2021).

By investigating how *size* (**Paper I**), *ecological niche* and *phylogeny* (**Paper II** and **Paper III**) and *visual conditions* (**Paper IV**) influence the straight-line orientation behaviour of these insects, I explore the challenges faced, and the solutions presented by their heading direction networks. With my work, I hope to provide an insight to the dynamic nature of the biological compass and its ability to change and adapt to different visual environments.

The ball-rolling dung beetle

With over 6000 species (Cambefort and Hanski, 1991*b*) dung beetles represent a substantial range and variety in morphological and ecological niche. Common for most is their affinity for dung, however the way it is consumed varies. In principle, dung beetles can be categorized into three functional types: *endocoprids* (dwellers), *paracoprids* (tunnelers) and *telecoprids* (rollers).

While *endocoprids* feed directly on the dung pat, *paracoprids* form tunnels underneath the pile, disappearing with a piece of dung to their chambers where they consume it in peace. For *telecoprids*, encompassing nearly 600 species of dung beetles, the interaction with dung can stretch several tens of meters away from the dung pile (**Paper I**). These beetles shape a piece of dung into a ball which they roll away from the pat. This behaviour is believed to be derived as a means of escaping the fierce competition for dung at the pat (Cambefort and Hanski, 1991*a*). After around 6 minutes of rolling (Dacke et al., 2019), the ball-rolling dung beetle will burrow into the ground with its ball. Once the beetle has consumed the dung, it emerges from the ground, commences the quest for food and starts the cycle all over again.

Box 1. Navigation and Orientation

Travelling insects can guide their forward route using one of two primary strategies:

Navigation. Navigation requires the use of a compass that informs the animal of its direction in relation to a set reference point, no matter where the animal is in space. Navigation can, in principle, be categorized into two classes: *long-distance migration* and *homing.*

Long-distant migrants, such as Bogong moths, navigate to the Alpine caves using a magnetic compass in conjunction with landmarks (Dreyer et al., 2018) and monarch butterflies reach their overwintering grounds in Mexico by the use of their time-compensated sun compass (Perez et al., 1997).

Homing by path-integration also requires an odometer. Ants and bees (Collett, 1996) continuously keep track of the distance travelled (by their odometer) and their global direction (by their compass) in relation to a select goal (their nest or food source). This information is then integrated to produce a single ‘home vector’ that takes them directly back to their point of origin.

Orientation. An orienting animal has the aim to travel along a given bearing, but does not necessarily have a select goal. The ball-rolling beetle is an animal that orients; once it has formed its ball of dung, it chooses a seemingly arbitrary heading direction (Baird et al., 2010) and continuously integrates sensory cue information to steer its trajectory straight across the sandy terrain. Essentially, contrary to navigation, the only requirement of the guidance system of an animal that orients is to hold a constant direction in reference to the directional cue.

(continues on next page)

Compass or heading indicator?

There is a notion that animals using directional cue information only for steering - like the ball-rolling dung beetles - do not truly rely on a compass, but instead possess a *heading indicator* (Guilford and Taylor, 2014). A heading indicator will not compensate for the apparent change in position of the external reference cues that are integrated, such as the apparent movement of the sun across the sky over the day. Therefore, simply travelling in constant bearing to this celestial reference cue would steer the animal in close to opposite directions in the morning and in the afternoon. For short term movements, such as the ball-rolling journey of the beetle (Dacke et al., 2019), this is however not a problem. What constitutes as a ‘heading indicator’ versus a ‘compass’ is still fairly vague, and has yet to be fully accepted in insect navigation literature. For this reason, this distinction is not made in this thesis. It is, nonetheless, important to note to the reader, that in the context of dung beetle orientation throughout this thesis, the term biological compass and heading indicator always refers to the orientation mechanism involving the integration of directional cue information from appropriate sensory signals to steer along a given bearing.

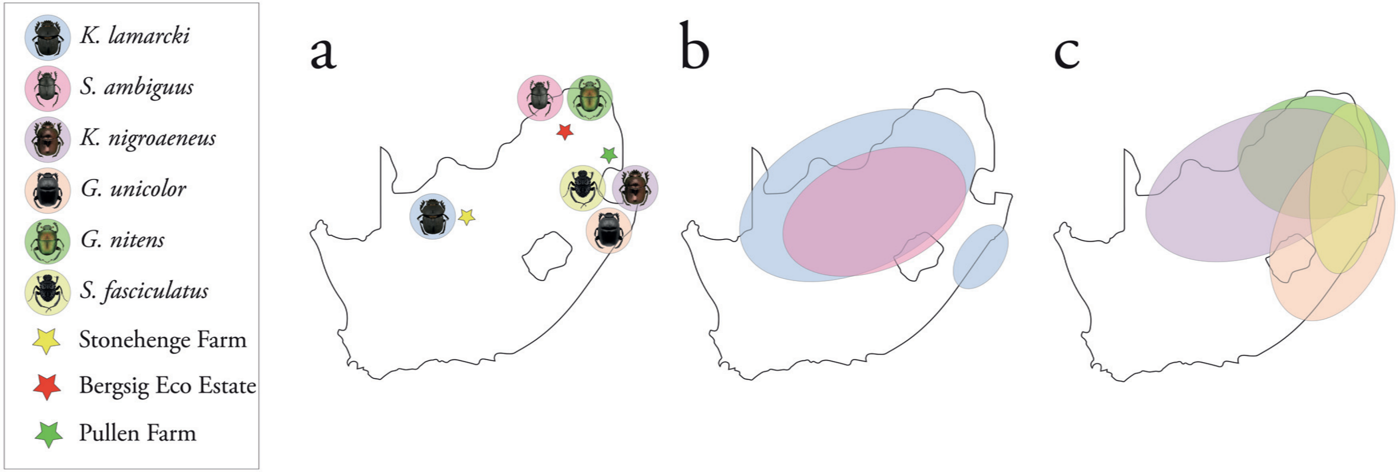
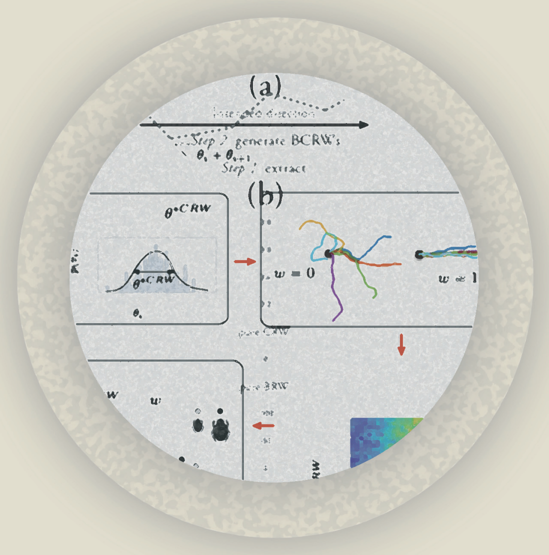


Figure 1. Map of field sites and distribution of species. The behavioural studies presented in this thesis focus on six species of South African ball-rolling dung beetles (*Kheper lamarcki* (**Paper I; II; IV**); *Scarabaeus ambiguus* (**Paper I**); *Kheper nigroaeneus* (**Paper III**); *Garreta unicolor* (**Paper III**); *Garreta nitens* (**Paper III**); *Sisyphus fasciculatus* (**Paper II; III**)), collected at three different field sites in South Africa (**a**). A rough estimate of the species distributions across South Africa is shown in **b** and **c** (data modified from *Scholtz and Ranwashe 2021*).


(a)
Step 2 generate BCRW's
$\theta_t + \theta_{t+1}$
Step 1 extract
(b)
$\theta^{*}CRW$
$\theta^{*}CRW$
θ_t
$w = 0$
$w = 1$
pure CRW
pure BRW

The influence of noise in a biological compass system

As the dung beetle rolls across the sandy terrain of the South African savanna, noise unavoidably accumulates in the beetle's motor and sensory system (Rung, 2007). Noise caused from the integration of internal cues generates **motor error**, where the animal's perceived joint position does not match its true joint position, and noise caused from the integration of external cues leads to **compass error**, where the perceived position of a cue does not quite match its true position, consequently affecting the motor output of its straight-line orientation behaviour with each ensuing step.

The ball-rolling dung beetle provides an excellent model to study the influence of noise

Previously, the detailed influence of noise on the ability to maintain a straight course had only been studied mathematically (Cheung et al., 2007). As the primary goal of ball-rolling beetles is to maintain a straight bearing while moving forward (**Paper II**; **Paper III**; Dacke et al., 2021), they offer an excellent model species with which to tackle this question from a behavioural point of view. With a wide array of species, ranging from a few millimetres to a few centimetres (Cambefort and Hanski, 1991*b*), this diverse group of insects can help understand how noise affects the biological compass in the absence and presence of external directional reference cues. By studying the effect of motor and compass error on straight-line orientation in two differently sized, but closely related, ball-rolling beetles; *Scarabaeus ambiguus* (pronotum width of 1 cm, body length of 1.5 cm and step size of 1.6 cm) and *Kheper lamarcki* (pronotum width of 2 cm, body length of 3 cm and step size of 2.6 cm) [Scarabaeini] (*Figure 2*), I set out, in **Paper I**, to investigate *i)* how the error associated with each step of the beetle (*step size error*) influences its straight-line orientation behaviour, in the absence and presence of external cues and *ii)* how external and internal directional cue information (self-generated motion signals) is weighted in its heading direction network. I behaviourally estimated the motor error generated per step in both species and used this as an input parameter into *a biased correlated random walk* (BRCW) model (Bailey et al., 2018), developed together with researchers from Harvard University. From the BRCW model, the compass error could be estimated (see *Box 2*) and the weight given to external visual cues over internal proprioceptive cues could be determined.

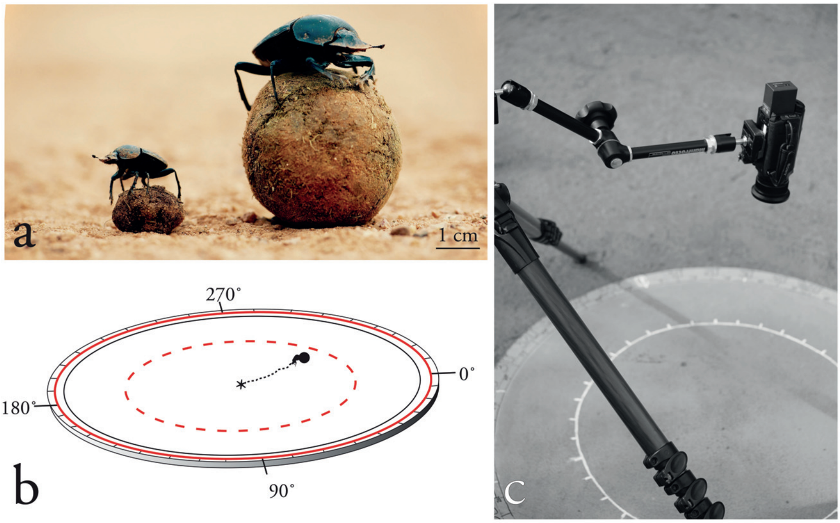


Figure 2. Description of the experimental design (Paper I). Individuals of *Scarabaeus ambiguus* (*left*) and *Kheper lamarcki* (*right*) are depicted side-by-side for size comparison (**a**). *Photo: Christopher Collingridge*. For all treatments, a beetle was placed alongside a ball in the centre of a circular, sand-coated arena (**b**) and filmed with an overhead camera (**c**). The beetle was allowed to roll its ball to the perimeter of the arena, where the exit angle was noted. Three differently sized arenas were used depending on the species tested (**b**): 50 cm (*S. ambiguus* and *K. lamarcki*, black solid line), 33 cm (*S. ambiguus*, red dotted inner circle) and 52 cm (*K. lamarcki*, red solid outer circle) radius.

The role of the sun in straight-line orientation of Scarabaeus ambiguus

To be able to roll along a straight trajectory, the dung beetle, and travelling insects in general, must integrate relevant directional information from appropriate sensory cues into their heading direction network (see *Box 1*). Usually, these cues are derived from two main sources of directional information; internal mechanosensory cues, such as body rotations or leg movements (Bisch-Knaden and Wehner, 2001; Wittlinger et al., 2006) and external reference cues such as sky compass cues (**Paper I-IV**; Byrne et al., 2003; Dacke et al., 2014), terrestrial cues (Cartwright and Collett, 1982; Fukushi and Wehner, 2004) or magnetic cues (Dommer et al., 2008; Fleischmann et al., 2020; Guerra et al., 2014).

Past studies on the large ball-rolling dung beetle, *K. lamarcki*, have undoubtedly demonstrated that in its heading direction network, the directional information provided by the sun is afforded the greatest weight when supporting straight-line orientation (see *Compass cues used by the ball-rolling dung beetle*). However, the role of the sun in the heading direction network of the smaller, closely related, ball-roller, *S. ambiguus*, was up until **Paper I** unknown. Therefore, in this study, I first demonstrated the role of the sun in the heading direction network of *S. ambiguus*. This was done by allowing individuals of this species to roll under an open, clear sky in the presence of a mirrored sun, while simultaneously shading the real sun from the beetle's field of view.

When the apparent position of the sun was changed by 180° with the use of a mirror, *S. ambiguus* responded to this azimuthal change of apparent sun position with the same order of magnitude as its larger cousin, changing its bearing direction by 150° (*K. lamarcki* changed its bearing direction by 140° when presented with the same experimental paradigm). My findings demonstrate that the heading direction network of *S. ambiguus* integrates directional information from the sun to orient, and suggests that, much like its larger cousin, the heading indicator of this beetle predominantly relies on directional information from the sun during straight-line orientation.

Box 2. Biased Random Walk and Correlated Random Walk

Two main random walk models are used to describe how an agent navigates through its environment:

Biased random walk. An agent moving forward, guided by an external cue, is moving by means of a biased random walk (BRW) (Hill and Häder, 1997). Here, the agent will move in a given direction in relation to an external directional cue.

