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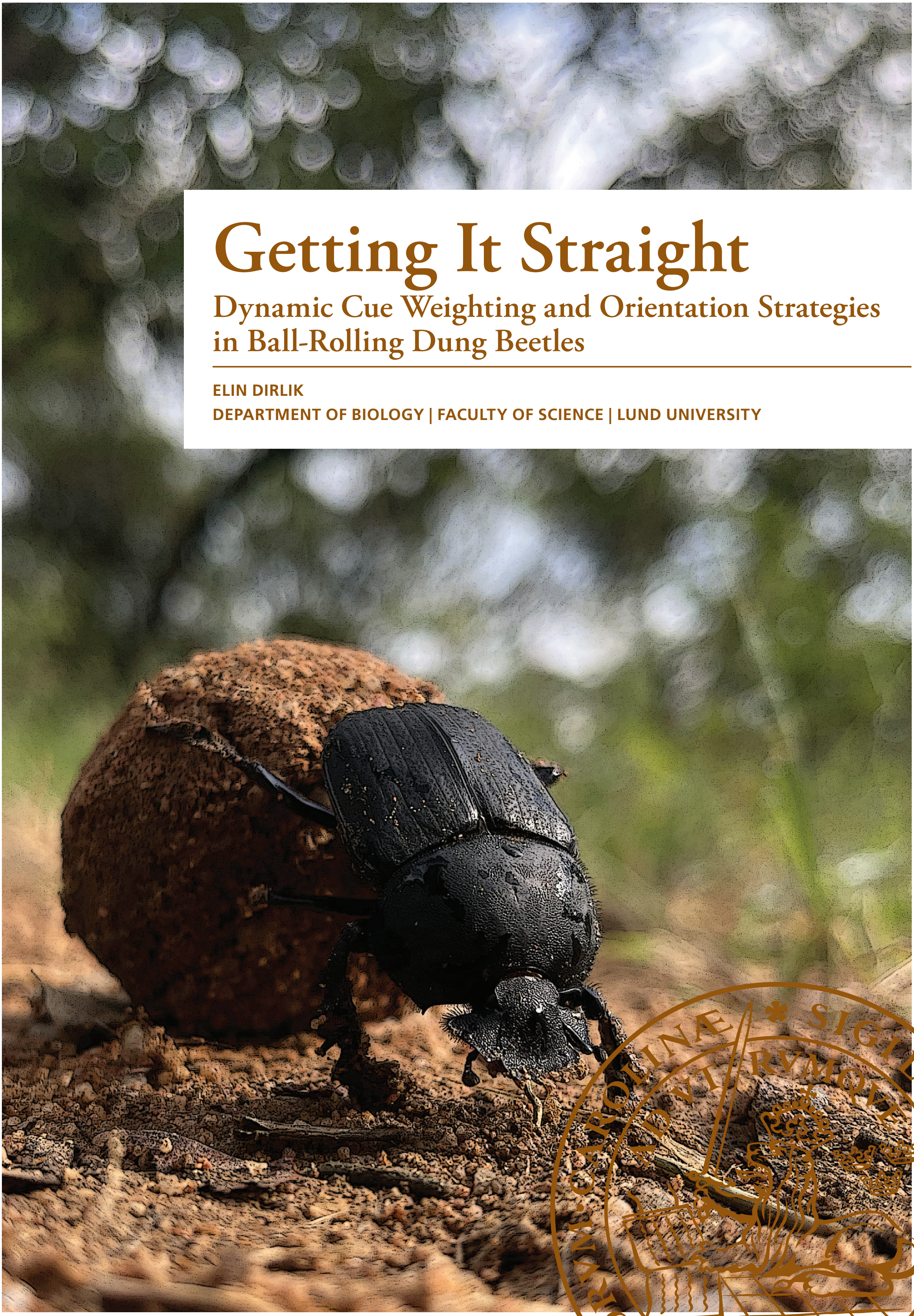

Getting It Straight

Dynamic Cue Weighting and Orientation Strategies in Ball-Rolling Dung Beetles

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DOCTORAL DISSERTATION

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Abstract

Directed movement is fundamental to animal behavior, yet the mechanisms underlying robust orientation remain incompletely understood. The ball-rolling dung beetle offers a unique model system for investigating these mechanisms due to its distinctive navigational challenges: maintaining a straight-line trajectory while moving backward and transporting a dung ball. In this thesis, I investigates oriented behavior in dung beetles, focusing primarily on the diurnal South African species *Kheper lamarcki* and its characteristic orientation dance.

I characterize the triggering factors and motifs of the orientation dance - yaw rotations performed atop the dung ball - demonstrating that these rotation events are triggered by terrain-related disturbances but also occur spontaneously during unimpeded travel (**Paper I**). Notably, I indicate that rotation events likely serve to map and re-map external directional cues onto the beetle's internal compass, restoring orientation to shifted cue positions and improving ambiguous directional signals (**Paper I**; **Paper III**).

I further demonstrate that dung beetles can maintain their bearings using idiothetic information alone only over short distances (**Paper III**). When external cues are available, beetles dynamically weight directional information from multiple sources, including the position of the sun and wind flow, into a combined directional signal. This weighting shifts according to cue usefulness, which is reflected in the relative influence of the cues on directional guidance (**Paper II**).

Finally, I describe cooperative brood ball transportation in two *Sisyphus* species, revealing that males control steering while females contribute passively during flat-ground travel but actively assist in obstacle clearance - a dynamic collaboration enabling efficient straight-line orientation without a predefined destination (**Paper IV**).

Together, these findings advance our understanding of how insects maintain robust directional guidance through the dynamic integration of multimodal cues, the functional role of rotational behaviors in compass calibration, and the coordination of oriented behavior between individuals.

Key words

orientation, behavior, compass, rotation, cue integration, cue weighting, cooperative transport

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Getting It Straight

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Cover illustration front: A ball-rolling dung beetle of the species *Kheper lamarcki*.

Cover illustration back: A dung-baited trap for dung beetle collection, with a fantastic view.

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Dedicated to
my family

Contents

List of publications

This thesis is based on the following publications, referred to by their Roman numerals:

I **E. Dirlik**, Y. Gagnon, L. Khaldy, C. Tocco, M. Byrne, E. Baird, M. Dacke. **Dirty dancing: The rotational component of the dung-beetle dance**. (*Manuscript submitted*).

II S. Shaverdian*, **E. Dirlik***, R. Mitchell*, C. Tocco, B. Webb, M. Dacke. **Weighted cue integration for straight-line orientation**. iScience 25, 105207. `https://doi.org/10.1016/j.isci.2022.105207`

III **E. Dirlik**, Y. Gagnon, M. Dacke. **The dung-beetles' dance remaps external directional cues.** (*Manuscript*).

IV C. Tocco, M. Byrne, Y. Gagnon, **E. Dirlik**, M. Dacke. **Spider dung beetles: coordinated cooperative transport without a predefined destination**. Proc Biol Sci B 291, 20232621. `https://doi.org/10.1098/rspb.2023.2621`

Author contributions

I **E.D.** and M.D. designed experiments. **E.D.**, C.T., and M.B., collected and identified the model species. **E.D.** conducted the experiments. **E.D.** and L.K. extracted data from recordings. **E.D.** and Y.G. analyzed the data. **E.D.** drafted the manuscript. **E.D.**, Y.G., L.K., C.T., M.B., E.B., and M.D. revised the manuscript.

II **E.D.**, S.S., and M.D. designed behavioral experiments. **E.D.**, S.S., and C.T. collected and identified the model species. **E.D.** and S.S. conducted behavioral experiments and analyzed behavioral data. R.M. did all of the modeling. **E.D.**, S.S., and R.M. drafted the manuscript. **E.D.**, S.S., R.M., C.T., B.W., and M.D. revised the manuscript. *First-authorship is shared between S.S., **E.D.**, and R.M.

III **E.D.** designed and conducted the experiments. **E.D.** and Y.G. analysed the data. **E.D.** drafted the manuscript. **E.D.**, Y.G., and M.D. revised the manuscript.

IV C.T. and M.D. designed experiments. C.T., **E.D.**, and Y.G. conducted the experiments. C.T. analysed the data. C.T. drafted the manuscript. C.T., **E.D.**, and M.D. revised the manuscript.

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*Shared first authorship.

Popular summary

You might be surprised to find that you have at least one thing in common with a dung beetle; you are both likely to steer away from a dung pat as quickly as possible. While you are probably doing so to avoid interacting with it at all, the dung beetle has its own reasons. It turns out that this dung pat makes up a fragrant feast for our beetle, as well as for any other dung beetle within range of the scent. To secure some of this precious resource for itself, the beetle shapes a piece of the dung into a ball and rolls away from the crowd of competitors accumulating at the buffet. To make sure every step takes it as far as possible from potential thieves, the beetle rolls its ball along a remarkably straight path. But how does it stay on course? As it turns out, the beetle relies on cues from the world around it for guidance.

The South African species *Kheper lamarcki* finds its way using the position of the sun in the sky, but also by sensing the wind blowing across the landscape. But conditions are not always ideal; clouds may hide the sun, or the wind may die down. How does the beetle cope? In **Paper II**, I found that beetles do not simply pick one cue and ignore the other. Instead, they pay attention to both at once, trusting each source according to how useful it is at that moment. When the sun rises high overhead around midday, for instance, it becomes harder to use for directional guidance, and the beetle shifts its trust in favor of the wind. This flexible strategy allows the beetle to keep rolling in a straight line even when conditions change.