Correlated random walk. If external cues are absent, the animal instead moves by means of a correlated random walk (CRW) (Bovet and Benhamou, 1988; Kareiva and Shigesada, 1983). Here, the agent relies on internal cues and each step is intended to point in the same direction as the previous.

The effect of noise on straight-line orientation

Based on my first findings in **Paper I**, a similar celestial orientation strategy for both the smaller, *S. ambiguus* and the larger *K. lamarcki* could be identified, but the question of the influence of size (or more specifically step length) emerged: if noise is generated by each ensuing step, how does the *step size* of a beetle influence its ability to maintain a straight bearing during straight-line orientation?

I first explored this question from a purely behavioural standpoint. This was done by defining the orientation precision of the beetles' straight-line trajectories when rolling across flat, sanded arenas of different sizes, 20 consecutive times. One arena had a radius of 50 cm, and another two had radii of 32 cm and 52 cm -equivalent to 20 step-lengths of *S. ambiguus* and *K. lamarcki* respectively (*Figure 2b*). In the context of straight-line orientation, orientation precision can be determined from the mean vector length, R, of 10 or more consecutive rolls (Dacke et al., 2019; Foster et al., 2019*; Foster et al., 2021*), where a value of 0 indicates a random distribution of angles (where data is not clearly bimodal), and a value of 1 indicates no dispersion in distribution of angles (*Figure 3*).

From the angular spread in bearing direction over 20 consecutive rolls performed by each species in each paradigm (across a radial distance of 20 steps or 50 cm), it became evident –as expected– that, even under an open sky, with several external directional cues available, the headings travelled by the beetles are subject to noise. In addition, when moving over the same distance, this noise appears to be inversely proportional to the step size of the beetle: when individuals of the smaller *S. ambiguus* and the larger *K. lamarcki* were allowed to roll across a radial distance of 50 cm, the smaller beetle had a significantly shorter mean vector length compared to that of its larger cousin. However, when instead allowed to roll over a radial distance equal to 20 steps, no significant difference in mean vector length was found between the two ball-rollers. The results demonstrate that, over the same absolute distance, the smaller beetle is less able to maintain a straight bearing when rolling under an open sky.

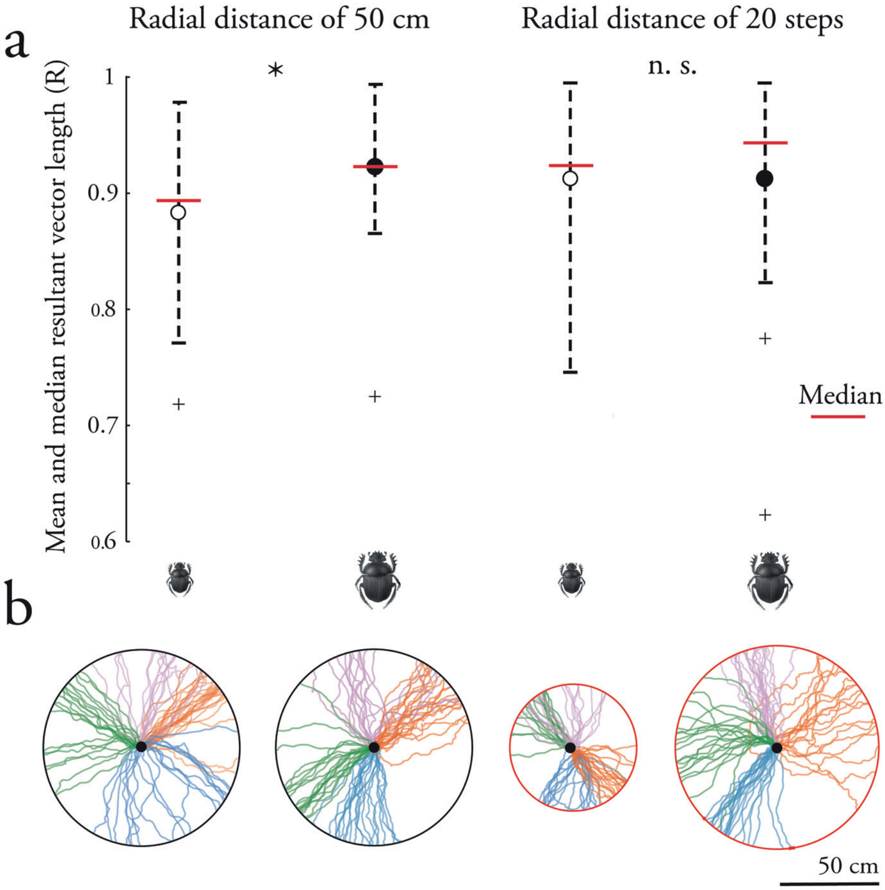


Figure 3. Orientation performance in the presence of external visual cues (Paper I). As a measure of orientation performance (**a**), the mean vector length for each beetle was calculated from 20 trajectories over a radius equivalent of 50 cm, as well as of a radius equivalent of 20 step lengths of the corresponding species (32 cm for *Scarabaeus ambiguus* and 52 cm for *Kheper lamarcki*) (*white circle*: mean value for *S. ambiguus*; *black circle*: mean value for *K. lamarcki*; *red solid line*: median value for *S. ambiguus* and *K. lamarcki*). An R-value of 1 indicates that the beetles maintained the same direction over 20 rolls. When rolling over a radius of 50 cm, the smaller species, *S. ambiguus*, showed a significantly shorter resultant vector length compared to its larger cousin (R(*S. ambiguus*): 0.88 ± 0.02; R(*K. lamarcki*): 0.92 ± 0.01, $p < 0.1$, $N = 20$). However, no significant difference was seen when both species rolled over a distance equivalent to 20 steps (R (*S. ambiguus*): 0.91 ± 0.015; R (*K. lamarcki*): 0.91 ± 0.02, $p = 0.42$, $N = 20$). Paths travelled by four individuals for each species are shown in **b** (from left: *S. ambiguus* (50 cm); *K. lamarcki* (50 cm); *S. ambiguus* (32 cm); *K. lamarcki* (52 cm)). Each colour represents 20 trajectories of one individual. * = $p < 0.05$; n. s. = $p > 0.05$.

The effect of the greater accumulation of noise in smaller verses bigger species of dung beetles can be observed when tracking beetles in their natural habitat: when allowed to roll from the same dung pile in nature (a likely occurrence for these beetles, as they are observed to actively forage within the same habitat (see *Figure 1*)), the total path length to the final burial spot did not differ between the smaller *S. ambiguus* and the larger *K. lamarcki*. Yet, if measured radially, the smaller sized beetles clearly appeared to bury their dung balls at a significantly shorter radial distance from the pile (*Figure 4b*). The correlation between the distance an insect travels and its body size can also be observed in bees and darkling beetles: here, similar to what has been observed in the dung beetles, larger conspecifics tend to forage further than smaller ones (Crist et al., 1992; Greenleaf et al., 2007). A possible explanation for these dispersal differences can be that the accumulation of noise in the compass system of these insects is, much like for the beetles, proportional to the size of the animal. This same size-related phenomenon can also be observed in ants, where over an absolute distance, smaller sized individuals travel more tortuous paths than their larger conspecifics (Palavalli-Nettimi and Narendra, 2018). Interestingly, the results observed in nature suggests that the heading indicator of the beetle does not compensate for the directional challenges faced by the smaller beetles rolling across the same terrain as their bigger relatives and competitors; the noise is inversely proportional to the step size of the beetle. However, the proportion of the noise allotted to motor error versus compass error could not be analysed from the behavioural data alone. For this, a mathematical model was implemented (*Box 3*) with the help of my collaborators at Harvard University, MA, USA.

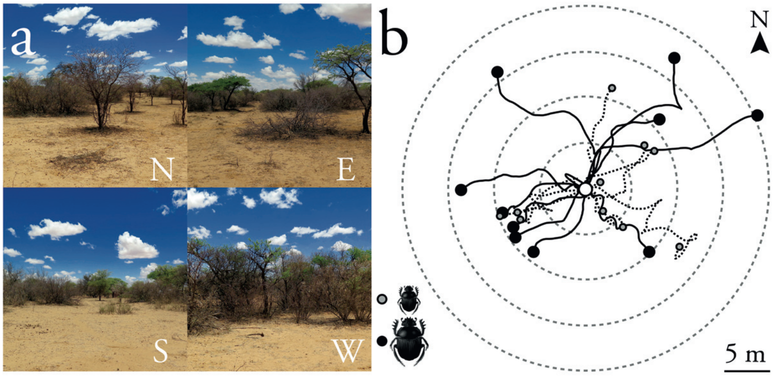


Figure 4. Rolling trajectories of *Scarabaeus ambiguus* and *Kheper lamarcki* in natural terrain (Paper I). The smaller *S. ambiguus* and the larger *K. lamarcki* were allowed to form a dung ball and roll it away from a dung pat in their natural environment (*N*: north; *E*: east; *S*: south; *W*: west.) (**a**). Their trajectories (*dashed black line*: *S. ambiguus*; *solid black line*: *K. lamarcki*), were recorded until they started to bury their balls (*grey circles*: *S. ambiguus*; *black circles*: *K. lamarcki*) (**b**). Compared to the larger *K. lamarcki*, *S. ambiguus* rolled a significantly shorter radial distance from the pat before burying its ball (*S. ambiguus*; 7.56 m ± 1.05 m, *K. lamarcki*; 12.45 m ± 1.28 m, *N* = 10) ($p < 0.01$, Wilcoxon Rank Sum).

Box 3. Compass error can be estimated using a biased correlated random walk model

A biased correlated random walk model (Bailey et al., 2018) was used to estimate the compass error and determine the relative weighting of internal and external cues in the heading direction network of the beetle. The behaviourally extracted values given for the motor errors for each species, were implemented in the model as input parameters (*Figure 5, step 1*). From here, trajectory examples were extrapolated, ranging from conditions when the agent is only reliant on internal cues (a pure CRW), to when the agent is only reliant on external cues (a pure BRW) (*Figure 5, step 2*). From these simulations, mathematically generated mean vector length (R) values were created that were in turn compared to the experimentally obtained mean vector length values attained from rolling the beetles under an open sky (*Figure 5, step 3*). When fitting the experimentally obtained R-values with the modelled ones, compass errors of 1.16° (*S. ambiguus*) and 1.31° (*K. lamarcki*) could be extracted. Furthermore, the balance between compass errors and motor errors (termed w, where the limit of a pure CRW is $w = 0$, and a limit of pure BRW is $w = 1$) was estimated by the model and determined to $w = 0.84$ for *S. ambiguus* and $w = 0.83$ for *K. lamarcki*. Interestingly, like the motor errors, the compass errors and the balance between these two sources of errors did not differ for the two species (*Figure 5, step 4*). This indicates that the compass system of the differently sized beetles is not designed to compensate for the faster accumulation of errors generated by the smaller navigator as it exits from the dung pat.

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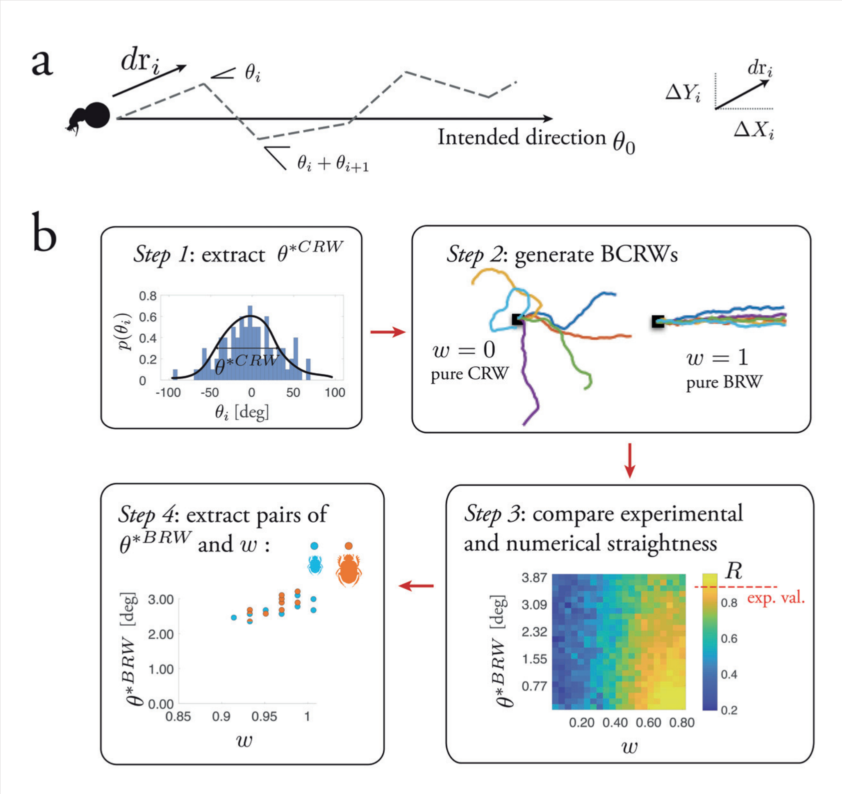


Figure 5. Estimation of motor errors, compass errors, and their balance (Paper I). A model of a beetle performing a random walk, where θ_i is the direction of movement of the previous step and ΔX_i, ΔY_i are the distance travelled in step *i* along the x and y directions, respectively (defined in Eq. 1,2 of **Paper I**) (**a**). A flow diagram describing the process of estimating the acquisition error, θ^*BRW , and the balance between the two sources of noise, *w*, for the two differently sized beetles, *S. ambiguus* and *K. lamarcki*. ***Step 1***: In the absence of external cues, the directional error generated by the beetle is equal to the execution error, θ^*CRW, and can thus be behaviourally estimated. ***Step 2***: From the model, BCRW trajectories ranging from the limit of pure CRW (*w* = 0) (*left*) to a of pure BRW (*w* = 1) (*right*) can be generated. ***Step 3***: The mean vector length (R) for each species is generated from the simulation and compared to the experimentally measured values (shown as red dotted line on the colour bar). ***Step 4***: From step 3, pairs of the acquisition error, θ^*BRW, and the balance between the two sources of noise, *w*, can be extracted for each species.

Determining motor and compass error

When integrating directional information from both internal and external cues to steer straight under a clear sky, the directed movements of the dung beetle could best be represented by the means of *a biased and correlated random walk* (BCRW). According to this model, the noise accumulated in each step is generated from the integration of internal as well as external directional cues. In order to separate these two sources of noise, we needed to first extract the noise generated by internal cues exclusively. In the absence of other cues, motor output is governed solely by proprioceptive cues. For a beetle rolling in complete darkness, the angular error generated by each step can therefore acts as a proxy for motor error.

Motor error is determined in the absence of external directional cues

Any agent moving forward relying on internal mechanosensory information alone, will not succeed in travelling any greater distance from its initial location. This is because each subsequent step taken by the agent will deviate slightly from the former direction, ultimately causing the agent to stray from its intended route (Cheung et al., 2007; Cheung et al., 2008). Despite this predicament, there are animals that rely solely on internal proprioceptive cues for directed movements. These include hunting spiders, that find their way back to the food site using internal information from their lyriform slit-sense organs alone (Barth and Seyfarth, 1971), or cockroach larvae, that navigate back to their shelter using only kinaesthetic cues (Durier and Rivault, 1999). However, in these situations, the distances travelled are comparably short, limiting the accumulation of mechanosensory noise. Animals that travel relatively far, like the dung beetles (around 10-20 m, see *Figure 4b*), must instead use external compass cues in combination with internal cues to successfully orient or navigate (Cheung et al., 2007; Collett, 1996; Dacke et al., 2020; Heinze et al., 2018; Kim and Dickinson, 2017; Srinivasan et al., 1996).

To determine the motor error generated by each beetle species, individuals were allowed to roll in complete darkness. Interestingly, when rolling devoid of external visual cues, the trajectories of each species differed in straightness (Batschelet, 1981) over a radial distance of equal absolute length (50 cm), but not equal relative length (20 steps of the species) (*Figure 6*). These results are similar to those found under the open sky, indicating that the noise generated per step is the same in the two beetle species. From the trajectories of both species, angular error per step was calculated as the absolute difference in bearing direction between two consecutive foreleg-surface contacts, and from this, motor errors of 33° for *S. ambiguus* and 29° for *K. lamarcki* could be determined.

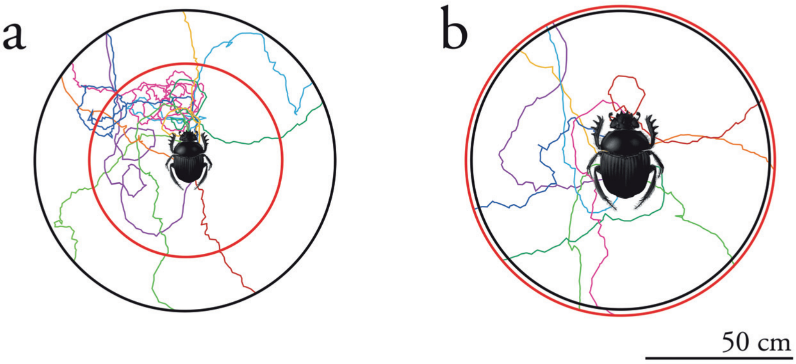


Figure 6. Rolling trajectories in the absence of visual cues (Paper I). When allowed to roll a dung ball from the centre of a flat, sand-coated arena, in complete darkness, *Scarabaeus ambiguus* (**a**) obtained a significantly higher tortuosity than *Kheper lamarcki* (**b**) over a radial distance of equal absolute length (50 cm radius, *black perimeter*). Over a radial distance corresponding to 20 steps for each species respectively (*red perimeter*), no significant difference in tortuosity was recorded between the species.

Compass error is estimated through a biased and correlated random walk model

Once the amount of motor error was estimated, this could be included in our model and used to estimate the noise generated by the integration of external compass cues into the heading direction network (compass error). This then allowed us to estimate the weight given to internal and external cues in the heading direction network of the beetle as it rolls across the savanna.

From the trajectories of the beetles under the open sky, it is apparent that there is some noise present in the beetle's heading indicator when rolling outside. However, due to their relatively straight trajectories across the flat, sanded arena (R value over a radius of 20 steps: R (*S. ambiguus*) = 0.9; R (*K. lamarcki*) = 0.9), it is clear that this noise is smaller than what is generated in the dark (compare *Figure 3* and *Figure 6*). Not surprisingly, from our model (see *Box 3*) the compass error of 1.16° per step for *S. ambiguus* and 1.31° per step for *K. lamarcki* was significantly less than the motor error found for each species (33° for *S. ambiguus* and 29° for *K. lamarcki*). What is interesting is that the noise generated by the integration of internal cues as well as external cues is inversely proportional to the step size of the beetle. This indicates that the heading direction network of the smaller beetle is just as precise as that of the larger, further highlighting that the heading direction network of the smaller beetle is not evolved to compensate for the directional challenges that arise due to differences in stride length. This can be an energetically expensive disadvantage for an orienting insect that aims to travel the same distance irrespective of size, but as my study suggests (*Figure 4b*) burying at different distances from the dung pile might be an advantage, as it decreases the chances of beetles ending up burying in the same spot, thus limiting the opportunity of competitors to steal another beetle's ball.

In addition to estimating the compass error, our model also estimated the relative weight of internal proprioceptive cues and external reference cues under the open sky. It was found that this relative weight in the heading indicator of the beetle, when rolling outside, was significantly shifted to external reference cues, allotting approximately 85% of the directional weight in the heading direction network to external cues. This applied to both species, and stand in line with our previous observations of ball-rolling dung beetles and their dependence on celestial cue input for straight-line orientation (Dacke et al., 2013b; Dacke et al., 2019; Foster et al., 2021*; el Jundi et al., 2015a*).

Compass cues used by the ball-rolling dung beetle

As it makes its way around small bushes and tufts of grass, a savanna-living ball-roller –or rather, its brain– integrates relevant directional information from several different compass cues. To maintain its bearing, the brain continuously compares the desired heading with the current one, adjusting for any deviations in the beetle's path, until a suitable place to bury and consume its ball is found. The end of the ball-rolling adventure is very likely determined by the terrain (Osberg et al., 1993; Osberg et al., 1994), as well as the size of the ball-roller (for more see *The influence of noise in a biological compass system*). In general, the directional information used to guide animals throughout their journey, depends on the availability of cues and the navigator's ability to detect them. Here, I describe the most prevalent compass cues used by ball-rolling dung beetles (and other travelling insects).

The sun

The sun plays a dominant role in the heading direction network of many diurnal ball-rolling dung beetles

The sun compass in honeybees was discovered over 60 years ago (Frisch and Lindauer, 1956), clearly demonstrating that honeybees use directional information from the sun to navigate to their food source. Ever since then, a vast range of arthropods have been confirmed to utilise directional information from the sun to guide their navigational tasks: monarch butterflies and other migratory butterflies use this information to guide their routes over long distances (Merlin et al., 2009; Mouritsen and Frost, 2002; Nesbit et al., 2009; Perez et al., 1997), sandhoppers reference this celestial body to get themselves to and from the shore (Forward et al. 2009; Scapini, Fallaci and Mezzetti 1996; Williamson 1951), desert ants integrate directional information from the sun to navigate back to the nest (Lebhardt and Ronacher 2015; Muller and Wehner 2006) and dung beetles use it to steer straight across the savanna (**Paper I**; **Paper III**; Byrne et al., 2003; Dacke et al., 2014; Dacke et al., 2019; el Jundi et al., 2015a*; Smolka et al., 2016).

For most diurnal ball-rolling dung beetles studied in the context of straight-line orientation, directional information from the sun receives the greatest relative weight in their heading direction network (**Paper I**; **Paper II**; Byrne et al., 2003; Dacke et al., 2014; Dacke et al., 2019; el Jundi et al., 2015a*). This is demonstrated by using the simple, yet powerful method of reflecting the apparent position of the sun with a mirror, while simultaneously obstructing the real sun from the animal's field of view. Responding to the positional change of the apparent sun, while the position of all other celestial cues, such as the celestial polarised light pattern (Horváth et al., 2014; Pomozi et al., 2001; Suhai and Horváth, 2004) as well as the intensity (Warrant et al., 2020) and colour gradient of the sky (Coemans et al., 1994) remain unchanged, is a clear indication of the relatively high weight given to the directional information provided by the sun in the heading direction network of the animal.

Apart from studies in dung beetles, this classic 'mirrored sun' method has also been used in various other studies of arthropods, such as ants (Wystrach et al., 2014), sandhoppers (Pardi and Papi, 1953) and marine isopods (Ugolini and G, 1988). For the dung beetle, a dominant use of the sun as a directional cue is not only demonstrated for *Kheper lamarcki* (Dacke et al., 2014; Dacke et al., 2019; el Jundi et al., 2015a*), but also for *Pachysoma femoralis* (Byrne et al., 2003), *Scarabaeus ambiguus* (**Paper I**) and *K. nigroaeneus* (**Paper III**), all present in similar visual environments.

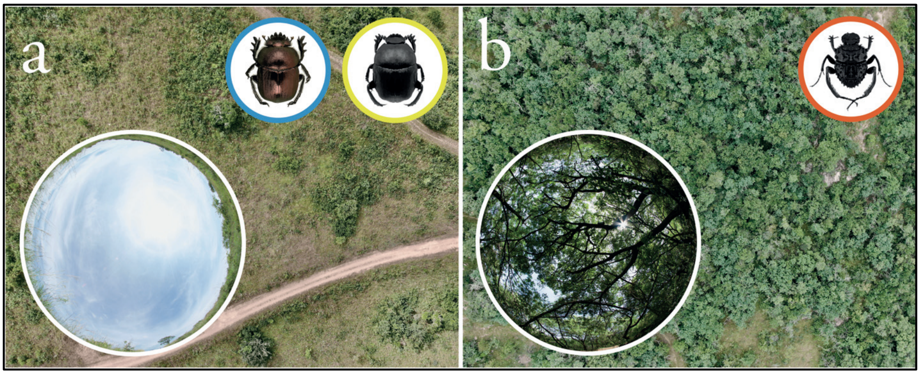


Figure 7. Beetles from three tribes of ball-rollers and the bioregions they inhabit (Paper III). Beetles from three tribes of ball-rollers (*blue circle*: Scarabaeini; *yellow circle*: Gymnopleurini; *orange circle:* Sisyphini) can be found in the same bioregion. *K. nigroaeneus* and *G. unicolor* are predominantly found actively foraging the open region (**a**) and *S. fasciculatus* predominantly forages within the closed region (**b**) of this bioregion. A 180° view of the sky as seen from the ground perspective of the beetle is included at the bottom of each panel.

The influence of visual environment on the weight relationship of cues

Since the weight relationship of directional cues in the heading direction network of an animal could depend, in part, on the availability of the cues and the ability of the navigator to detect them, the visual environment is very likely to affect the navigational strategy. For example, desert ant species present in largely landmark-free saltpans, have a higher propensity to rely more on their path integrator over terrestrial cues, while species inhabiting cluttered, landmark-rich environments rely more heavily on landmarks for route guidance (Bühlmann et al., 2011; Cheng et al., 2012). This suggests that the visual ecology of the animal can influence how directional information is weighted in the heading direction network of the animal.

Our knowledge regarding the role of the sun in diurnal dung beetles had, prior to my work in **Paper II**, been limited to species primarily orienting under open, blue skies. However, as ball-rolling beetles are found on all continents except Antarctica, in habitats spanning the deserts of South Africa, to the rainforests of Brazil, I sought out to study the straight-line orientation strategy of beetles in a different visual environment, exploring how the weighting of directional information of the sun in the compass of the dung beetle is influenced by the habitat in which it is active.

The role of the sun in the woodland-living beetle

Contrary to its distant cousins, who are primarily found in dryer, sandy savanna regions (Cambefort and Walter, 1991*c*), the tiny woodland-living beetle, *Sisyphus fasciculatus*, is often found in more humid and vegetation-rich areas (Daniel et al., 2020; Mucina and Rutherford, 2006; Paschalidis, 1974; Scholtz and Ranwashe, 2020) (**Paper III**) (*Figure 1* and *7*). In these types of habitats, the sun is frequently obstructed from view, while wide-field cues (such as the pattern of polarised skylight) remain visible through the overhead canopy (Endler, 1993; Hegedüs et al., 2007; Shashar et al., 1988). Is it possible that beetles active in this type of habitat, attribute the greatest relative weight to directional information provided by this wide-field sky cue, rather than by the sun itself?

To test this hypothesis, I allowed individuals of the beetle *Sisyphus fasciculatus* to steer their dung balls in the presence of a mirrored sun under a clear sky, while simultaneously blocking the real sun from view. In accordance with my hypothesis, the tiny beetles would keep rolling in the same direction as before, completely ignoring the apparent positional change of the sun (*Figure 8a, graph 1*), indicating that the sun compass does not dominate the heading direction network of *S. fasciculatus*.

Considering that nearly all insects, such as bees (Evangelista et al., 2014; Frisch and Lindauer, 1956), ants (Lebhardt et al., 2012; Reid et al., 2011), crickets (Herzmann and Labhart, 1989), locusts (Mappes and Homberg, 2004) and flies (Hardcastle et al., 2020; Warren et al., 2019), derive compass information from the skylight polarisation pattern, a natural second step in my study was to test how the beetles respond to the rotation of the celestial polarisation pattern. Placed underneath a UV transparent polariser, I allowed individuals of *S. fasciculatus* to exit underneath the filter in full view of a clear sky. Prior to the second roll, the polariser was rotated by 90°, in effect turning the artificial band of skylight polarisation. Under this condition, these tiny rollers would change their bearings by approximately 85°, demonstrating that, under the bright, clear sky, with the sun fully available, the heading direction network of these beetles attributed greatest relative weight for guidance to the directional information provided by the pattern of polarised skylight (*Figure 8b, graph 1*). It is however important to note that, under the appropriate circumstances, the woodland-living beetle can indeed obtain directional information from a point-light source. If presented with a single green light spot (a credible replacement for the sun to a beetle (el Jundi et al., 2015a*), *S. fasciculatus* responds in accordance with a 180° azimuthal displacement of this light (*Figure 8c, graph 1*), by a 185° change in bearing. In summary, my results clearly show that the heading direction network of *S. fasciculatus* attributes greatest relative weight to the directional information provided by the wide-field celestial polarisation pattern, contrary to what has been shown previously in other diurnal beetles.