Every now and then, something curious happens: the beetle stops mid-stride, climbs on top of its ball, and spins around before continuing along its straight-line travel. This little pirouette, sometimes called the ”orientation dance”, is impossible to observe without wondering why. In **Paper I**, I found that these dances are often triggered by the terrain; perhaps a bump on the ground makes the beetle lose its grip on the ball, or it stumbles and tips over. After such a disturbance, the rotation helps the beetle find its bearings again and return to its original course. But the dance also seems to serve another purpose: in **Paper I** and **Paper III** I found that when directional cues become confusing or unreliable, rotating atop the ball appears to help the beetle recalibrate its internal compass to the world around it.

The beetle continues its travel in this way - rolling steadily, occasionally dancing - until it finds a suitable spot to bury itself with its prize, so that it can feast undisturbed. However, not all dung beetle journeys are solo affairs. At times, beetles travel in pairs, rolling a larger brood ball destined for their future offspring. In **Paper IV**, together with colleagues, I studied how two species of dung beetles, *Sisyphus fasciculatus* and *Sisyphus schaefferi*, manage to steer together without disagreeing on which way to go. The answer turns out to be elegantly simple: the male takes charge of the steering while the female plays a supporting role, pushing only when he pulls. With only one navigator making the decisions, there is no bickering over direction. The female, however, is far from useless; when the pair encounters an obstacle, she steps up to help lift and maneuver the ball over the hurdle. In this way, the two beetles divide their labor, cooperating smoothly to transport their precious cargo across the landscape.

The dung beetle, with its simple goal and remarkable precision, offers a window into the fundamental mechanisms that allow animals to orient themselves in space.

Populärvetenskaplig sammanfattning på svenska

Det kanske förvånar dig att du har åtminstone en sak gemensamt med en dyngbagge: ni vill förmodligen båda ta er ifrån en dynghög så fort som bara möjligt. Fast medan du antagligen vill undvika den helt och hållet, har dyngbaggen sina egna skäl. Det visar sig nämligen att dynghögen utgör en fantastisk festmåltid för vår bagge – liksom för alla andra dyngbaggar som är innom räckvidd av dess doft. För att säkra en portion av denna värdefulla resurs åt sig själv formar dyngbaggen en bit av dyngan till en boll som den kan rulla iväg från myllret av konkurrenter som samlats vid buffébordet. För att varje steg ska ta den så långt som möjligt från potentiella tjuvar rullar baggen sin boll längs en anmärkningsvärt rak bana. Men hur håller den sin kurs så väl? Det visar sig att baggen skannar sin omvärld och bibehåller sin riktning i relation till specifika referenspunkter.

Den sydafrikanska arten *Kheper lamarcki* orienterar sig med hjälp av solens position på himlen, men också genom att känna av vinden som sveper över landskapet. Men väderförhållanden är inte alltid ideala; moln kan dölja solen, eller vinden kan mojna. Hur klarar baggen av att bibehålla sin riktning då? I Paper II fann jag att baggarna inte bara väljer solen *eller* vinden som referenspunkt. Istället uppmärksammar de båda *samtidigt* och litar på dem utefter hur användbara de är från stund till stund. När solen står som högst på himlen mitt på dagen blir den till exempel svårare att använda för att hålla riktningen, och baggen skiftar sitt förtroende till förmån för vinden. Denna flexibla strategi gör att baggen kan fortsätta hålla sin raka kurs även när förhållanden i dess omgivning ändras.

Då och då under dyngbaggens resa händer något märkligt: baggen stannar tvärt, klättrar upp på sin boll och snurrar runt innan den fortsätter sin raka färd. Denna lilla piruett, ibland kallad "*orienteringsdansen*", går inte att observera utan att man undrar vad som försigår. I Paper I fann jag att dessa danser ofta utlöses av terrängen som dyngbaggen färdades över; en ojämnhet i marken kan få baggen att tappa greppet om bollen eller få den att snubbla och ramla omkull. Efter en sådan störning hjälper dyngbaggens dans den att återfå sin orientering och hitta tillbaka till sin ursprungliga kurs. Men dansen verkar också tjäna ett annat syfte: i Paper I och Paper III fann jag att när referenspunkterna blir opålitliga att syra efter, verkar rotationen ovanpå bollen hjälpa baggen att kalibrera sin inre kompass i förhållande till omvärlden på nytt.

Baggen fortsätter sin färd på detta sätt – rullar stadigt, dansar då och då – tills den hittar en lämplig plats att gräva ner sig med sin skatt, så att den kan äta i fred. Men alla dyngbaggeresor är inte ensamäventyr. Ibland färdas baggarna i *par* och rullar en större dyngboll avsedd för deras framtida avkomma. I Paper IV studerade jag tillsammans med kollegor hur två arter av dyngbaggar, *Sisyphus fasciculatus* och *Sisyphus schaefferi*, lyckas styra en boll tillsammans utan att bli oense om vilken väg de ska ta. Svaret visar sig vara elegant enkelt: hanen tar hand om styrningen medan honan spelar en passiv roll; hon sjkuter endast på när han drar i bollen. Med bara *en* navigatör som fattar besluten uppstår inget käbbel om riktningen. Honan är dock långt ifrån värdelös; när paret stöter på ett hinder lägger hon manken till och hjälper till att lyfta och manövrera bollen över hindret. På så sätt delar de två baggarna upp arbetet och samarbetar smidigt för att transportera sin dyrbara last över landskapet.

Dyngbaggen, med sitt enkla mål och sin anmärkningsvärda precision, erbjuder ett fönster in i de grundläggande mekanismer som gör det möjligt för djur att orientera sig i världen.

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Here goes one of the hardest parts about writing this thesis; successfully expressing the extent of my gratitude towards everyone who has made my work possible and/or made my time as a PhD-student as great as it has been.

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Linnéa, I am beyond happy that we made sure to get to know each other in between all of your travels (maybe you would make a good model organism to study oriented behavior?). I have particularly appreciated our exchanges while carrying out a range of sweaty activities.

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Evri, even though our overlap in the lab will not have been the most extensive, I am glad that you are part of this group. I want to thank you for your willingness to discuss things with me.

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While I am still harping on about people from the lab group, I extend my thanks to Marcus (who I consider an ’honorary’ forever-member of the lab group). I appreciate all the time I got to spend with you in the field, you truly are inspiring.

I would also like to thank my supervision committee. Emily, thank you for the scientific input and discussions, as well as for the fun in the field. Susanne, thank you for your input throughout the years. Eric, I would like to thank you in both your capacity as my institutional representative, as well as the head of the Vision Group. You are incredibly positive and supportive, and I always feel like your door is open; I appreciate all of it.

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Valentin, you are simultaneously one of the most serious and one of the most unserious people I know. It makes for a perfect mixture of fun and safe, and I really appreciate you for that. I am incredibly grateful to you for both your tough-love attitude and your genuine support of me; thanks for being in my corner.

I am also really grateful to everyone who has been part of the Biology Show crew throughout the years: Therese, Lina, Julian, Jacob, Sherry, Valentin, Auguste, Saroja, Sofie, Janka, Griffin, Linnea, Jana. It really has been a fun (and exhausting) experience. Through the tired, but hyped, haze we often moved in together, I really enjoyed solving issues and goofing around with all of you.

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Lastly, I am grateful to my friends outside of this bubble, as well as my family. I am lucky to have the support of all of you. Thank you so much.

Preamble

Even though you rarely consciously think about it, you have a sense of where and how you are located in space as you move. You can recognize familiar environments to know your location, or learn surrounding features to navigate in new ones. If lost in a featureless landscape, you can use a compass, the sun, or the stars to maintain a steady direction. All of this relies on external information from the environment and sensors, such as your eyes, that enable me to perceive it. Simultaneously, inertial sensors - detecting idiothetic information - give you an internal sense of your body's orientation and motion through space; you have an idea of your pitch (looking up or down) and your roll (tilting from side to side), as well as your yaw angle (rotating on the spot) and your translational motion (movement in any direction).

These components of navigation are common to most animals and give rise to a wide range of navigational behaviors. Even among insects, we find strategies spanning long-distance migration to orientation over just a few meters. Due to their small size, often stereotyped behaviors, and highly conserved brains, insects provide excellent systems for studying complex questions about navigation. In my work, I utilize the oriented behaviors of ball-rolling dung beetles to investigate how a consistent direction of travel can be maintained.

Chapter 1

Insect navigation and ball-rolling dung beetles

1 Navigation strategies in insects

Directed movement is a fundamental aspect of animal behavior and insects employ diverse navigational strategies suited to the spatial scale and purpose of their movements (reviewed in Freas and Cheng, 2022; Freas and Spetch, 2022). At one extreme, long-distance seasonal migrants such as Monarch butterflies and Bogong moths undertake journeys spanning hundreds to thousands of kilometers between breeding sites and overwintering or estivation refuges (Mouritsen and Frost, 2002; Mouritsen et al., 2013; Reppert et al., 2010; Warrant et al., 2016). These migrants must maintain consistent headings over extended periods of time, often across multiple nights or days, to reach specific destinations that may be beyond their detection range during most of the journey. At shorter spatial scales, central-place foragers including bees, wasps, and ants regularly leave their nests on meandering foraging trips that can extend from a few meters to several kilometers (Collett and Hempel de Ibarra, 2023; Zeil and Fleischmann, 2019). These foragers face the challenge of returning accurately to a small nest entrance after extensive journeys, relying on path integration to maintain an ongoing estimate of their position relative to home (Collett et al., 2013; Green et al., 2019; Heinze, 2017a). Finally, at the shortest scales, insects such as fruit flies and dung beetles engage in goalless orientation behaviors (with respect to a specific end destination), maintaining straight-line travel in an arbitrarily chosen direction for dispersal or resource transport (Byrne et al., 2003; Warren et al., 2018). Across all these navigational strategies, insects continuously compare their current direction of travel with their desired direction and make corrective adjustments whenever the two do not align (Collett et al., 2013; Green et al., 2019; Heinze, 2017a; Stone et al., 2017). These processes rely on stable

Figure 1.1: Three species of ball-rolling dung beetles. All three species are diurnal but inhabit different habitats, and even different continents. I studied aspects of their straight-line orientation throughout my thesis work. From left to right: the South African *Kheper lamarcki* (**Paper I**, **Paper II**, and **Paper III**), the mediterranean *Ateuchetus laticollis* (**unpublished data**) and *Sisyphus schaefferi* (**Paper IV**). Picture of *S. schaefferi* by courtesy of Claudia Tocco.

external references that provide directional sensory information. Such references include local landmarks and panoramic views (Cartwright and Collett, 1983; Collett et al., 1992; Fleischmann et al., 2016; Graham and Cheng, 2009; Warrant et al., 2004; Wehner et al., 1996), as well as more global directional cues such as the magnetic field (Fleischmann et al., 2020), and celestial information (Freas and Cheng, 2022).

2 Ball-rolling dung beetles

There is close to 10,000 dung beetle species across the world, most of which, as implied by their name, consume dung for sustenance. About 10% of these species can be observed to transport dung before consuming it (Hanski and Cambefort, 1991). Upon finding a fresh pat of dung, such a beetle shapes a piece of dung into a transportable sphere, places its hind legs on this dung ball, its front legs on the ground, and rolls the ball away from the competition at the dung pat along a straight trajectory (see **Figure 1.1**). When encountering a favorable microhabitat sufficiently far from the pat, the beetle digs itself into the ground with its ball and consumes it undisturbed. Not all ball-rolling beetles are straight-line dispersers; some species inhabit temporary nests that they fill with small dung pieces from a nearby source over several trips. Additionally, ball-rolling beetles regularly transport relatively larger brood balls for mating purposes. The challenges and solutions for the transportation of a heavy brood ball over complex terrain are explored further in **Chapter 6** (and **Paper IV**).

3 Straight-line orientation in diurnal beetles

Throughout a foraging occasion, each individual dispersing ball-rolling dung beetle strives to travel along a consistent bearing. Between different foraging occasion, however, the beetle will steer along different bearings (Baird et al., 2010). The direction traveled from the dung pile is thus arbitrary but maintained throughout a single journey, indicating true menotactic orientation (movement at a constant angle relative to stimuli) rather than simple taxis away or towards stimuli. To support their journeys away from the dung pile, beetles maintain their traveling directions relative to external references (see **Figure 1.2**). This is particularly well-studied in the Sub-Saharan African dung beetle *Kheper lamarcki* (MacLeay) which maintains its direction relative to celestial cues such as the position of the sun (Dacke et al., 2014, 2019), as well as the spectral gradient (el Jundi et al., 2015a), and the pattern of polarized light (el Jundi et al., 2014b; Khaldy et al., 2022) that the sun produces across the sky. Indoors, *K. lamarcki* can use a simulated sun, consisting of a green LED, to maintain its arbitrarily chosen bearing (el Jundi et al., 2015a; Khaldy et al., 2020; **Papers I** to **III**). This remains true across a range of elevations of the simulated sun (see **Figure 1.2**, **unpublished data**). Beyond visual cues, *K. lamarcki* can also maintain its direction with respect to a wind flow (Dacke et al., 2019; **Paper II**), demonstrating that directional information from different sensory modalities can be can be used by the beetle to maintain its heading.

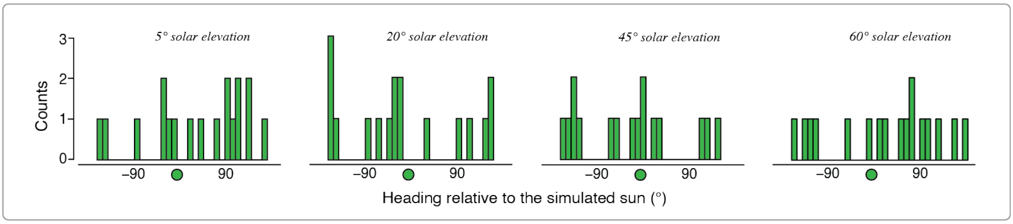

Figure 1.2: Headings of beetles orientating in the presence of a simulated sun at different elevations. The distribution of headings from *Kheper lamarcki* relative to the azimuthal position of the "sun" (green circles) are shown on the x-axes, binned by 5°, and the number of individuals heading in these directions are shown on the y-axis (**unpublished data**). This clearly illustrates that beetles chose arbitrary headings relative to a directional cue at a range of solar elevations.

The ability to use celestial cues for straight-line orientation is in no way limited to *K. lamarcki*, but extends to several other species of ball-rolling dung beetles, including species from different tribes inhabiting a range of habitat types (Khaldy et al., 2021). In addition to my main model system, *K. lamarcki*, my thesis work includes observations from the African species *Sysiphus fasciculatus* Boheman, as well as the Mediterranean species *Sisyphus schaefferi* (Linnaeus) and *Ateuchetus laticollis* (Linnaeus), which also steer using celestial cues (see **Figure 5.1**, **unpublished data**). Homing beetles, which do not use local landmarks to steer their paths between a food location and home (Dacke et al., 2020), also likely rely on celestial information for guidance. Different species, however, prioritize different sources of celestial directional information to steer their desired course (Khaldy et al., 2020, 2021), suggesting that they apply varying weights to the available directional references (discussed further in **Chapter 5**). In *K. lamarcki*'s compass system, the sun typically dominates over other cues. This can be tested by shifting the apparent position of the sun using a mirror while simultaneously hiding its real position with a screen (see **Figure 1.3**); if the beetle updates its direction of travel according to the positional change, it is primarily guided by the sun. To replicate this test indoors, a simulated sun can be set to different elevations and azimuthal directions (see **Figure 1.3**).

Figure 1.3: Experimental setups. Left: The apparent position of the sun from the view of the beetle is shifted by the use of a mirror, while the real sun is hidden from the beetle’s view by the use of a shading board. This apparent 180° azimuthal shift of the sun was a key component of the methods for **Paper III**. Right: An indoor setup with a green LED as a simulated sun, which can be set to any elevation along arcs representing a hemisphere. A circular, 0.5 m radius, arena is located in the center and three wind generators are present at different positions along a 1.5 m radius from the arena center. For a detailed description of this setup and its components, see **Paper II**. Beetles were presented with a simulated sun in **Paper I**, **Paper II**, and **Paper III** and the wind generators were used in **Paper II**.

K. lamarcki has also been described to perform yaw rotations on top of its dung ball, a behavior referred to as ”the dung beetle orientation dance” (Byrne et al., 2003; Baird et al., 2012; see also Hanski and Cambefort, 1991). This peculiar rotation on the spot (see **Figure 2.1**) is one of several features that make the dung beetles a unique model system to advance our understanding of the fundamental mechanisms behind robust orientation. Other such features include the sustained orientation while transporting a load that can be several times the beetle’s own body weight, and the fact that they move backwards along their straight paths (see **Figure 1.1**). These features, combined with their behavioral robustness to experimental manipulations, make straight-line ball-rolling beetles excellent models for investigating how a desired heading is maintained, how directional information from external references is dynamically weighted, and what role rotational behaviors play for orientation.

Chapter 2

The motifs and function behind rotational behaviors

Before departing on oriented journeys, as well as during their travels, many insects, as well as other arthropods, perform stereotyped rotational movements.

1 Rotations for learning of surroundings

Central place foragers such as bees, wasps, and ants execute controlled orientation flights or learning walks upon emerging from their nests, moving along arcs and loops with clear rotational components while gradually increasing the distance from their nest entrance (Collett and Hempel de Ibarra, 2023; Zeil and Fleischmann, 2019). Ground-borne ants perform circular paths and pirouette-like rotations, with regular pauses facing their nest entrance (Fleischmann et al., 2017). Even without a fixed nest location, sandhoppers perform left and right oscillations around their body axis to detect the Earth's magnetic field for their shore-line orientation (Ugolini, 2006). These rotational behaviors serve to learn the surrounding environment: orientation flights and learning walks allow foragers to memorize local landmarks and visual scenes around the nest, while pirouettes provide particularly

Figure 2.1: The dung beetle "orientation dance". In this particular example, the rotation event of an individual *Kheper lamarcki* consists of a complete yaw rotation atop its dung ball. For a detailed characterization of the orientation dance, see **Paper I**.

stable moments during which ants can acquire snapshots of important views (Fleischmann et al., 2017; Zeil and Fleischmann, 2019). Rotations also appear to calibrate the navigator's internal compass against external directional references such as the position of the sun (Collett and Hempel de Ibarra, 2023). The ”orientation dances” performed by straight-line ball-rolling dung beetles provide an excellent system for investigating the role of rotations for oriented behavior in greater detail.

2 Characteristics of the dung beetle orientation dance

The ”orientation dances” of the straight-line ball-rolling dung beetle *Kheper lamarcki* are essentially pirouettes in the form of yaw rotations performed atop its dung ball (Byrne et al., 2003; Baird et al., 2012; see **Figure 2.1**). Such rotation events at the beginning of a journey have been suggested to contribute to setting the intended direction of travel (Baird et al., 2012), and have proven critical for the beetles' ability to integrate different visual directional cues into a common frame of reference (el Jundi et al., 2016).