The findings of **Paper II** ascribe to a weighting strategy similar to that found in the ant; as homing ants, that find their way back home using their path integrator and the guidance of landmarks, are further displaced from their nest, the relative weight of these two reference cues shifts in favour of the former, affording greatest relative weight to the most reliable source of directional information in the habitat (Wystrach et al., 2015). In the case of *S. fasciculatus*, this is naturally the polarised pattern of skylight.

My findings of this little wood-land living dung beetle prompted a deeper investigation into the possible adaptive values of assigning the greater relative weight to directional information provided by a particular celestial cue. In addition to the marked differences in their habitat preference (*Figure 7*), there are distinct inter-tribal discrepancies in body size, eye shape and rolling strategy in the beetle species of these two tribes (Tocco et al., 2019; Tocco et al., 2021) (for an in-depth discussion regarding these properties, see *The influence of noise in a biological compass system* and *The Compound Eyes*) (*Figure 14* and *16*). Owing to, not only the ecological differences, but also the morphological inter-tribal differences, the question arose: Is the relative weight influenced exclusively by the visual ecology of the species?

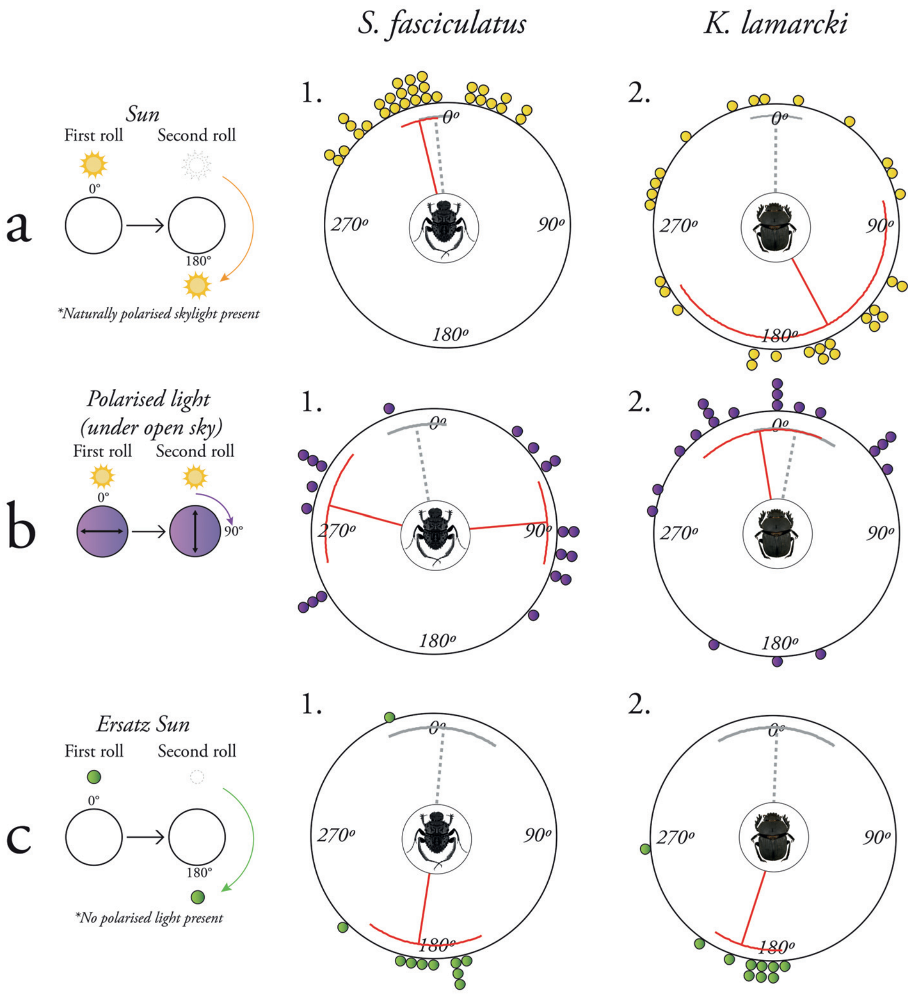


Figure 8. Response to directional changes of compass cues (Paper II). *Sisyphus fasciculatus* and *Kheper lamarcki*, were allowed to roll their dung balls to the perimeter of a circular arena under an open sky (**a**, **b**) or in the presence of an artificial sun in an indoor lab (**c**). Once the beetle had reached the periphery of the arena, it was removed from its dung ball and placed back in the centre alongside its ball. At this time, the position of the tested cue (**a**: sun, **b**: polarised light or **c**: green light spot) was changed. The apparent position of the real sun (**a**, *orange arrow*) or the green light spot (**c**, *green arrow*) was switched by 180° and the apparent e-vector direction was turned by 90° using a polarisation filter (**b**, *purple arrow*) The absolute angular difference between the first and the second exit angle represent the response to the treatment (*test*) (**a**, *yellow circles*; **b**, *purple circles*; **c**, *green circles*). Beetles were then allowed to roll a third time, with the manipulated cue moved back to its initial position. The mean angular difference between the first and second exit (*test*), and the first and third exit (*control*), is represented by a red solid vector and a grey dotted vector, respectively, in each graph. Error bars represents one circular standard deviation.

Directional information from the sun is integrated differently in beetles from different tribes

To answer my questions concerning the possible relationship between the visual ecology of the species and its heading direction network, I next chose to study the straight-line orientation strategy of three species from three different tribes of dung beetles: *Kheper nigroaeneus* [Scarabaeini], *Sisyphus fasciculatus* [Sisyphini] and *Garreta unicolor* [Gymnopleurini], all present in the same region, but actively foraging in vastly different habitats (*Figure 7*).

To understand the relative weight of directional information from the sun and the celestial polarisation pattern in these three species, I allowed individuals from each species to roll in the presence of a sun, as well as underneath a UV transparent polariser in the presence of the sun. When changing the apparent position of the sun by 180°, only *K. nigroaeneus*, showed a marked response to this change through a changing in heading of 200° (*Figure 9b, graph 1*). This was not unexpected; although *K. nigroaeneus* is primarily found in a different region to its very close relative, *K. lamarcki* (known to rely primarily on the sun), both species carry large dorsal eyes (the size of the eyes might play a role in weighting strategy: see *The Compound Eyes*) and forage under open, clear skies. Only when the sun was obstructed from the beetle's view, would *K. nigroaeneus* respond to the 90° turn of the polariser with a change in bearing approaching 70° (compare *Figure 9c, graph 1* and *Figure 9d, graph 1*). This is similar to previous results in *K. lamarcki* (el Jundi et al., 2014a); when the predominant cue (the sun) is hidden from view, the beetles respond to the 90° e-vector turn of the polarised skylight. Following this logic, *S. fasciculatus* (which attributes the greatest weight to the skylight polarisation (**Paper II**)), should not respond to a mirrored sun under a clear sky, but turn with the polariser under the same clear sky. This was exactly what was observed (*Figure 9b-c, graph 3*).

What is interesting is that *Garreta unicolor* (and *G. nitens,* data not shown) did not respond to either of these manipulations (*Figure 9b-c, graph 2*). Only when the position of both compass cues was manipulated, by mirroring the sun by 180° while simultaneously turning the polariser by 90°, did these beetles change their bearings (*Figure 9e, graph 2*). However, the response appeared to be randomly distributed. It is important to note that the beetles maintained a straight trajectory when rolling, and as soon as the real sun was revealed and the polariser was turned back to its original position, would the beetles resume their initial direction of travel. In addition, *K. nigroaeneus* was also tested under this multi-conflict paradigm, and showed a clear response to the mirrored sun (*Figure 9e, graph 1*). Most likely, a similar outcome would have been seen for *S. fasciculatus* but, no matter how hard we tried, we could not manage to get these small beetles to behave under this paradigm. Another important note is that *G. unicolor*, just like *K. nigroaeneus* and *S. fasciculatus*, is able to orient to a green light spot (*Figure 9a*), indicating that all three beetles can orient to directional information provided by a point-source light.

G. unicolor is found actively foraging under open skies, much like *K. nigroaeneus*, but contrary to its larger distant cousin, it has a narrow, oval-shaped dorsal eye region, much like that found in *S. fasciculatus* (*Figure 14* and *16*). A narrow dorsal eye might encompass a smaller visual field (Cronin et al., 2014; Land, 1997; Land and Nilsson, 2012; Rutowski et al., 2009; Taylor et al., 2019), therefore it could be more beneficial for *S. fasciculatus* and *G. unicolor* to rely on directional information from a sky-wide cue, rather than using the position of a single light source. Thus, these inter-tribal differences might be an additional influence on how species within each tribe weight the sources of directional information they can reliably use higher.

The differing strategy seen in *G. unicolor* can perhaps be explained by the fact that each individual follow their own weighting strategy, wherein some individuals afford greatest relative weight to the sun, turning towards 180° in response to the mirror, some turn with the 90° turn of the polariser, and some remain on the same path, following the remaining sky cues, such as the intensity and colour gradient (see *Spectral and intensity gradient*). However, if this would have been the case, we would have seen a similar spread in bearings in the other conditions as well, which we did not (*Figure 9a-d, graph 2*). Another, more plausible, explanation could be that directional information from the sun and polarised light are near equal in weight, therefore any small individual 'preference' of one cue over the other will be seen as large differences in angular change. It would be of great interest to see how these beetles would respond if both the azimuthal position of the sun and the band of skylight polarisation were rotated by the same angular distance. Would a 90° turn of both cues elicit a 90° turn of the population? Or will the response of the population also here appear random? Unfortunately, due to experimental constraints, this was not possible to test in this study. In **Paper IV** this problem is solved (for more, see *Examining the weight relationship of the sun and polarised skylight by proxy*). For the moment however, the random spread of changes in bearings observed for *G. unicolor* cannot be fully explained.

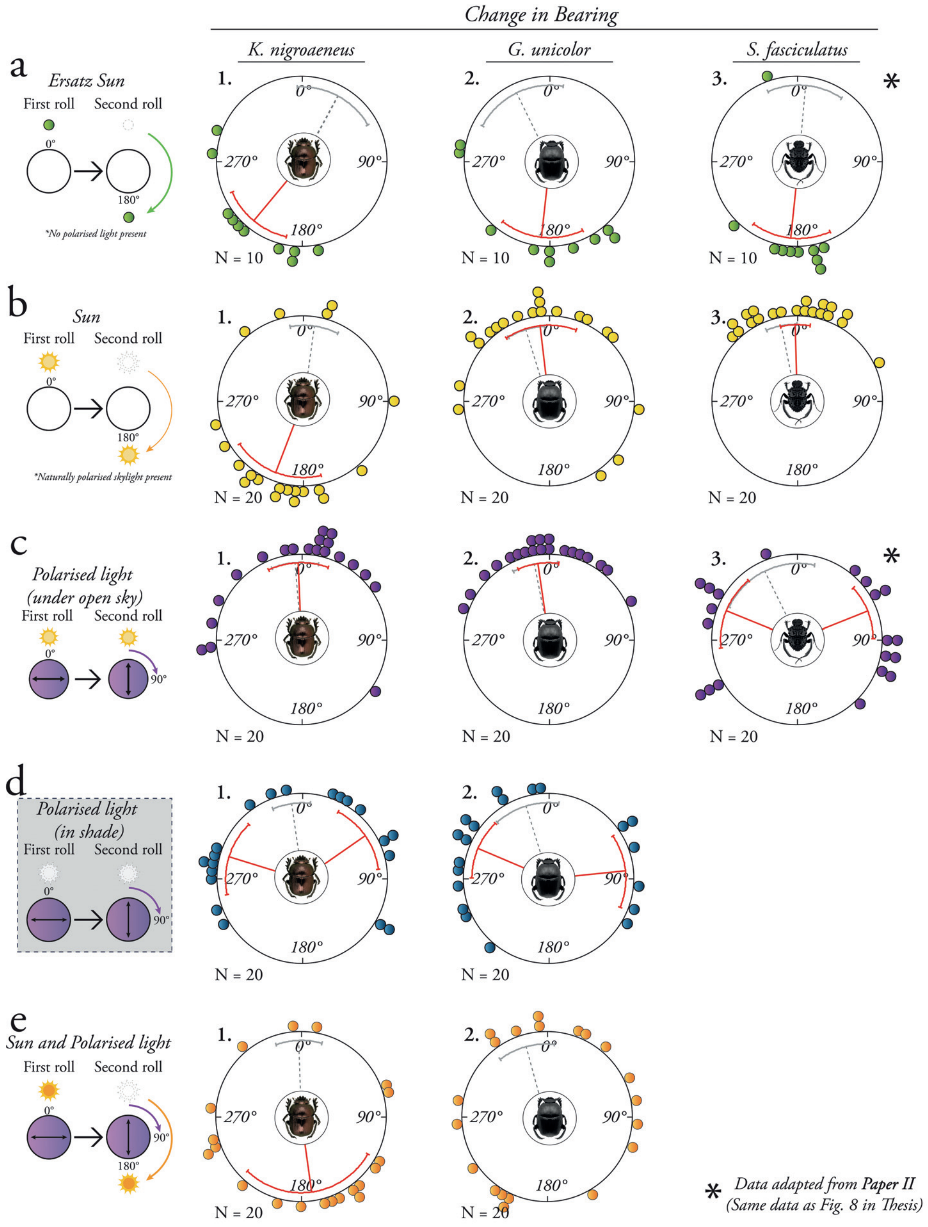


Figure 9. See next page for legend.