A rotation event can be experimentally induced by placing obstacles along the beetle's path (Baird et al., 2012), or by a temporary separation of the beetle from its dung ball (Baird et al., 2010, 2012; Byrne et al., 2003; Dacke et al., 2014; **Paper I**). While the dung beetle has been known to dance atop is ball for a long time, neither what naturally triggers these rotations during unimpeded travel, nor their angular components had been described.

In **Paper I**, I systematically characterized the triggering factors that made beetles spontan-

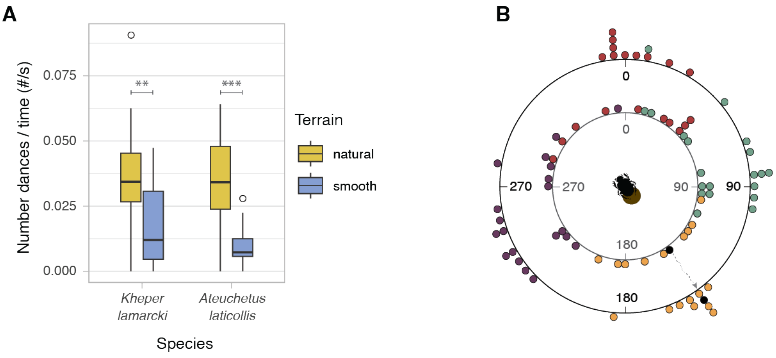

Figure 2.2: Outcomes from studies of beetles spontaneously performing orientation dances along their paths and after repeated temporary separations from their dung balls. A) The number of dances over traveling time for two species of ball-rolling beetles (*Kheper lamarcki* and *Ateuchetus laticollis*), rolling their balls over natural terrain or the artificially smooth "terrain" of a tennis court (*K. lamarcki*: **Paper I**; *A. laticollis*: **unpublished data**). B) Individual ***K. lamarcki*** rotated ten times each atop their dung balls, interspersed with 0.5 m of ball-rolling along a consistent course. Color coded examples from 4 beetles' body orientations as they stop rotating atop the ball (inner circle), and their corresponding bearings after having traveled 0.5 m following the rotation events (outer circle). The two black dots highlight an example body orientation and its corresponding bearing, connected with a gray arrow. Figure B is modified from **Paper I**.

eously stop and rotate atop their dung balls while transporting them over natural terrain, as well as across the leveled surface of a tennis court. When traversing the sandy, grassy, and bushy terrain that *K. lamarcki* naturally inhabits, the beetles performed significantly more rotation events than on smooth ground, indicating that terrain-related factors induced rotations (see Figure 2.2, Paper I). This study was replicated in a second species of ball-rolling dung beetle, *Ateuchetus laticollis*, which similarly performed more frequent orientation dances when traversing natural terrain compared to when traversing the smooth ground of a tennis court (see Figure 2.2, **unpublished data**). Further categorization of terrain-related disturbances revealed that the beetles spontaneously performed a rotation event after an unpredicted halt, temporarily losing contact with the dung ball, or falling on their side while still holding the ball (Paper I). This aligns well with the experimentally induced triggers previously identified under controlled conditions, where obstacles and physical disturbances prompted the beetle to climb atop its ball and rotate (Baird et al., 2012). However, a substantial proportion of rotations occurred without any identifiable external disturbance (Paper I). In these cases, the beetle simply stopped mid-stride, swiftly rotated atop its ball, and continued along a similar bearing. Additionally, spontaneous rotations are sometimes induced when beetles climb their balls for thermoregulation (Smolka et al., 2012), and are regularly induced when the position of the sun is experimentally shifted by a mirror (Baird et al., 2012; Paper III).

The rotation event has been suggested by Baird et al. (2012) to return the beetle to its dir-

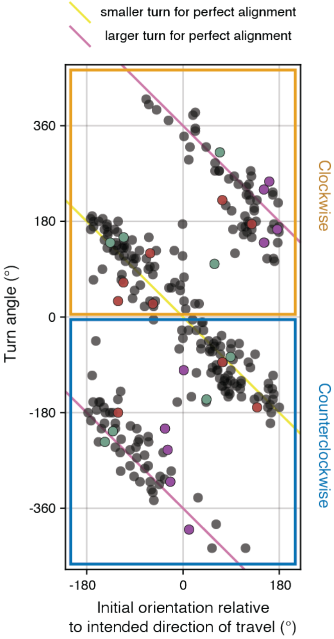

Figure 2.3: Angular characteristics of rotation events by Kheper lamarcki under the natural sky. Each beetle was temporarily separated from its dung ball and placed back onto it with a systematically controlled angular deviation from the beetle's *intended direction of travel*. The exact angle of placement defined its *initial orientation* atop the ball. The beetle then rotated atop the ball, resulting in a ***turn angle***, before climbing down to continue rolling its ball along its intended direction. Each beetle performed ten rotation events, interspersed with 0.5 m ball-rolling. Data points indicate the turn angles for unidirectional rotation events (n=272). The x-axis shows the beetle's initial body orientation relative to its intended direction of travel: positive values indicate a CW introduced angular displacement from this intended direction of travel, negative values a CCW introduced angular displacement. The y-axis indicates the angle turned: positive values indicate CW turns (orange box), negative values CCW turns (blue box). Diagonal lines indicate the smaller ($\leq 180°$, yellow line) and larger ($< 180°$, pink line) turn required for perfect alignment with the intended direction of travel. Data from three individuals are highlighted in red, green and purple. Modified from **Paper I**.

ection of travel after a disturbance, and in **Paper I**, I extended this line of research. Indeed, the beetle's body orientation at the end of a rotation aligned with the bearing along which it continued to roll its ball (see **Figure 2.2**B; **Paper I**). My characterization of these rotation events further revealed that they were predominantly unidirectional, either clockwise or counterclockwise, with beetles rotating in this single direction until aligned with their intended bearings (see **Figure 2.3**; **Paper I**). The choice of rotation direction appeared random, with no individual preference for clockwise or counterclockwise rotations. Thus, the rotation event requires no directional decision-making for the beetle to purposefully minimize - or maximize - its rotation atop the ball, and it is terminated when the beetle aligns with its intended bearing.

Taken together, rotations appear critical for insects' use of external references for oriented behavior, a notion also supported by calcium imaging from the fruit fly brain (Fisher et al., 2022). To better understand how rotations shape internal representations of direction, we must first become more familiar with the internal compass of insects.

Chapter 3

The insect internal compass

The internal compass of insects is found in a region of their brain called the central complex. This part of the brain is neatly structured into columns and layers, with neurons connected in distinct networks which allows for directional computations.

1 The central complex structure

The central complex, located on the midline of the insect brain, consists of four synapse-rich neuropils: the ellipsoid body (EB), the fan shaped body (FB), the protocerebral bridge (PB) and a pair of noduli (NO)(Wolff and Rubin, 2018; Pfeiffer and Homberg, 2014; Turner-Evans and Jayaraman, 2016; Honkanen et al., 2019; Hulse et al., 2021; Immonen et al., 2017; see **Figure 3.1**A-C). The EB, FB and PB are divided into columns according to the projection patterns of neurons that innervate these regions. Both the EB and the FB are typically divided into 8 or 9 columns, depending on the insect. In the PB, the columnar pattern (of 8 or 9) is repeated across the right and left hemispheres (see **Figure 3.1**C).

The nomenclature of the columnar neurons of the central complex, is based on which neuropils the cell type arborizes within (see **Figure 3.1**C-D). For example, the columnar neuron types EPG and PEG have the same projection patterns by innervating the EB, the PB and the gall (located in the lateral complex), but different directionality (also see **Figure 3.2** for EPG projections). According to the same naming convention, PEN neurons arborize in the PB, EB and NO, whereas PFN neurons arborize in the PB, FB and NO.

In contrast to columnar neurons that project into specific columns between neuropils, tangential neurons arborize *across* columns (see **Figure 3.1**C-D). They project from outside the central complex into a single target neuropil, where they generally extend across its width.