Figure 9. Response to directional changes of compass cues (Paper III). Three diurnal dung beetle species (from left to right: *Kheper nigroaeneus*, *Garreta unicolor* and *Sisyphus fasciculatus*) were allowed to roll their balls of dung out of a circular arena in a darkened room (**a**) or outdoors under the open sky (**b**), or with a polarisation filter placed above the arena with the sun visible (**c**, **e**) or with a polarisation filter placed above the arena with the sun shielded from view (**d**). Once the beetle had reached the periphery of the arena, it was removed from its dung ball and placed back in the centre alongside its ball. At this time, the apparent position of the ersatz sun (**a**, *green arrow*) or the real sun (**b**, *orange arrow*) was switched by 180°, the apparent e-vector direction was turned by 90° using a polarisation filter (**c**-**d**, *purple arrow*) or the position of the sun was changed by 180° while simultaneously turning the apparent e-vector direction by 90° (**e**, *orange arrow*: sun, *purple arrow*: polarisation filter). The beetle was then allowed to exit the arena a second time. The absolute angular difference between the first and the second exit angle represent the response to the treatment (*test*). The beetles were then allowed to roll a third time, with the manipulated cue(s) moved back to its/their initial position. The mean angular difference between the first and second exit (*test*), and the first and third exit (*control*), is represented by a red solid vector and a grey dotted vector, respectively, in each graph. Error bars represents one circular standard deviation. The data presented for *S. fasciculatus* in **a** and **c** (graph 3, respectively) is adapted from **Paper II.**

Box 4. The celestial pattern of polarised light

Linear polarised light

The light emitting from the sun is composed of light waves with electric field vectors, *e-vectors*, oscillating in all possible orientations perpendicular to their direction of travel (*Figure 10*). As sunlight reaches the atmosphere, it collides with air molecules and scatters. Following this, the e-vector component of the light wave oscillates to a higher degree in one plane over others, becoming partially polarised. The extent to which this component oscillates in one certain direction over others determines the light's *degree of linear polarisation* (Strutt, 1871; Suhai and Horváth, 2004). A light wave that contains an e-vector in only one plane is considered fully linearly polarised (100% polarisation). The highest degree of linear polarisation in the sky is present directly perpendicular to the sun and decreases sinusoidally towards the sun and anti-sun (Strutt 1871) (*Figure 10a*).

Although largely invisible to us, many insects, such as dung beetles (**Paper II**; Dacke et al., 2003; Foster et al., 2019*; Jundi et al., 2015a*), ants (Legge et al., 2014; Müller and Wehner, 2007; Wehner, 2003), bees (Evangelista et al., 2014), locusts (Mappes and Homberg, 2004), crickets (Henze and Labhart, 2007), flies (Warren et al., 2019; Weir and Dickinson, 2012) and butterflies (Froy et al., 2003; Heinze and Reppert, 2011; Reppert et al., 2004) perceive this celestial pattern of polarised light through their *dorsal rim area* (a specialized region in the compound eyes of insects (see *The Compound Eyes*), and use it as a directional cue during navigation and orientation.

(*continues on next page*)

Circularly polarised light

Under certain circumstances, the e-vector component of two light waves can be out of phase. In this case, the resultant e-vector changes its direction over time, resulting in a spiral of the e-vector direction (*Figure 10b*). If the light waves are out of phase by 90°, the light becomes *circularly polarised* (Cronin et al., 2014; Land and Nilsson, 2012). While circularly polarised light does exist in nature, its production and detection are limited to only a few groups of animals, including some scarab beetles and marine stomatopods (Brady and Cummings, 2010; Brink et al., 2007; Chiou et al., 2008). However, as most behaviours known to be controlled by polarised light, are done so by linearly polarised light, all references to polarisation and polarised skylight throughout this thesis refers to its linear form.

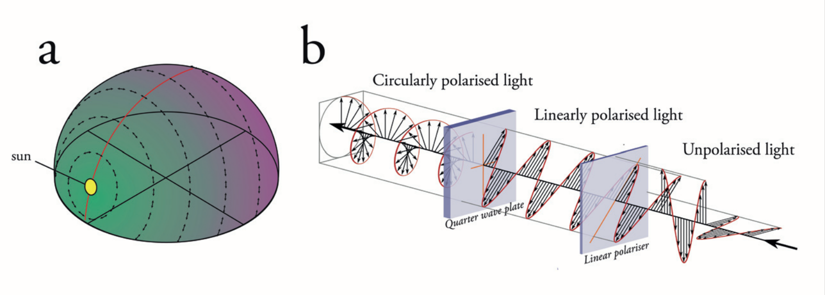


Figure 10. Polarised light and the alignment of e-vectors in relation to the sun. In the sky, the electric field vectors (*e-vectors*) (*black small arrows*) of the polarised skylight are arranged in concentric circles around the sun in a symmetrical fashion along the solar meridian (*red line*) (**a**). The maximum degree of polarisation can be found 90° from the sun. In addition, as the solar hemisphere contains a relatively higher amount of long-wavelength light (green), and the antisolar hemisphere contains relatively more short-wavelength light (UV, depicted in the image as purple), a spectral gradient forms across the sky. A schematic drawing of an *unpolarised*, *linearly polarised*, and *circularly polarised* light beam (*orange wave*) is shown in **b**. The direction of the light beam is depicted by the large black arrow. The e-vector direction along the light beam is depicted by small black arrows. Image in *a* is modified from *el Jundi et al. 2016*; image in *b* is modified from *https://commons.wikimedia.org/w/index.php?curid=9862692*.

Polarised Light

The role of polarised light in the heading direction network of the ball-rolling dung beetle

In **Paper III**, when the apparent position of the sun was displaced by 180°, or the apparent e-vector direction of the celestial polarised light was turned by 90°, *Garreta unicolor* did not respond to either of these manipulations. Only when both cues were manipulated simultaneously would *G. unicolor* change its bearing (*Figure 8b-c* and *e, graph 2*). Based on this curious behaviour of *G. unicolor*, I wanted to further explore the interplay of these two cues in the heading direction network of the dung beetle. More specifically, I aimed to examine how straight-line orientation is affected when the three properties of a polarised light cue (intensity, degree and direction of polarisation) are manipulated and presented with a single, unpolarized light cue (simulating the sun) to the ball-rolling beetle. Could the observed result of *G. unicolor* be a consequence of an equal weighting of directional information of this pair of celestial cues in the heading direction network of the beetle?

Although the obvious choice of species to investigate this interplay would have been *G. unicolor*, geographical constraints, abundancy, and overall fussiness of the beetle, makes it a poor candidate for this investigation. Instead, because of its robust nature, calm temperament, and high availability, *Kheper lamarcki* was selected to address this question. In addition, and perhaps more importantly, close to twenty years in the field studying the straight-line orientation of this species have provided a plethora of knowledge regarding its orientation system, on a behavioural as well as neuronal level, making it a superb candidate for my last study of this thesis.

Examining the weight relationship of the sun and polarised skylight by proxy

Exploring the interplay of the sun and the polarised skylight under natural conditions presents some obvious challenges. First, as discussed previously for **Paper III**, changing the azimuthal position of both cues equally, i.e., turning the apparent position of the sun by 90° to match the maximum possible angular change of the e-vector, presents its own set of challenges. Second, manipulating the reliability of each cue without compromising the properties of the remaining celestial cues is a difficult (if not impossible) task. Third, there are significant restrictions regarding the properties that can be manipulated. Across a bright savanna sky, the sun and the polarised skylight has virtually reached their upper limit concerning light intensity and degree of polarisation (Foster et al., 2019*; Johnsen et al., 2006; Lythgoe, 1979; Warrant et al., 2020). Due to these constraints, in **Paper IV**, I introduced *K. lamarcki* to artificial compass cues as a proxy for the sun and the polarised skylight pattern (*Figure 11*). By altering the qualities of the polarised light cue, this allowed me to examine how the weight relationship of these two sources is influenced and altered by their reliability in the heading direction network of the beetle.

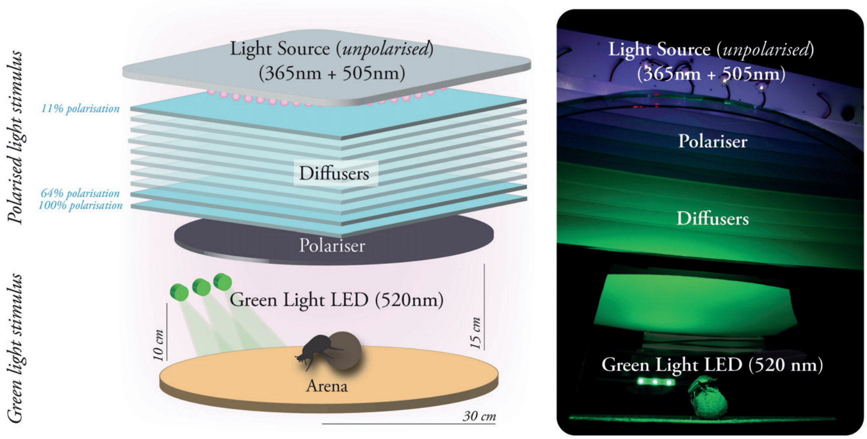


Figure 11. Description of the experimental setup of Paper IV. The experimental setup combined an overhead *Polarised light stimulus* and a laterally presented *Green light stimulus*. The overhead light stimulus was suspended 15 cm above a circular arena of 30 cm radius and consisted of an unpolarised light fixture ('Light Source') of 80 UV light-emitting diodes (365 nm) and 21 cyan light-emitting diodes (510 nm) centred on a square shaped aluminium plate, along with ten sheets of 'Diffusers' (Plexiglas®) arranged in a stacked fashion 1 cm apart, and a polarisation filter ('Polariser'). Depending on the placement of the polarisation filter within the stack of diffuser, the degree of polarisation of light emitted from the overhead light source could be determined. For my experimental purposes, the polariser was placed in three different positions within the setup (highlighted in blue in the figure): *i)* before the stack of diffusers (*11 % polarisation*), *ii)* before the 9th diffuser (*64 % polarisation*), or *iii)* after the stack of diffusers (*100 % polarisation*). The green unpolarised light stimulus (520 nm) consisted of 3 horizontally aligned LEDs (9.5 cm x 0.5 cm) presented to the beetle from either of the four sides of the arena (0°, 90°, 180° and 270°), 30 cm from the arena centre, at a height of 10 cm. *Left image*: schematic depiction of the experimental setup. *Right image*: real image of the experimental setup.

Evidence for two spectrally distinct photoreceptors in the dorsal rim area of Kheper lamarcki

Across the clear, sun-lit sky, the celestial polarisation pattern is highly distinguishable over all wavelengths of light. However, if observed underneath a tree canopy or experienced through a layer of clouds, the maximal degree of polarisation is in the UV range (Barta and Horváth, 2004; Hegedüs et al., 2007; Seliger et al., 1994; Wang et al., 2014). Perhaps, this is why most insects, including honeybees, ants, maybeetles, butterflies and flies (Duelli and Wehner, 1973; Frantsevich et al., 1977; Hardie et al., 1979; Labhart, 1980; Stalleicken et al., 2006) analyse this pattern through a set of UV sensitive photoreceptors. Interestingly, for the diurnal dung beetle *K. lamarcki*, the findings of my co-authors Ayse Yilmaz (Lund University, Sweden) and Gregor Belušič (University of Ljubljana, Slovenia) in **Paper IV** show evidence for polarisation sensitivity in the UV *as well as* the green part of the spectrum (*Figure 12*). This relatively rare finding of two spectrally distinct, polarisation-sensitive types of photoreceptors, has also been observed in the diurnal homing dung beetle, *Pachysoma striatum* (Dacke et al., 2002). This type of spectral sensitivity across a broader spectrum of light can for example favour the absolute polarisation sensitivity of the eyes (Belušič et al., 2017; Eggers and Gewecke, 1993; Labhart et al., 1992). For experimental purposes, the artificial overhead polarised light source presented to the beetles in **Paper IV** was designed to match the maxima of the two spectral sensitivity peaks of the photoreceptors in the dorsal region of the dorsal eye of *K. lamarcki* (*Figure 11* and *12*).

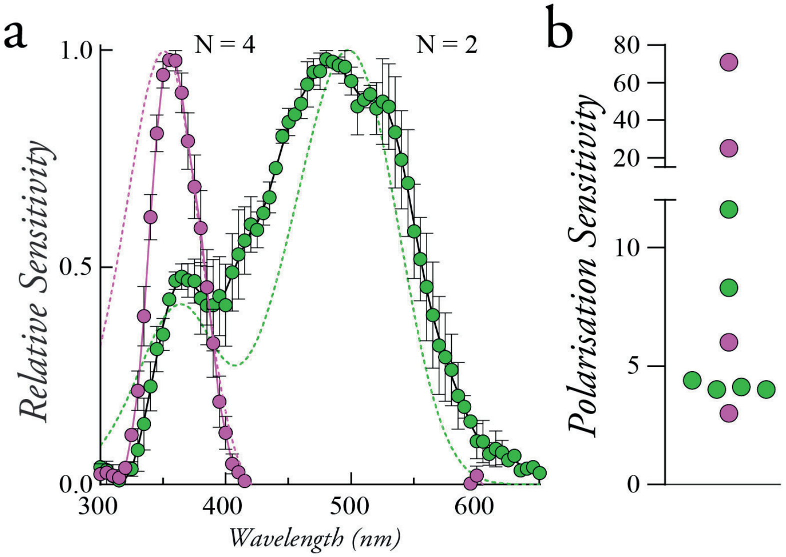


Figure 12. Spectral sensitivity of photoreceptors in the dorsal region of the dorsal eye of *Kheper lamarcki* (Paper IV). Intracellular recordings in the dorsal region of the dorsal eye of *K. lamarcki* revealed two types of spectrally distinct, but highly polarisation sensitive photoreceptors (**a**). The spectral sensitivities of the ultraviolet sensitive photoreceptor (λmax ≈ 350 nm) (*pink graph*) and the green sensitive photoreceptor (λmax ≈ 500 nm) (*green graph*) are fitted with rhodopsin nomograms (*pink dashed line*: λmax = 352 nm; *green dashed line*: λmax=501 nm). The range of measured polarisation sensitivities of the ultraviolet (*pink circles*) and green (*green circles*) photoreceptors can be seen in **b**. *Courtesy of Ayse Yilmaz and Gregor Belušic.*

Directional information is weighted according to Bayesian reasoning

As the degree of polarised light is determined by the intensity of the electric field component in proportion to the light beam's overall intensity (Strutt, 1871; Suhai and Horváth, 2004) (*Box 4*), this is also a measure of signal strength: the higher the degree of polarisation, the stronger the signal. It is thus plausible to assume that the reliability of the polarised light source as a directional cue decreases as a function of its degree. When beetles of *K. lamarcki* were allowed to roll under an overhead polarised light source of three differing degrees of polarisation (*100%*, *64%* or *11%*) (*Figure 11*) of equal intensity, they showed a clear response to the 90° rotation of the artificial band of polarised light under all three degrees of polarisation (*Figure 13, b-d*) (**Paper IV**). In addition, our data revealed a significant correlation between the degree of polarisation and the probability of a turn (45° or more), demonstrating that turning probability decreases with decreasing degree of polarisation. A similar trend is also observed in crickets, where the polarotactic response diminishes as the animal is presented a stimulus of lower degree of polarisation (Henze and Labhart, 2007; Labhart, 1996).