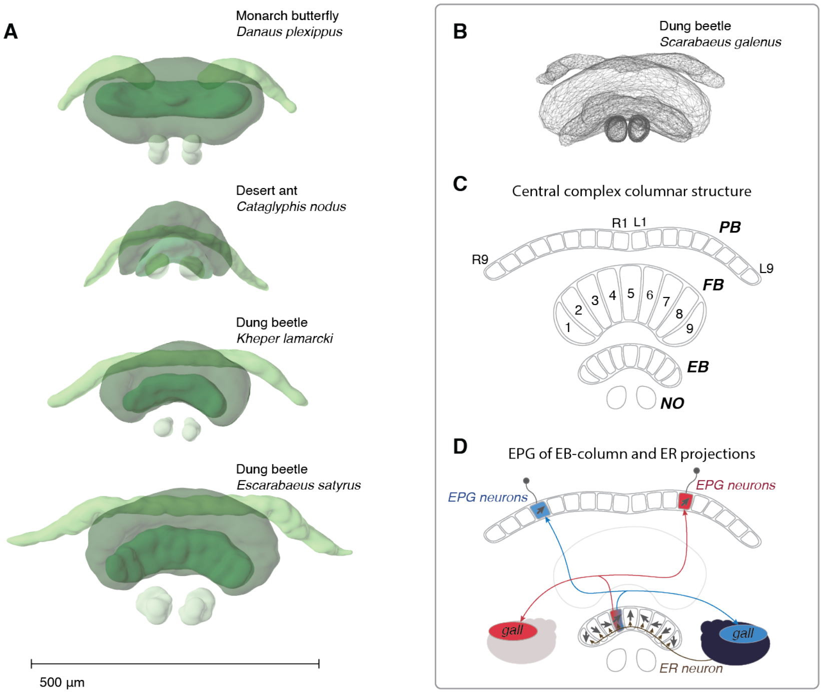

Figure 3.1: Central complex reconstructions, structure layout and example neuron projections. A) Central complex reconstructions retrieved from InsectBrainDB (insectbraindb.org; Heinze et al., 2021). Data (top to bottom): Monarch butterfly (***Danaus plexippus***; Heinze and Reppert, 2012), desert ant (***Cataglyphis nodus***; Habenstein et al., 2020), and dung beetles (***Kheper lamarcki*** and ***Escarabaeus satyrus*** (Boheman, 1860); Immonen et al., 2017). Scale bar; 500 μm. B) The central complex of the dung beetle ***Scarabaeus galenus*** (reconstruction by Auguste de Pennart, unpublished data). C) Schematic of the central complex neuropils: the protocerebral bridge (PB), fan-shaped body (FB), ellipsoid body (EB), and a pair of noduli (NO). The columnar pattern (8-9 columns depending on the species) of the EB and FB is replicated in the left (L) and right (R) parts of the PB. D) The projection pattern of EPG neurons (a type of columnar neuron) from the ***same*** column of the EB and of an ER neuron (a type of tangential neuron). EPG neurons have synaptic sites in the EB, PB, and gall (located in the paired lateral complexes which flank the central complex), and the EPG neurons innervating the same column of the EB split into either the right or the left PB. The activity of EPG cells moves across columns as the insect rotates, thereby tracking its angular orientation in space. In contrast to the columnar organization of EPG neurons, the ER neuron spans the width of the EB and has synaptic sites ***across*** its columns, as well as in the lateral complex.

Tangential neurons which target the EB or FB are organized in horizontal layers perpendicular to the columnar structure (Hulse et al., 2021; von Hadeln et al., 2020). One such cell type is the ER neuron (also known as ring, or R, neuron) that innervates the EB and has presynaptic partners in the lateral complex, a region that receives sensory input (see Figure 3.1). Other types of tangential neurons include the Δ7 cells which arborize across the PB, and LNO neurons that innervate the NO.

Together, the cell types described above, with their projection patterns, create the circuitry underlying the insect's internal compass.

2 The head direction network and its inputs

Theoretical models based on anatomical data along with functional evidence indicate that insects keep track of their angular orientation in space through a neuronal network within the central complex: the head direction network (Green et al., 2017; Turner-Evans et al., 2020). An important characteristic of this network is that the connectivity of the neuron types involved form a closed circle. Within this circuit, the columnar EPG cells in the EB function as ”compass neurons” by carrying a bump of neuronal activity (generated by the action of multiple cell types), that moves across columns as the insect rotates. In other words, this bump of activity acts like the needle of a compass, continuously tracking the insect's head direction (Seelig and Jayaraman, 2015; Heinze, 2017a; Stone et al., 2017). Due to the projections of EPG neurons, this activity bump in the EB is replicated twice in the PB, once in each hemisphere. Together, the PEG and EPG neurons create a recurrent loop between the EB and PB, effectively maintaining the bump of activity. In parallel, Δ7 cells prevent the generation of several simultaneous bumps by inhibiting EPG neurons corresponding to the angular orientation opposite the current position of the bump.

An array of sensory information is transferred through peripheral parts of the brain and reach the central complex via specific pathways. For example, information about self-motion (angular and translational velocity from optic flow, proprioception, and motor feedback) is transmitted to the lateral accessory lobe (LAL) of the lateral complex. From here, tangential GLNO neurons from each hemisphere notably relay rotational self-motion information to PEN neurons in the ipsilateral NO (Hulse et al., 2023, 2021). These PEN neurons are columnar neurons that, apart from innervating the NO, also project to the PB and EB. The PEN neurons innervating the *same* column as EPG neurons in the PB, are however contralaterally shifted by one column in the EB. When an animal turns, causing rotational velocity to be larger on one side of it, asymmetric input to PEN neurons from GLNO neurons shifts activity from one column of the EB to its neighbor. PEN neurons thus push the compass activity bump to adjacent columns as the animal turns (Green et al., 2017; Turner-Evans et al., 2017). Consequently, as idiothetic cues (motor information and proprioception) contribute to rotational velocity signals (Hulse et al., 2023), the ”compass bump” could theoretically keep tracking the insect's head direction in darkness. Evidence from fruit flies show that while this ”compass bump” does indeed track the insect's head direction for a short while, it quickly starts to drift in the absence of external references (Green et al., 2017; Kim et al., 2017; Seelig and Jayaraman, 2015; Turner-Evans et al., 2017).

External directional information counteracts this drift of the ”compass bump” and also follows specific pathways from sensors to the central complex. Directional information from the eyes, for example, travels through the distal optic lobes to the bulb of the lateral complex (Homberg et al., 2011; el Jundi et al., 2014a; Heinze et al., 2013; Held et al., 2016;

Hardcastle et al., 2021) while mechanosensory input, such as wind flow direction, ends up in the lateral accessory lobe (LAL) of the lateral complex (Homberg, 1994). Subtypes of tangential ER neurons then feed this directional information from the lateral complex to columnar EPG neurons in the EB (Seelig and Jayaraman, 2013; el Jundi et al., 2015b, 2018; Heinze et al., 2013; Okubo et al., 2020; Hardcastle et al., 2021; Omoto et al., 2017). Here, the direction of external cues are arbitrarily mapped relative to the bump of activity in the EB (Seelig and Jayaraman, 2015; Kim et al., 2019), a process that appears to occur through co-activation of ER and EPG neurons (Cope et al., 2017; Mitchell et al., 2023; Basnak et al., 2025). Initially, a population of ER neurons encoding different azimuthal positions of a cue has equal inhibitory connections to EPG neurons across columns. Over time, ER-to-EPG connections are weakened when an ER neuron is active at the same time as the bump is present in the target EPG column. This means that less inhibition is exerted onto EPG neurons in columns where the bump coincided with the directional signal from an ER neuron. As a result, a new connectivity weights between ER and EPG emerges, which tethers the bump location to the position of the cue (Fisher et al., 2019; Seelig and Jayaraman, 2015; Kim et al., 2017, 2019; Basnak et al., 2025). Consequently, after mapping, the external reference informs the insect about its angular orientation in space and provides feedback on its rotational velocity.

Together, directional information from external cues (from ER to EPG neurons) and self-motion cues in the shape of rotational velocity information (from PEN to EPG neurons) track the head direction of the insect by moving the activity bump to adjacent columns as the insect rotates, and update it about its current direction in the world (Seelig and Jayaraman, 2013, 2015; Green et al., 2017; Sun et al., 2017; Turner-Evans et al., 2017; Kim et al., 2017; Fisher et al., 2019; Kim et al., 2019; Okubo et al., 2020; Kim et al., 2019; Fisher et al., 2022; Haberkern et al., 2022; Hulse et al., 2021; Basnak et al., 2025). But how general is this ”internal heading representation” across insects, and what is it ultimately used for?

3 Steering towards goals

Insects that disperse, orient, navigate, or migrate share a common computational challenge: maintaining a goal direction, or desired heading (Collett et al., 2013; Green et al., 2019). Recent studies indicate that the spatial tuning of goal neurons within the central complex can remain invariant despite changes in the compass signal in the Monarch butterfly (Beetz et al., 2023) and the fruit fly (Mussells Pires et al., 2024). They have also put forward a central complex circuit that may facilitate the comparison of this internal goal representation with the insect’s current heading, consequently converting the difference between the two into a steering signal (Westeinde et al., 2024).

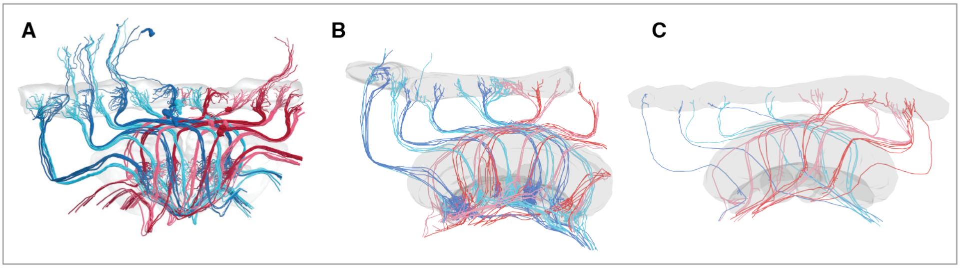

Figure 3.2: The projections of "compass neurons" (EPG neurons) of the head-direction network of three insect species. The neuropils of the central complex (top: protocerebral bridge (PB), middle: fanshaped body (FB), bottom: ellipsoid body (EB), and behind the FB/EB: a pair of noduli (NO)) are displayed in gray to highlight the different areas into which neurons of the central complex project. Individual neurons could be visualized following a protocol including ***a***) histological preparation of an insect brain, eventually embedded in resin, ***b***) this sample going through serial block-face electron microscopy (SBEM) for imaging the area of interest, and ***c***) the images from the SBEM going through steps of processing, resulting in an image stack (for the full protocol, see Sayre et al., 2021). From the resulting image stacks, individual neurons can be traced using a collaborative software. EPG neurons from the right PB (in blue) and from the left PB (in red) were in this way manually traced using the software Collaborative Annotation Toolkit for Massive Amounts of Image Data (CATMAID) in A) a bumblebee ***Bombus terrestris***, (data and image from Sayre et al., 2021), B) *Kheper lamarcki* (**unpublished data**), and C) *Scarabaeus galenus* (**unpublished data**). These neurons project into the EB and PB of the central complex and extends to the gall of either side.