Interestingly, my results from **Paper IV** revealed that *K. lamarcki* can extract and utilise directional information from a degree of polarisation as low as 11% (*Figure 13d*), a value corresponding to the threshold limit suggested for its nocturnal cousin, *Scarabaeus satyrus* Fabricius (Foster et al., 2019*). However, it is important to note that the light intensity presented to the diurnal beetle in **Paper IV** is four orders of magnitude higher than that presented to *S. satyrus* in Foster et al. 2019*, and nearly three orders of magnitude higher than the intensity of polarised light in the diurnal sky (Johnsen et al., 2006). Although the light intensity under a moon-lit night is significantly dimmer (approximately six orders of magnitude darker (Johnsen et al., 2006; Lythgoe, 1979), the degree of polarisation is comparable to a diurnal sky, with approximately 60% polarisation of the skylight (Foster et al., 2019*; Horváth et al., 2014). If the heading direction network of the beetle only evaluates the degree of the polarised light cue for directional information, *K. lamarcki* should in theory also be able to steer in reference to the night sky polarisation. Coerced to roll during a moon-lit night, with the apparent position of the real moon covered from the beetle's field of view, these diurnal beetles do, however, fail to maintain a straight bearing (Smolka et al., 2016). This indicates that the lowest detectable intensity (but not degree) of polarised light varies between the species.

When introducing and rotating a green light spot in combination with an overhead polarised light source at 11% polarisation, *K. lamarcki* turned in response to the 90° displacement of the green light (*Figure 13g*). It appears that this single bright spot generates a stronger and more reliable directional signal relative to the artificial band of polarised light. This weighting relationship is directly comparable to that observed outdoors; when the apparent position of the sun is changed by 180° with the aid of a mirror, while simultaneously blocking the real sun from view under a natural sky, *K.*

lamarcki will turn in response to the mirrored sun (see *Compass cues used by the ball-rolling dung beetle*). When instead presented with a fully (100%) polarised light source in the lab, in addition to the same laterally presented green light source as above, the beetles no longer turned in response to a 90° azimuthal change of the green light (*Figure 13e*). Instead, they now steer straight according to the polarised light stimulus. This demonstrates that *K. lamarcki* alters its weighting of directional cues in a stimulus-dependent manner to steer straight. That is, as the relative strength or reliability of the directional cues change, the relative weighting of these cues in the heading direction network of the beetle changes accordingly.

The weighting strategy of the beetle appears to be performed according to Bayesian reasoning (Körding, 2007; Körding and Wolpert, 2006). According to this theory, directional information conveying the highest certainty at the given moment is afforded the greatest weight in the navigational system of the animal. This influence of reliability on weighting strategy is also apparent in homing ants, that will rely more on path integration over terrestrial cues at visually unfamiliar locations (Wystrach et al., 2015), and vice versa when located in more familiar terrain (Legge et al., 2014). Similarly, sandhoppers, that predominantly rely on directional information from the sun (Ugolini et al., 2002; Ugolini et al., 2015; Ugolini et al., 2016), will utilise radiance and spectral gradient cues to direct their movements when this celestial body is out of sight (Ciofini et al., 2021), and Myrmica ants, that rely on visual guidance for navigation, resort to olfactory cues as the light intensity decreases (Cammaerts, 2012).

Along the same line of reasoning, following a 'Bayesian weight strategy', this would also imply that when two directional cues of equal weight are set in conflict with eachother, an intermediate heading direction to that of both sources of directional information is chosen. Although only hypothesized for *G. unicolor* in **Paper III**, this outcome has been repeatedly observed in ants: when the apparent e-vector direction of the celestial pattern of polarised light is set in conflict with the artificial panorama (Freas et al., 2017; Reid et al., 2011) or the artificial panorama is set in conflict with celestial cues (Legge et al., 2014; Wystrach et al., 2015), these insects choose an intermediate bearing to the dictates of both sources of directional information. When ball-rolling *K. lamarcki* was presented with a 64% polarised overhead light in combination with a green light spot, the beetles changed their bearings by about 45° in response to a 90° rotation of the light (*Figure 13f*). This could be because the two sources of input signals under this paradigm are providing directional information of similar reliability. Interestingly, as soon as the intensity of the overhead polarised light was lowered, the beetles again turned with the ersatz sun (*Figure 13h*), demonstrating that weakening the relative input of directional information from the polarisation cue again effectively shifted the relative weighting towards the ersatz sun.

From my results in **Paper IV**, I can safely conclude that *K. lamarcki* integrates multiple sources of directional information in a Bayesian manner (Cheng et al., 2007; Kӧrding, 2007; Körding and Wolpert, 2006), strongly suggesting that directional information conveying the highest certainty at any given moment is afforded the greatest weight in the navigational network of the animal.

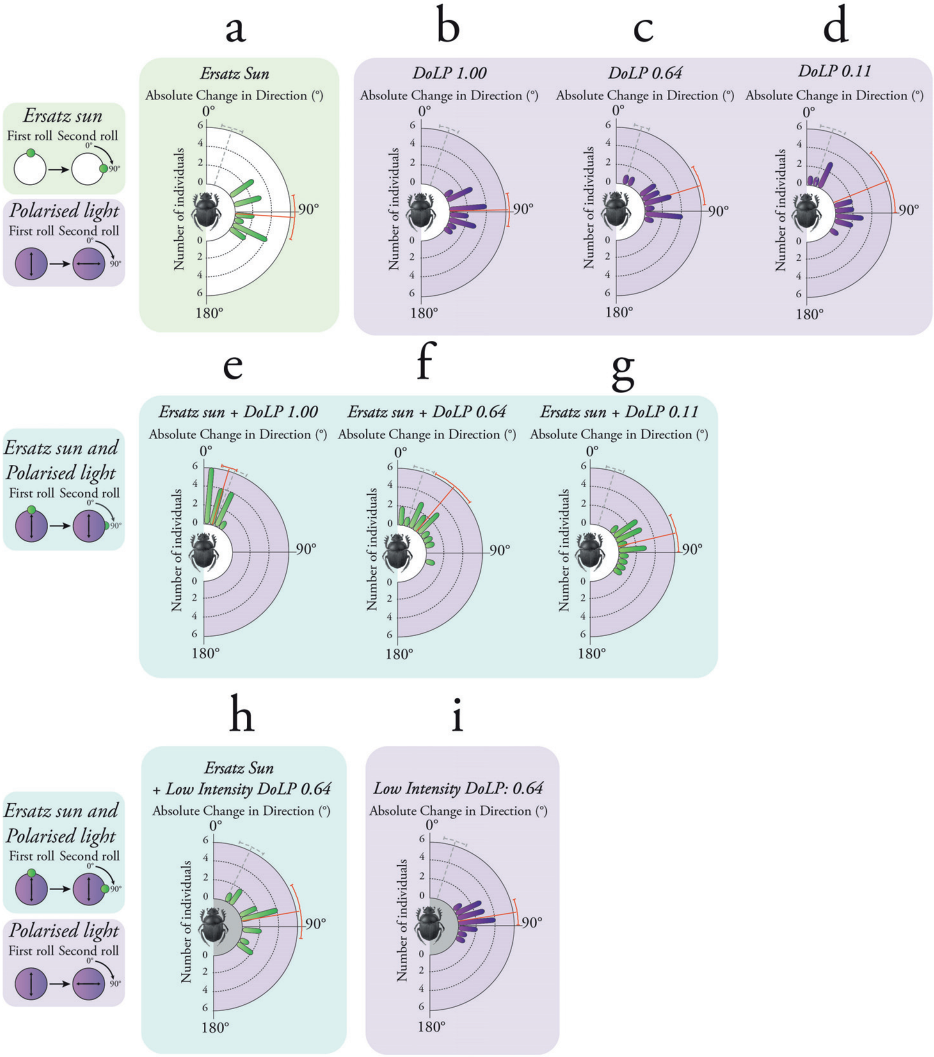


Figure 13. See next page for legend.

Figure 13. Response to directional changes of compass cues (Paper IV). *Kheper lamarcki* was allowed to roll its dung ball from the centre of a 30 cm radius arena presented with a lateral green light source (ersatz sun) in the presence of an overhead unpolarised light source (**a**), a single overhead polarised light source (**b**: 100% polarisation; **c**: 64% polarisation; **d**: 11% polarisation), a laterally presented green light source in combination with an overhead polarised light (**e**: ersatz sun in the presence of 100% polarisation; **f**: ersatz sun in the presence of 64% polarisation; **g**: ersatz sun in the presence of 11% polarisation; **h**: ersatz sun in the presence of 64% polarisation of lower light intensity), or in the presence of a single overhead polarised light source of 64% polarisation of lower light intensity (**i**). Once the beetle had reached the periphery of the arena, it was removed from its dung ball and placed back in the centre alongside its ball. This procedure was repeated five times. After the fifth exit from the arena, the apparent position of the ersatz sun (**a**, **e-h**) or the e-vector direction of the artificial band of the overhead polarised light source (**b-d**, **i**) was turned by 90° (*test*), or remained in position (*control*) and the beetle was allowed to exit the arena again for five consecutive rolls. The absolute angular change between the mean direction of the five rolls prior to the treatment and the mean direction of the five rolls preceding the treatment in the test condition is depicted as coloured bars in all graphs. When a single stimulus was presented in isolation (**a-d**), *K. lamarcki* changed bearing direction in accordance with the 90° angular change of the stimulus presented (*red vector*, all graphs). When rolling in the presence of an ersatz sun under 100% polarised light, *K. lamarcki* did not respond to the positional change of the ersatz sun (**e**). Contrarily, when rolling in the presence of an ersatz sun under 11% polarised light, *K. lamarcki* changed its bearing in accordance with the 90° angular turn of the ersatz sun (**g**). If presented with an ersatz sun in the presence of 64% polarised light, this beetle showed an intermediate response to the azimuthal change of the stimulus (**f**). However, when the intensity of the 64% polarised light decreased by tenfold, the beetle would now turn in response to the 90° turn of the ersatz sun (**i**). The absolute angular difference between the mean direction of the five rolls prior to the treatment and the five rolls preceding the treatment during the control condition is represented by a grey dotted vector in each graph. Error bars represent one circular standard deviation.

Spectral and intensity gradient

Spectral skylight and the intensity gradient of the sky as directional information