The central complex neuropils and the neurons behind the underlying head direction network have been characterized across a range of different insects with varying ecology and navigational strategies. Despite this diversity, the architecture of the central complex, and potentially the underlying circuits, is remarkably conserved across species (Heinze, 2017b; Honkanen et al., 2019). This holds true also for ball-rolling dung beetles (el Jundi et al., 2015b; Immonen et al., 2017; see **Figure 3.1**).

Ongoing work continues to highlight similarities and differences between species, allowing for further inferences about the necessity of specific neuronal pathways for different behavior. Notably, technological advances and years of manual work has lead to full projectomes and connectomes of the central complex of the fruit fly (connectome: Scheffer et al., 2020) and the bumblebee (projectome: Sayre et al., 2021). To the same end, I have initiated and advanced the mapping of neurons in the central complex of the straight-line ball-rolling dung beetle *Kheper lamarcki* and the path integrating dung beetle *Scarabaeus galenus* Westwood (see **Figure 3.2**, **unpublished data**). Although this labor-intensive work is far from complete at the moment of writing, it its well on its way to further our insights into the structure of the dung-beetles compass network.

Ultimately, all navigating insects likely need to compare "where I am heading" with "where I want to go" to guide corrective turns toward a goal, or at least a goal direction. But how robust is this goal-directed steering to varying conditions?

Chapter 4

Oriented behaviors are best guided by external references

To maintain a consistent bearing, an insect continuously compares its current heading representation to its internal goal direction. Because this heading representation is anchored to external references, these cues are essential for robust orientation over any longer distances. Yet, in the natural world of insects, there are many situations in which stable external references can become temporarily unreliable or even unavailable.

1 Orientation in the absence of external references

In the absence of external directional references, an animal must rely on self-motion information from proprioception, motor efference, or its vestibular system to maintain a consistent direction or to return to known locations. Indeed, in darkness, internally generated directional signals appear sufficient for fruit flies to find their way back to a food location across an 8 cm radius arena in darkness (Kim and Dickinson, 2017). However, if continuously walking for even a couple of minutes, flies are not able to maintain their initial directions of travel (Basnak et al., 2025). A similar dependence on external visual cues for directional guidance has been demonstrated in humans, where blindfolded participants relying solely on idiothetic information could only maintain a straight path for about ten meters (Mittelstaedt and Mittelstaedt, 2001). Beyond this distance, they soon began to walk in loops or circles (Souman et al., 2009; Dacke and el Jundi, 2018). This is because a directional estimation based on self-motion signals alone is prone to accumulating motor or sensory errors, which over time will lead to deviations from the intended direction of travel (Cheung et al., 2007; Heinze et al., 2018; Khaldy et al., 2019; Wystrach et al., 2015).

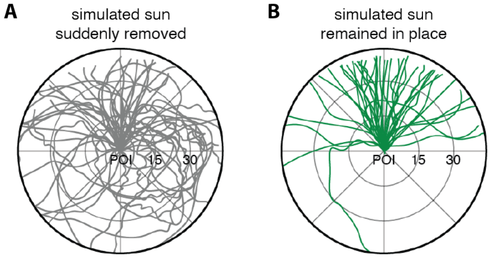

Figure 4.1: Directedness of beetles' (*Kheper lamarcki*) paths over a 0.5 m radius arena indoors. The beetles started to roll away from the arena center in the presence of a simulated sun as their sole visual reference. Once a beetle had traveled a radial distance of 0.1 m along its ***initial direction*** (represented by the upward direction in the circular plots), the simulated sun A) was suddenly removed, or B) remained in place. The beetles' continued travel from this point indicates how well they can maintain their initial direction, i.e., their trajectories highlight the directedness of each group. While beetles stayed well directed in the presence of the simulated sun, they did not manage to maintain their initial directions for long in the absence of directional cues. Modified from **Paper III**.

Some animals, however, can sustain oriented behavior with surprising accuracy over some distance without useful external references. Mantis shrimp, for example, manage to use idiothetic information to return to their burrows after visiting a food source 50 cm away (Patel and Cronin, 2020). Another remarkable example is the wandering spider, which can return with high precision to prey it left behind 75 cm away, even in the absence of external cues (Seyfarth et al., 1982; Zill and Seyfarth, 1996). This spider's remarkable accuracy in darkness can be attributed to specialized strain sensors in its legs which provide highly accurate proprioceptive signals. Clearly, the precision of orientation in darkness depends on the accuracy of the idiothetic system, which in most animals is limited.

It has been shown that without a clear view of the sky, the straight-line orientation of nocturnal and diurnal ball-rolling dung beetles is significantly impeded, as evidenced by more tortuous paths compared to when moving with a clear sky visible (Dacke et al., 2013b,a; Khaldy et al., 2019). To further define the ability of dung beetles to maintain their bearings with only idiothetic information, I took *Kheper lamarcki* into an indoor setup which allowed for total darkness (for an illustration of the setup, see **Figure 1.3**; **Paper III**). I found that, after suddenly removing their sole directional reference (a simulated sun), dung beetles could somewhat maintain their already established bearings (see **Figure 4.1**A; **Paper III**). However, their paths became progressively less directed with distance. Already within a radial distance of 25 cm from the point of the sun's removal, the directedness of beetles had dropped substantially compared to those which had continued access to a simulated sun (see **Figure 4.1**, **Paper III**). This suggests that, like other animals, dung beetles can use idiothetic information for short-range orientation but cannot sustain accurate directional travel in the absence of external references.

In parallel, a loss of directional precision in the absence of external references has been described for the internal heading representation of insects, where the position of this directional signal drifts in darkness (Green et al., 2017; Seelig and Jayaraman, 2015; Kim et al., 2019), consequently failing to accurately track the animals' angular orientation in space (Basnak et al., 2025). Given these limitations and challenges associated with relying on idiothetic information alone, it is no wonder that animals rely on external references to maintain their bearings. However, even these signals can be more or less reliable for directional guidance.

2 External references support oriented behavior

Celestial cues are well known to be used for directional guidance (reviewed in Freas and Spetch, 2022). Monarch butterflies (Perez et al., 1997; Reppert et al., 2010), homing ants (Wehner and Müller, 2006), and dispersing fruit flies (Warren et al., 2019), for example, use the position of the sun and polarized light to sustain their oriented behaviors. Beyond celestial information, the Earth's magnetic field can also serve as a directional reference (reviewed in Fleischmann et al., 2020), and Monarch butterflies (Mouritsen et al., 2013) and Bogong moths (Warrant et al., 2016) are believed to rely on odor cues to locate specific sites such as their estivation destinations. While pin-pointing exact goal locations, central place foragers such as bees (Cartwright and Collett, 1983; Collett et al., 2013; Warrant et al., 2004) and ants (Wehner and Duelli, 1971; Graham and Cheng, 2009; Fleischmann et al., 2016) also commonly use local landmarks and panoramic views for guidance. Interestingly, the only homing dung beetle that has been extensively studied to date does not take advantage of local landmarks as guiding cues (Dacke et al., 2020). Perhaps this is a reflection of its backward travel, where its gaze is facing away from the burrow upon arrival, leaving local landmarks rather unhelpful in locating this goal. Similarly, straight-line ball-rolling beetles guide their journeys without the added benefit of landmarks (Dacke et al., 2013b). Instead, the diurnal *K. lamarcki* predominantly maintains its straight trajectory away from the dung pile by maintaining a relative position to the azimuthal position of the sun (Dacke et al., 2014, 2019; Khaldy et al., 2020). If moved to a controlled indoors setup, dung beetles (el Jundi et al., 2015b; Smolka et al., 2016; **Paper II**), as well as other insects (for example, fruit flies: Giraldo et al., 2018 and Monarch butterflies: Beetz and el Jundi, 2023), can also maintain their intended directions of travel relative to the position of a simulated sun.

3 Sun guidance throughout the day

At low and medium solar elevations, *K. lamarcki* will consistently and robustly turn in accordance with an apparent 180° azimuthal shift of the sun's position in the sky (see **Figure 1.3**A for a mirrored sun), convincingly illustrating its role as the dominant cue in the compass system of the beetle. At high solar elevations, however, beetles display a greater orientation error (their difference in bearing between two consecutive runs from the center of a circular arena) compared to when steering at medium or low elevations of the sun (Dacke et al., 2014). The same loss in orientation accuracy can be observed in ants that

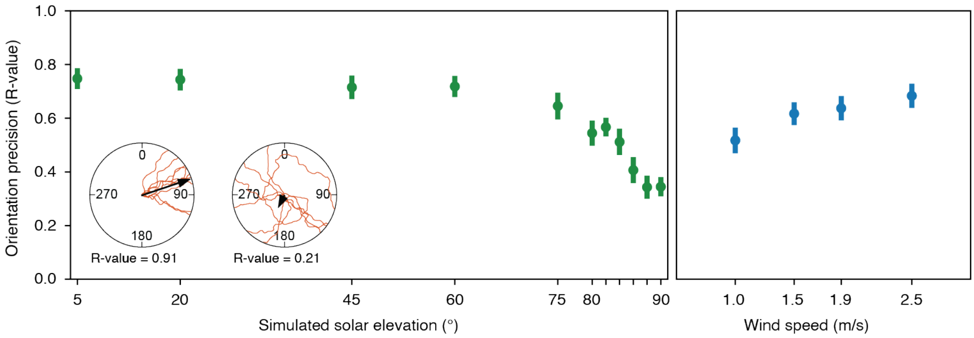

Figure 4.2: Mean orientation precision (R-value) across elevations and wind speeds. Each beetle (*Kheper lamarcki*) traveled from the center of a circular 0.5 m arena to its perimeter ***ten times*** (see figure **Figure 1.3** for the setup) in the presence of ***left***: a simulated sun (green data) and ***right***: a simulated wind (blue data). A beetle's directedness was determined by the mean vector length (R-value) from its ten bearings from the circular arena. For each simulated solar elevation and simulated wind speed, the population mean orientation was calculated (simulated sun: green data; wind: blue data). Vertical bars indicate standard error of the mean. Circular insets illustrate ten paths traveled by a highly directed (left, R-value = 0.91) and a weakly directed (right, R-value = 0.21) beetle. This shows that beetles were well directed at solar elevations between 5-75°, after which their precision quickly decreased with increasing solar elevation. They also became increasingly directed with higher speeds of the wind current. Modified from **Paper II** (Shaverdian et al., 2022).

display an increased scattering of directional choices based on the position of the sun at higher elevations (Müller and Wehner, 2007; Lanfranconi, 1982, as cited in Müller and Wehner, 2007). In line with these findings, the equatorial sandhopper also loses its ability to orient to the sun at elevations above 80° (Ugolini, 2001).