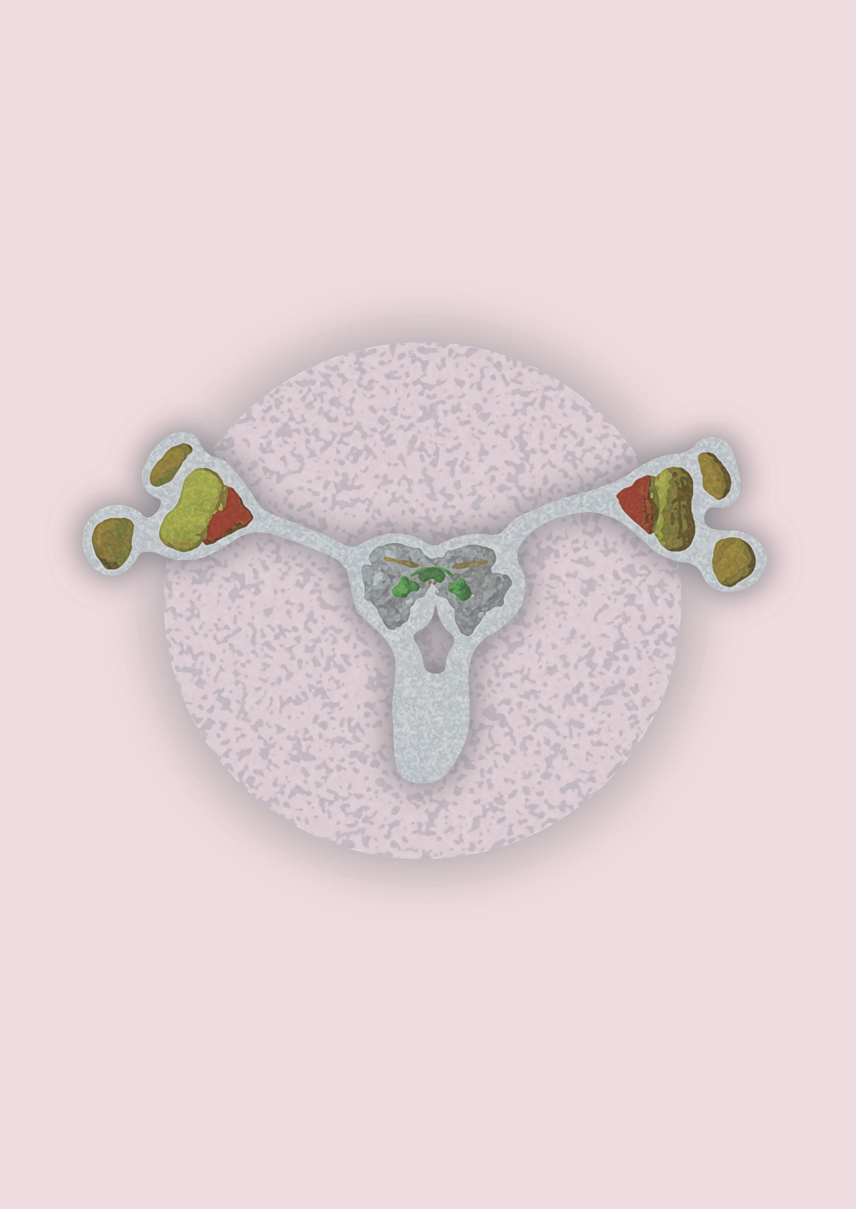
The atmospheric scattering of sunlight also generates a spectral (and intensity) gradient across the sky (*Figure 10a*). With increasing angular distance from the sun, the dominant wavelength of light decreases (Strutt, 1871), creating a chromatic contrast between long and short wavelength of light along the solar meridian. Consequently, the relative intensity of green light is stronger in the direction of the sun, and the relative intensity of ultraviolet (UV) light is stronger towards the antisolar direction (*Figure 10a*) (Coemans et al., 1994). This gradient can be exploited as a directional reference; honeybees are able to distinguish between the sun and the antisolar direction in the sky by associating long wavelengths to the solar half, while short wavelengths are associated to the antisolar half (Edrich et al., 1979; Rossel and Wehner, 1984) and sandhoppers are able to orient to the correct seaward direction of their home beach using the spectral gradient (Ciofini et al., 2021). The ability to derive compass information from spectral cues has also been demonstrated in the ball-rolling dung beetle *Kheper lamarcki* (el Jundi et al. 2015a*; el Jundi et al., 2016*). When presented with two green light spots positioned 180° apart, the beetles could not adhere to the same original direction over two consecutive rolls. However, if presented with one green light spot and one UV light spot, positioned 180° apart, the beetles had no difficulty in maintaining their bearing over two rolls. Their ability to adhere to the same direction persisted even when one of the light spots (UV or green) where turned off prior to the second roll. This clearly demonstrates that the beetles consider the position of both spectral cues in relation to one another, and shows that they can, much like honeybees and sandhoppers, use the celestial chromatic contrast for orientation. Dung beetles are also able to orient by the celestial light intensity gradient. If allowed to roll under an intensity gradient filter (a filter that becomes progressively darker from one side to the other) with the sun and the polarised skylight blocked from view (with the aid of a shading board and a depolariser, respectively), the dung beetle will turn in response to the 180° turn of the intensity gradient filter, demonstrating that *K. lamarcki* is able to use the light intensity gradient as an orientation cue (el Jundi et al., 2014a).

In principle, spectral and/or intensity gradient information only provides the navigator with information about whether it is moving towards or away from the solar hemisphere. Therefore, it is a great supplement to a more robust compass (el Jundi et al., 2014a), rather than a primary source of directional information. It might be for this reason there are, as far as I know, no insects that rely primarily on this type of directional information. Instead, most insects will exploit the spectral and light intensity gradient of skylight in addition to other cues, such as the sun and polarised skylight (reviewed by el Jundi et al. 2014b).

Wind

Dung beetles can utilise directional information from wind for straight-line orientation

Although repeatedly demonstrated that ball-rolling dung beetles utilise directional information from celestial cues to perform straight-line orientation (see previous sections), these peculiar insects are also able to extract directional information from the wind. If presented with a wind cue (or air accelerated by a fan) in the presence of the sun (or a single green light spot), dung beetles will increasingly rely on directional information from the wind as the sun is approaching zenith (Dacke et al., 2019; Shaverdian, Dirlik, Mitchell et al., 2021, *in prep*). This indicates that directional cue information can be transferred over several modalities, and much like has been observed in **Paper IV**, the beetles effectively shift the weight relationship towards the more reliable source of directional information, regardless of modality. This is also observed in ants, where, if experimentally deprived of their polarisation information, the weight relationship of the directional information from the sun and wind cue shifts in favour of wind as the solar elevation increases (Müller and Wehner, 2007).



The compass pathway: from visual input to behavioural output

Having provided a fair overview of the behaviour of the ball-rolling dung beetle, and the directional information utilised and integrated by the dung beetle compass as the beetle is rolling, I have yet to describe *how* this information is believed to be integrated. For this, we need to start at the beginning, where the directional information is first detected by the compass: the compound eyes.

The compound eyes

Compass cue information is first processed through the compound eyes of the dung beetle

As the beetle gets ready to depart with its dung ball from the pat, it is believed to register the compass information in the sky (Baird et al. 2010; el Jundi et al. 2016*) through its compound eyes (Byrne and Dacke 2011). Most ball-rolling dung beetles have four eyes (two dorsal, and two ventral) separated by a *canthus* (*Figure 14*). There are, however, some species of ball-rollers, such as *Sisyphus fasciculatus*, *Garreta unicolor* and *G. nitens* that possess only one pair of eyes. In these beetles, the dorsal and ventral regions of the eyes are only partially separated by the canthus (**Paper III**; Tocco et al., 2019) (*Figure 14*). At the time of this thesis, it is not fully understood what role the morphology of the eye plays in the orientation behaviour of the beetle (**Paper II** and **III**).

The compound eye comprises several optical units, **ommatidia** (*Figure 15*), that together form the image of the world perceived by the insect. The number of optical units in an eye varies across different groups of arthropods, ranging from very few, such as the 22 ommatidia in the eye of the water flea *Daphnia magna* (Smith and Macagno

1990), to the approximate thousand carried by the ball-rolling dung beetle (Byrne and Dacke 2011), to over tens of thousands, as in the eye of a dragonfly (Sherk 1978).

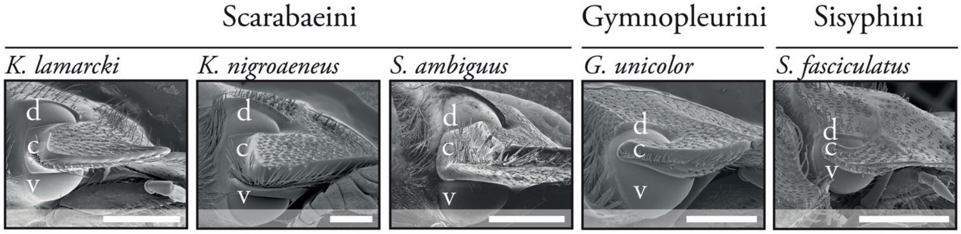


Figure 14. External eye design in three tribes of ball-rolling dung beetles. To facilitate straight-line orientation, diurnal species within the tribe Scarabaeini under most natural conditions attribute the highest weight to directional information provided by the sun. In contrast, *Sisyphus fasciculatus*, from the tribe Sisyphini, relies predominantly on polarised skylight for directional information. For beetles from the tribe Gymnopleurini, neither directional information from the sun nor from the polarisation pattern dominates the output from its compass network (**Paper III**). The canthus (*c*) completely separates the dorsal (*d*) and ventral (*v*) eyes of Scarabaeini spp., while the only partially separated dorsal part of the eyes of Gymnopleurini spp. and Sisyphini spp. are significantly smaller than their ventral parts. Scale bar is 1mm.

The compound eye functions as a light gathering unit

In general, there are two main types of compound eyes; *apposition compound eyes* and *superposition compound eyes*. In the **apposition eye**, each ommatidium is optically isolated from the other. As follows, each rhabdom receives light through the facet of one single ommatidium, forming an image of only a small part of the visual field of the entire eye. Together, the light gathering units of the eye create a mosaic of the whole visual field. In a **superposition eye**, there is a space between the facet and its rhabdom in the form of a *clear zone* (*Figure 15*). Here, light from one certain direction can be imaged onto neighbouring ommatidia. Superposition eyes are very common in nocturnal insects, as it supports higher summation of light per rhabdom, making the eye more light-sensitive in contrast to the apposition eye (Land and Nilsson, 2012; Cronin et al. 2014). However, superposition eyes are not limited to nocturnal insects, but can also be found in diurnal species, including ball-rolling dung beetles (**Paper III**; Byrne and Dacke 2011) (*Figure 14 and 16*), hawkmoths (Warrant, Bartsch and Günther, 1999) and owl flies (Belušič G, Pirih P, Stavenga DG, 2013).

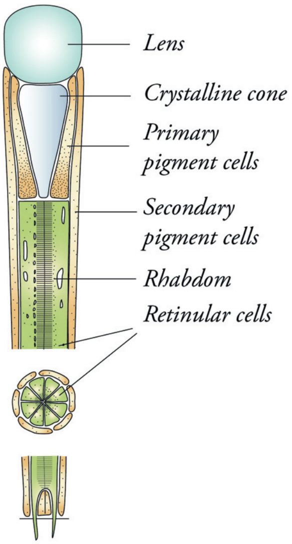


Figure 15. Schematic drawing of an ommatidium. Visual information in the form of light reaches the lens of the ommatidium and travels down to the rhabdom via the crystalline cone. Pigment cells lining the walls of the ommatidium help prevent incoming light from spreading to neighbouring ommatidia. In the rhabdom, the absorption of light initiates an electrical signal that is sent to the brain for further processing. Adapted from Cronin et al. (2014).

The rhabdom detects the light and converts it to a neural signal

As light from the outside world reaches the compound eye of the beetle, the light first passes the lens of the ommatidium, travelling down through the crystalline cone underneath, and finally reaches the **rhabdom**. While the lens and crystalline cone can be thought of as the 'light gathering' unit of the ommatidium, the rhabdom functions as the 'light detecting' unit. It is in this part of the eye that incoming light is translated to a neural signal. The rhabdom is (usually) formed by seven or eight *photoreceptor cells* (or retinular cells) (*Figure 16*) in which the microvillar component of each of these cells run along its entirety and is oriented inwards, towards the centre of the rhabdom (*Figure 15*). These microvilli all contain light sensitive pigments, *rhodopsin*, composed of an opsin protein bound to a light-absorbing chromophore. Depending on the configuration of opsin and chromophore type, the visual pigment will be more or less sensitive to certain wavelengths of light, affectively determining the wavelength sensitivity of the entire photoreceptor cell.

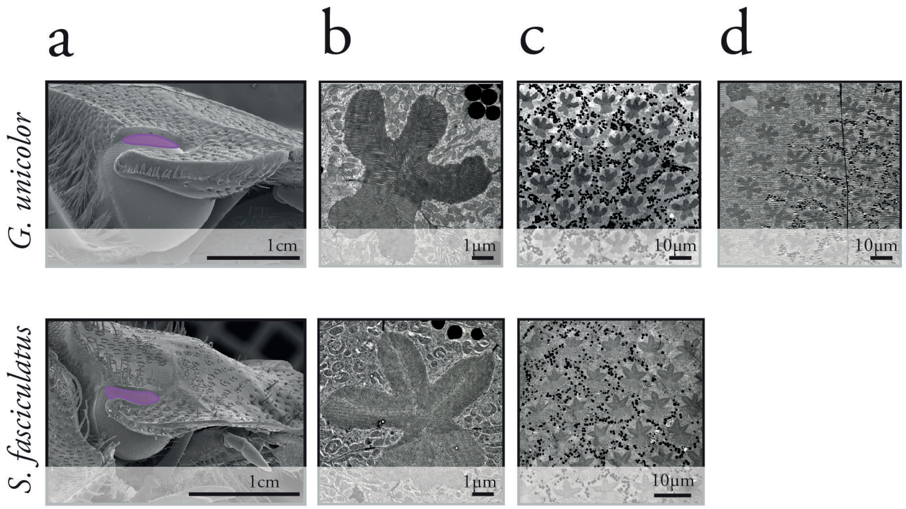


Figure 16. Rhabdoms in the dorsal region of the dorsal eye of *Garreta unicolor* and *Sisyphus fasciculatus*. The rhabdoms of dung beetle eyes are formed by seven receptor cells and differ in shape and microvillar orientation in different eye regions. The rhabdoms of the dorsal rim area (DRA) (**b** and **c**) possess orthogonally arranged microvilli, while the rhabdoms in the rest of the dorsal eye (**d**) are flower shaped with varying microvillar orientations. Based on my preliminary data, the presumed DRA of each species is highlighted in purple in **a**.

The opsins are the building blocks of wavelength sensitivity

Despite the incredible diversity within the insect realm, the wavelength sensitivity of arthropod photoreceptors is quite conservative. In general, insects possess three types of **opsin groups** of different wavelength sensitivities, with absorbance peaks in the *ultraviolet* (also known as *short*, ranging around 350 nm), *blue* (also known as *medium*, ranging around 440 nm) and *green* (also known as *long*, ranging around 520 nm) wavelength range (Briscoe and Chittka, 2001). Throughout evolution, the possession of these three opsin paralogues have been modified, and in some insects, such as the dung beetle, only two out of the three opsin types, effectively the UV and long wavelength opsins remain (**Paper IV**; Lord et al., 2016; Sharkey et al., 2017) (*Figure 12*).

The dorsal rim area detects polarised light

The majority of an insect compound eye consists of rhabdoms with microvilli arranged in all different directions (*Figure 15* and *16d*). In addition to this, many insects have a region of specialized ommatidia commonly found in the most dorsal part of the eye. In this region, termed **the dorsal rim area** (DRA) (*Figure 16b-c*), the microvilli of each photoreceptor within the rhabdom are distributed exclusively in two different directions, orthogonal to each other (*Figure 16b*). This causes each photoreceptor cell to be sensitive to light oscillating in one specific plane (*Figure 10b*, also see *Box 4*), essentially forming a polarisation detector in each ommatidium.