To further define how the sun's usefulness as an orientation cue varies with its elevation, I set out to define the orientation precision of dung beetles (their ability to maintain an individual bearing over consecutive runs from the center of a circular arena) at different elevations of a simulated sun in a controlled indoor setup (see **Figure 1.3**B). I found that the orientation precision of dung beetles remained high at elevations between 5° and 75°, but then quickly decreased with further increasing solar elevation (see **Figure 4.2**; **Paper II**). One way to cope with this decrease in precision of their solar compass at high elevations would be to avoid foraging in the middle of the day. This is not what is observed among these beetles Dacke et al. (2019); Tocco et al. (2021). Instead, as the sun becomes less useful, they rely more on other, more useful, directional cues (**Figure 5.2**; **Paper II**), as will become apparent in **Chapter 5**.

From the perspective of an animal, turning motions in the presence of a sun that is approaching zenith will generate less relative motion of the cue across the visual field than a sun at lower elevations will, reflecting a physical decrease in angular resolution. This can in turn explain the difficulty of animals, including the dung beetle (**Paper II**) to successfully orient themselves when the sun reaches extremely high elevations. The same reasoning has been explored in the case of ants, linking the spatial resolution of different parts of their eyes to a varying degree of *'accuracy of compass readings'*, or angular acuity (Zollikofer et al., 1995; Müller and Wehner, 2007).

Beyond elevation, the brightness of a light cue also affects its usefulness for directional guidance. This was recently demonstrated in the fruit fly through an elegant set of experiments that visualized the compass bump in the brain of the walking fly (Basnak et al., 2025). The study revealed how this improved orientation accuracy to a brighter cue was reflected in the internal heading representation of the insect. They showed that with increased brightness of the light cue: *a*) the movement of the bump corresponded better to the turning of the insect and *b*) the bump profile narrowed. Although not reflecting naturalistic conditions, this neatly illustrates the underlying mechanism behind more or less precise orientation relative to a single directional cue.

4 Wind for directional guidance

Beetles (Bell et al., 1989; Böhm, 1995; Linsenmair, 1972; **Paper II**, as well as other insects (Bell and Kramer, 1979; Wehner and Duelli, 1971; Wolf and Wehner, 2000; Müller and Wehner, 2007; Suver et al., 2019; Basnak et al., 2025) can also rely on the direction of wind flow to guide their travels. This directional information is most likely sensed through deflection of its antennae in which a stretch receptor organ called the Johnston organ resides (Bell and Kramer, 1979; Linsenmair, 1972; Shaverdian, 2025). Indeed, dung beetles and ants that have missing or immobilized antennae can no longer successfully orient to a wind cue (Shaverdian, 2025; Wehner and Duelli, 1971; Wolf and Wehner, 2000).

To further define how the usefulness of wind for directional guidance varies with its speed, my colleagues and I evaluated the straight-line orientation of the diurnal dung beetle *K. lamarcki* in the presence of an artificial wind current in a controlled indoor setup (see **Figure 1.3**B). We found that beetles successfully performed anemomenotaxis at wind speeds from 1 m/s to 2.5 m/s and that their orientation precision increased with increasing speed (see **Figure 4.2**; **Paper II**). This improved precision at wind speeds around and above 2 m/s matches the prevailing wind conditions that these beetles experience during their active period in their natural habitat (Dacke et al., 2019).

The ability to use wind can be particularly helpful during mid-day journeys when the precision of the directional information from the sun decreases, and illustrates that even when a preferred cue is unreliable, there are others to fall back on. In a similar manner, the equatorial sandhopper which can no longer use the sun at elevations exceeding 80° continues orienting using the magnetic field (Ugolini, 2001). But what happens when multiple reliable directional cues are available simultaneously?

Chapter 5

Dynamic cue weighting

Oftentimes, animals have more than one directional cue available for guidance at any given moment in time. Consequently, there must be some underlying processes in place to control *which* directional cue(s) are to be utilized, or *to what degree* the directional information from these cue should be trusted and followed. Indeed, such weighting of cues not only occurs, but differs between species and shifts dynamically with context.

1 Celestial cues are dynamically weighted

One way to quantify cue weighting is to first present an animal with two cues and allow it to establish a bearing, then experimentally shift the relative positions of the cues and observe how the animal responds to this cue conflict. In the context of homing, directional information from global cues can be put in conflict with local landmarks; and ants tend to steer intermediate courses, i.e., courses in-between the directions indicated by the two sources (Legge et al., 2014; Collett, 2012; Narendra et al., 2013; Wystrach et al., 2014; Wehner et al., 2016). Ants also appear to rely more on local landmarks as they approach their nest location (Wystrach et al., 2015). Here, distance can be used as a measure of when to trust what cue, and closer to a familiar location previously learned, landmarks should indeed be reliable. The same logic cannot be applied to global cues, including a range of celestial cues, whose usefulness does not change when walking. When the directional information from the sun's position and polarized light pattern conflict, ants have been shown to either primarily rely on polarized light (Wehner and Müller, 2006; Müller and Wehner, 2007) or again steer intermediate courses (Lebhardt and Ronacher, 2014; Wystrach et al., 2014).

Similar cue conflict experiments have been performed on ball-rolling dung beetles, and in one such experiment, el Jundi et al. (2015b) showed that *K. lamarcki* preferentially steer

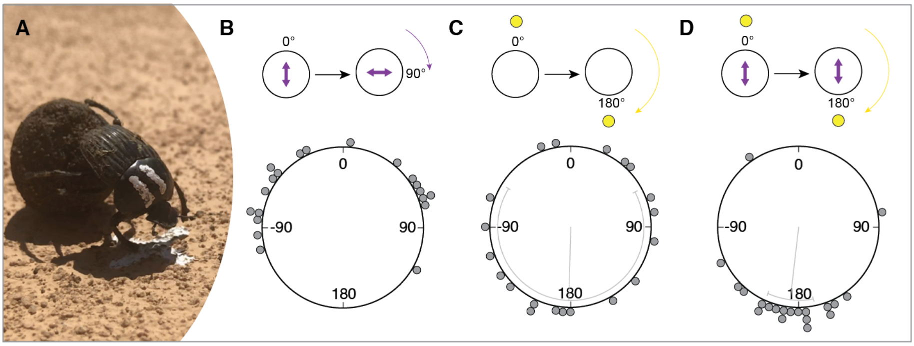

Figure 5.1: Directional changes in response to a cue manipulation of the polarized pattern or the sun. Beetles of the species *Ateuchetus laticollis* traveled from the center of a circular 0.5 m radius arena to its perimeter two times in a row. During its travels across the arena, each beetle was either given C) full access to the natural sky, or B, D) a full view of the sky through an overhead polarizing filter. A) *A. laticollis* (with the number "11" painted to its pronotum for individual identification) rolling a dung ball. B-C) Between the two consecutive runs over the arena performed per beetle, I introduced a cue conflict by rotating the polarizing filter by 90° (***top row***: purple arrows indicate e-vectors), or by mirroring the sun by 180° (***top row***: yellow circles indicate relative solar position). The directional change of each beetle was recorded (***bottom row***: gray data points indicate the directional change between two exits of the same individual; **unpublished data**). This shows that beetles changed their directions according to the rotated polarized pattern, as well as the shifted sun when the overhead polarizing filter was present. When the sun's position was shifted without an overhead polarizing filter, beetles instead changed directions seemingly randomly.

to the available celestial body (sun or moon) over the polarized pattern regardless of the time of day. This preference, however, is not universal; comparisons between diurnal dung beetle species from different habitats reveal that some preferentially follow a mirrored sun while others instead turn in response to a shifted polarization pattern when both cues are present (Khaldy et al., 2020, 2021). These findings could be interpreted as beetles simply attending to one cue at a time. However, with a more detailed manipulation of different cue parameters - such as varying the intensity or elevation of a sun cue, the degree of light polarization, or the speed of a wind current - a more complex interplay between the cues emerges. Experiments with *K. lamarcki* show that the weight given to different cues depends on what sensory inputs are available. When directional information from a simulated sun and a polarization pattern are put into conflict, the beetles' response depends on light intensity and degree of polarization (Khaldy et al., 2022). At higher light intensities and lower degrees of polarization, the beetles preferentially orient using the sun cue, whereas at lower intensities and higher degrees of polarization, they use the polarization pattern. Perhaps a similar dynamic weighting of cues could explain why ants have sometimes been described to steer according to the directional information from polarized light when in conflict with the sun's position, while at other times taking intermediate courses.