Most insects (Labhart and Meyer, 1999), including dung beetles (Dacke et al., 2002; Dacke et al., 2003), crickets (Brunner and Labhart, 1987), honeybees (Wehner and Strasser, 1985) and ants (Labhart, 1986) possess compound eyes with a DRA. For many of these insects, the photoreceptor cells within this region are UV wavelength sensitive (Labhart, 1986; Nilsson et al., 1987). However, in some insects, such as in crickets (Herzmann and Labhart, 1989) and locusts (Schmeling et al., 2014), the DRA presents blue wavelength sensitive photoreceptors. Although less common (Hegedüs et al., 2006), green wavelength sensitive photoreceptors in the DRA have also been found in the cockchafer (Labhart et al., 1992) and very recently also in the diurnal beetle, *Kheper lamarcki* (**Paper IV**) and the nocturnal beetle, *Scarabaeus satyrus* (Yilmaz, *unpublished*).

The size of the dorsal rim area affects the polarisation sensitivity of the dung beetle

Prior to this thesis, all studies of straight-line orientation in diurnal ball-rolling beetles have shown that diurnal ball-rollers attribute greatest relative weight to the directional information provided by the sun (**Paper I**; **Paper II**; **Paper III**; Byrne et al., 2003; Dacke et al., 2014; Dacke et al., 2019; el Jundi et al., 2015a*). However, if the sun gets out of view, due to cloud cover or vegetation, the beetles continue to steer straight according to the celestial pattern of polarised light (Jundi et al., 2014a) or the colour and intensity gradient spanning across the sky (Jundi et al., 2014a; el Jundi et al., 2015b), with no decrease in performance.

In **Paper II** and **III** I showed that when changing the position of the apparent sun by 180°, while shading the real sun from view, under the natural sky, *Sisyphus fasciculatus* along with *Garreta unicolor*, remained unresponsive to this change. A possible rationale for this could be the simple constraints of the external eye: both species possess much narrower dorsal eyes compared to that of any other diurnal dung beetle studied in this thesis (*Figure 14*). A smaller compound eye could possibly contribute to a smaller visual field (Cronin et al., 2014; Land, 1997; Land and Nilsson, 2012; Rutowski et al., 2009; Taylor et al., 2019). Hence, it might be more beneficial to integrate information from a sky-wide signal, such as the celestial polarisation pattern, rather than determining the position of a single light source. Although yet to be confirmed, the mentioned beetles, specifically *S. fasciculatus* – which clearly weights directional information from polarised skylight over the sun (**Paper II**), could also possess a DRA covering a larger part of the dorsal eye (see *Figure 16*). A narrow dorsal eye limiting the visual field of the beetle, in combination with a large DRA could support a higher sensitivity of polarised light input, contributing to the behavioural responses documented for *S. fasciculatus* and *G. unicolor*.

It is important to note that the size of the DRA does not necessarily correlate with the sensitivity to polarised skylight in insects (Labhart and Meyer, 1999), however, based on past and previous behavioural observations in the dung beetle, the size of the DRA in the dung beetle is very likely to influence the weighting strategy of the animal's orientation system. This is at least observed for the nocturnal and crepuscular beetles, *Scarabaeus satyrus* and *Scarabaeus zambesianus* Péringuey. These animals rely on directional information from the polarised skylight above that from the moon (Dacke et al., 2004; Dacke et al., 2003; Dacke et al., 2011; Dacke et al., 2013b; Foster et al., 2019*). Interestingly, if instead coerced to roll during the day, the nocturnal *S. satyrus* will weight directional information from the sun over that provided by the celestial polarised light pattern (el Jundi et al., 2015a*). It is now most likely the drastic increase in light intensity (Lythgoe, 1979) that changes the weight relationship of the directional cues in the neural network of the beetle (**Paper IV**, *Figure 13*, and *The brain*). Comparably, if the diurnal analogous, *Kheper lamarcki*, is coerced to roll at night, it still primarily follows the directional information provided by a point-source light, i.e. the moon. It can be so that the eyes of *K. lamarcki* are just not be able to detect the polarised skylight pattern (or any other additional celestial cues) across the night sky. Only a single row of DRA has been found in *Kheper lamarcki* (Dacke, *unpublished*). This limited region of DRA, in combination with a subpar adaptation to dim light vision (Dacke et al., 2011; Smolka et al., 2016), can be contributing factors that constrain the beetle's ability to utilise the nocturnal celestial polarisation pattern as it rolls under the night sky.

The brain

The pathway to the central complex

Unlike locusts, monarchs and Bogong moths, that migrate over tremendous distances (Homberg, 2015; Perez et al., 1997; Warrant et al., 2016), or ants, bees and wasps, that need to return to their nests after a successful foraging trip (Collett, 2012; Mandal et al., 2017; Rossel and Wehner, 1984; Wehner, 1996; Wehner, 2003), the ball-rolling dung beetle 'simply' needs to move away from a single point in as straight of a trajectory as possible, for the duration of approximately 6 minutes (Dacke et al., 2019). Nonetheless, different navigational strategies aside, the neural pathway underlying these behaviours are highly conserved across the entire insect realm (Heinze and Pfeiffer, 2018; Homberg et al., 2011; Ito et al., 2014; el Jundi et al., 2018; Pfeiffer and Homberg, 2013; Stone et al., 2017; Zeller et al., 2015), strongly suggesting that all travelling insects rely on the same neural basis to achieve their guided movements.

Prior to rolling, the beetle climbs on top of its ball and begins to rotate around its vertical axis in a motion reminiscent of the learning walk pirouettes of ants (see Grob et al., 2019; Lent et al., 2010; Zeil and Fleischmann, 2019). During this pirouette, or dance, the beetle is believed to take a snapshot of the sky, that it then attempts to continuously match while rolling (Baird et al., 2012; el Jundi et al., 2016*). As the beetle dances, light reaches the photoreceptors and swiftly converts into neural signals, that in turn is transferred to the first processing centre for visual input; **the optic lobe** (Immonen et al. 2017). Here, the neural signal is received by the first two neuropils of the optic lobe; *the lamina*, proximally followed by *the medulla* (*Figure 17*), where polarised light information from the dorsal rim area, along with unpolarised light information from the rest of the retina are integrated and transferred by transmedulla neurons to the central brain, specifically **the anterior optic tubercle** (el Jundi, Pfeiffer and Homberg, 2011; Blum and Labhart, 2000; Kinoshita, Pfeiffer and Homberg, 2007; Homberg and Paech, 2002). Interestingly, in the dung beetle, the transmedulla neurons only project from the dorsal medulla, indicating that celestial information is only received from the dorsal eyes of the beetle (most dung beetles have four eyes, see *The Compound Eyes* and *Figure 14*) (Immonen et al. 2017). This neuroanatomical finding is very much reflected in the behavioural output of the beetle: when the diurnal dung beetle, *Kheper lamarcki*, is allowed to roll under an open sky, with an opaque black cap shielding its dorsal eyes from viewing the sky, it is unsuccessful in maintaining a straight trajectory (Dacke et al., 2013b), indicating the need of dorsal light input for orientation. After the anterior optic tubercle, the neural signal from the eye is carried to **the ipsilateral bulb of the lateral complex** (el Jundi et al., 2018). This is considered the 'last destination' prior to the brain region believed to possess the compass of the beetle; **the central complex** (*Figure 17*).

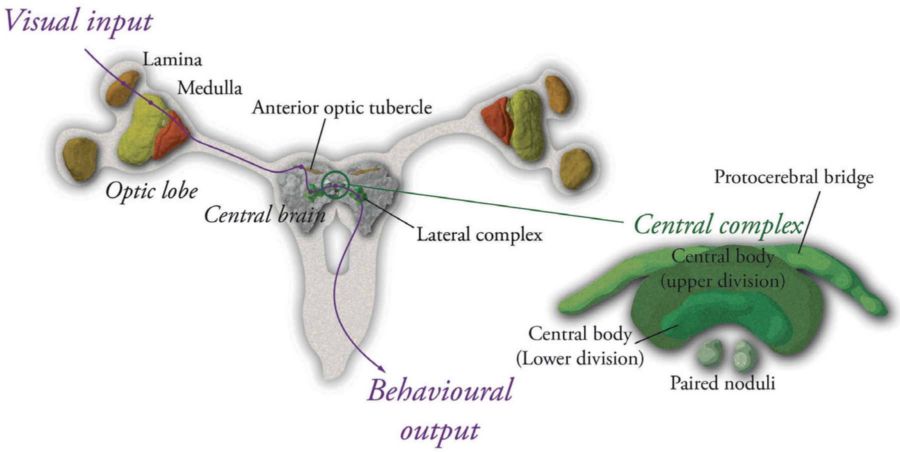


Figure 17. The light compass pathway in the dung beetle brain. Visual information from celestial cues, such as the sun or polarised skylight, first reaches the compound eye retina. The neural signals from the retinula cells are then transferred to the first processing centre for visual input; *the optic lobe*. From here, the information is transferred to the *anterior optic tubercle* and subsequently carried via the *lateral complex* to the *central complex*. This is where we find the heading direction network of the beetle. The central complex (here represented in green) is comprised of the protocerebral bridge, the upper and lower divisions of the central body and the paired noduli. *Adapted from Immonen et al. 2017 (3D model of the brain was generated using the website www.insectbrain.org).*

The composition of the central complex

The central complex (CX) can be divided into four neuropils, located across the midline of the insect brain: *the arch-like protocerebral bridge* (PB); *the upper division of the central body* (CBU, also termed fan-shaped body in flies); *the lower division of the central body* (CBL, also termed ellipsoid body in flies) and *the paired noduli* (NO) (*Figure 17*). These four regions can further be divided into slices and layers (Homberg et al., 2011; Immonen et al., 2017; el Jundi et al., 2018; Pfeiffer and Homberg, 2013), creating a highly organized neuronal network that provides connections between the individual components of the CX, as well as input from and output to other areas in the insect brain. Together, these connections transform visual information carried from the insect retina into premotor commands that guide navigation. This central region of the brain is believed to play a key role in spatial orientation (Homberg et al., 2011; Triphan et al., 2010; Varga et al., 2017; Zittrell et al., 2020), sky compass integration (Heinze and Homberg, 2007; Heinze et al., 2013; Homberg, 2004; Homberg et al., 2011; Pegel et al., 2018) and locomotor control (Martin et al., 2015; Ritzmann et al., 2012; Seelig and Jayaraman, 2015; Strauss, 2002).

While all celestial information is encoded in the central complex, the dorsally located protocerebral bridge is considered to carry a map-like representation of the polarised skylight. In locusts, polarisation sensitive neurons (often called POL neurons) within each slice are maximally activated by a certain e-vector direction and maximally inhibited by the 90° rotation of this e-vector direction. This polarisation opponency for a preferred e-vector orientation changes by around 20-30° for each neighbouring slice (Heinze and Homberg, 2007). Considering that the same neurons are sensitive to polarised light in the dung beetle brain (el Jundi et al. 2015*), this map likely also exists in dung beetles. As there are 8 slices in the protocerebral bridge of the dung beetle CX (Immonen et al., 2017), each hemisphere of the PB covers an angular range of 180°, covering the full span of the celestial e-vector map (*Figure 10a*).

Differing neural sensitivity to polarised and unpolarised light influences the orientation strategy of the beetle

To understand how the integration of celestial compass information is encoded, and how this information is weighted in the dung beetle compass, diurnal and nocturnal beetles were presented with a polarised light source in combination with an unpolarised light source, of brighter or lower light intensities (corresponding to sun -or moonlight conditions), while simultaneously recording from the CX of the beetle (el Jundi et al., 2015a*). When presented with either of the two intensity paradigms, the CX neurons of the diurnal *Kheper lamarcki* would always respond exclusively to the unpolarised light source. In contrast, the CX neurons of the nocturnal *Scarabaeus satyrus* would only respond to the unpolarised light source during bright light conditions. If presented with dim light conditions, the neural tuning of the CX neurons in the nocturnal species would be dominated by the polarisation stimulus. This neural response, elegantly matches the relative weighting strategy of both species during straight-line orientation: while the diurnal *K. lamarcki*, known to predominantly weight directional information from the sun (Byrne et al., 2003; Dacke et al., 2014), continues to orient to the moon at night (el Jundi et al., 2015a*), its nocturnal counterpart, *S. satyrus*, will shift its predominant weight of directional information, from polarised light at night (Dacke et al., 2004; Dacke et al., 2011; Foster et al., 2019*), to the sun during the day (el Jundi et al., 2015a*). In locusts, the absolute sensitivity of the CX neurons to polarised light is higher than to unpolarised light. Thus, depending on the light intensities presented to the animal, either polarisation input or unpolarised light input will dominate the response of the neurons (Kinoshita et al., 2007). The same is suggested to happen in the compass of the beetle; at dim-light intensities, the neural response is in favour of the polarised light source. However, this only applies for as long as the eye is sensitive enough to detect the signal. A larger dorsal rim area, such as in the crepuscular *S.*

zambesianus (Dacke et al., 2003) or the diurnal homing beetle *Pachysoma striatum* (Dacke et al., 2002), might also be found in *S. satyrus* (Dacke, *unpublished*). This can, at least partially, contribute to a higher sensitivity to polarised light, influencing the weight relationship between these two sources of information even at earlier stages in the brain. In the case of the diurnal *K. lamarcki*, the dim polarised light was perhaps simply undetectable due to its very limited dorsal rim area (see *The dorsal rim area detects polarised light*), resulting in no (or very weak) neural response for dim polarised light.

The results seen in the nocturnal *S. satyrus* might also explain the weighting strategy seen behaviourally in the diurnal woodland-living beetle, *Sisyphus fasciculatus*, studied in **Paper II** and **Paper III**. As previously mentioned, this beetle attributes higher relative weight to celestial polarised light, despite the sun being fully visible (*Figure 8a, graph 1*). It is feasible that the eye of *S. fasciculatus* has a substantial dorsal rim area (*Figure 16b*). However, at this time, this is merely a speculation.

Acknowledgements

Of all the sections of this thesis, this one was the hardest one to write. As the last part of my *kappa*, it dawns on me that this is the beginning of the end of my PhD journey! I am eternally grateful for everyone that has supported me and helped me throughout my PhD, but there are some I must give special thanks to...

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