The diurnal dung beetle *Ateuchetus laticollis* shows a more complex interplay between cues. In a set of experiments with this species, I repeatedly allowed individuals to travel from the center of a circular arena to its perimeter under a natural sky. In between two consecutive runs of one individual, I manipulated either the direction of the available polarization pattern (using a polarizing filter) or the position of the sun (using a mirror) and noted the beetle's directional response to the now *conflicting* information from the references (see Figure 5.1B: top row). I found that beetles changed their traveling directions at random when the sun was mirrored while the rest of the natural sky remained visible (see Figure 5.1C, **unpublished data**). When instead the sun was mirrored in the presence of an artificially high degree of polarization (provided by the polarizing filter), the beetles clearly followed the shift of the sun (see Figure 5.1, **unpublished data**). This again demonstrates that reliance on the sun for directional guidance changes depending on celestial conditions, but here in an unusual way. One possibility is that the unexpected outcome reflects the overall lower light intensity under the polarizing filter rather than the increased degree of polarization, causing the solar disc to appear more prominent relative to the rest of the sky. This hypothesis could be tested in future experiments by monitoring responses to a mirrored sun under a neutral-density filter that lowers light intensity without affecting the degree of polarization.

2 Multimodal cues are dynamically weighted

The weighting between sun and wind for directional guidance also depends on cue context. In a set of experiments conducted outdoors, *K. lamarcki* were allowed to set their individual bearings in the presence of an artificial wind flow under the natural sky, after which the sun was mirrored or the wind flow direction was rotated (Dacke et al., 2019). The beetles responded by orienting according to the mirrored sun at low solar elevations but instead steered using the wind cue at high elevations (Dacke et al., 2019). Whether this reflected a simple hierarchy dictated by solar elevation or a more complex interaction, however, remained unclear. Together with my colleagues, I could demonstrate that the relative weighting of an artificial sun and wind in *K. lamarcki* shifts with solar elevation *and* wind speed (see Figure 5.2; Paper II). Starting from 45° elevation, beetles preferentially used the sun over a 2.5 m/s wind current. At 75° and above, they instead preferred the wind cue, consistent with the reduced directional usefulness of a sun at high elevations (see Figure 5.2 and Figure 4.2; Paper II). When wind speed was lowered to 1.25 m/s, however, the preference shifted so that beetles oriented by the sun even at 75° elevation. These results indicate a dynamic cue weighting between the directional information from sun and wind (Paper II). A similar dynamic weighting between these cues has been observed for ants (Müller and Wehner, 2007). However, while many of the conflict conditions in beetles seemed to generate a stronger preference for one cue or the other, the ants in the study above steered according to intermediate courses, which shifted more towards the wind at high solar elevations.

We further showed that the dung beetles' behavior was not best explained by a winner-takes-all integration strategy nor a statistically 'optimal' integration strategy, but rather by a non-optimal weighted vector sum model with small individual biases (see Figure 5.3; Paper II).

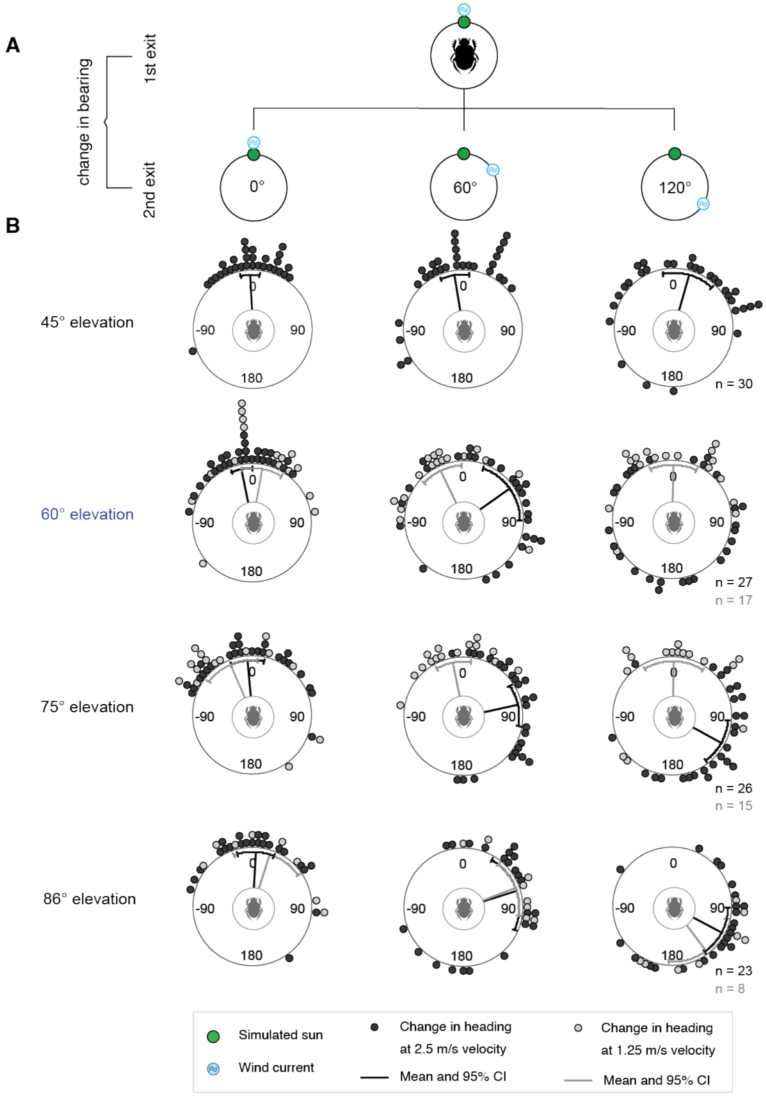

Figure 5.2: Behavioral results from a cue conflict experiment between a simulated sun and a wind current. A) Schematic representation of the cue conflict experiment conducted in an indoor setup (see **Figure 1.3**; **Paper II**). Change in bearing was calculated for individual beetles (***Kheper lamarcki***) between two consecutive exits from a circular arena; initial condition (1st exit where the initial bearing is established) to conflict condition (2nd exit where the wind current had changed direction by 0°, 60°, or 120° relative to the simulated sun). B) The changes in bearings at wind speed 2.5 m/s are illustrated as black circles and at 1.25 m/s as gray circles in the circular plots. Lines extending from the centers indicate mean vectors, black lines for 2.5 m/s and gray lines for 1.25 m/s, and end in a 95% confidence interval of the population spread. This shows that the relative influence that a simulated sun and wind exerted on beetles' bearings varied with the elevation of the sun, as well as the speed of the wind. Apparently, the directional information from the two cues was weighted according to their relative usefulness (see **Figure 4.2** for orientation precision of beetles presented with either cue in isolation). Adapted from **Paper II** (Shaverdian et al., 2022).

Under this model, beetles' directional choices varied according to the weight afforded to each cue, producing intermediate courses when conflicting cues carried similar weights.

When the weights differ dramatically, however, directional changes can resemble winner-takes-all behavior (see **Figure 5.2** for what can appear as a sun preference at 45° elevation and a wind preference at 75° elevation). Additionally, certain conflict angles with *similar* weights between the cues resulted in apparently random heading changes (see **Figure 4.2** and **Figure 5.2**B at 60° elevation and 2.5 m/s wind velocity; **Paper II**). Yet, beetles recovered their initial bearings when cues were returned to their original positions. This indicated that the beetles were not lost; the observed random distribution was instead an effect of the integration strategy, which the weighted vector sum model with small individual biases successfully accounted for.

A recent study on fruit flies orienting in the presence of either a simulated sun *or* a wind flow revealed individual differences in head-direction encoding accuracy (Basnak et al., 2025). This was indicated by the compass bump in the brains of different individuals matching the movement of a single cue to a varying degree. This in turn affected the relative weight given to the two cues when presented together. This is particularly noteworthy as it establishes a direct link between the weighting of cues observed from an animals' behavior and the accuracy in encoding of cues into the underlying compass circuit. It is also possible that the variation in weight attributed to specific cues, for example between dung beetle species living in different habitats (Khaldy et al., 2020, 2021), arise from how accurately the animal can encode them. Such a difference could stem from variation at any step between detecting the cue, processing it, and mapping it onto the compass network. In the case of *K. lamarcki* weighting directional information from sun and wind mentioned above, this would indicate that the sun is more accurately encoded than wind under solar elevations up to about 60° (see **Figure 4.2** and **Figure 5.2**). With elevations above this threshold, the sun instead appears to generate a less accurate directional signal than the wind current as the relative influence of the cues on the beetles' orientation shifts (see **Figure 5.2**).

Taken together, insects appear to integrate information, not only from one cue at a time, but from a range of available directional cues. The directional information from these cues is then dynamically weighted depending on their usefulness for directional guidance. This usefulness might rely on geometric limitations as with the elevation of the sun, or on salience as with the brightness of a simulated sun.

3 The dung beetles' rotations facilitate cue encoding and re-mapping

Rotational movements are commonly observed in insects and, based on behavioral studies, appear to serve the learning of visual scenes and the calibration of the compass system (see **Chapter 2**). In dung beetles, such rotations are triggered by disturbances to the path or by conflicting directional information (Baird et al., 2012; **Paper I**; **Paper III**). But why should a rotation be the response to these challenges?

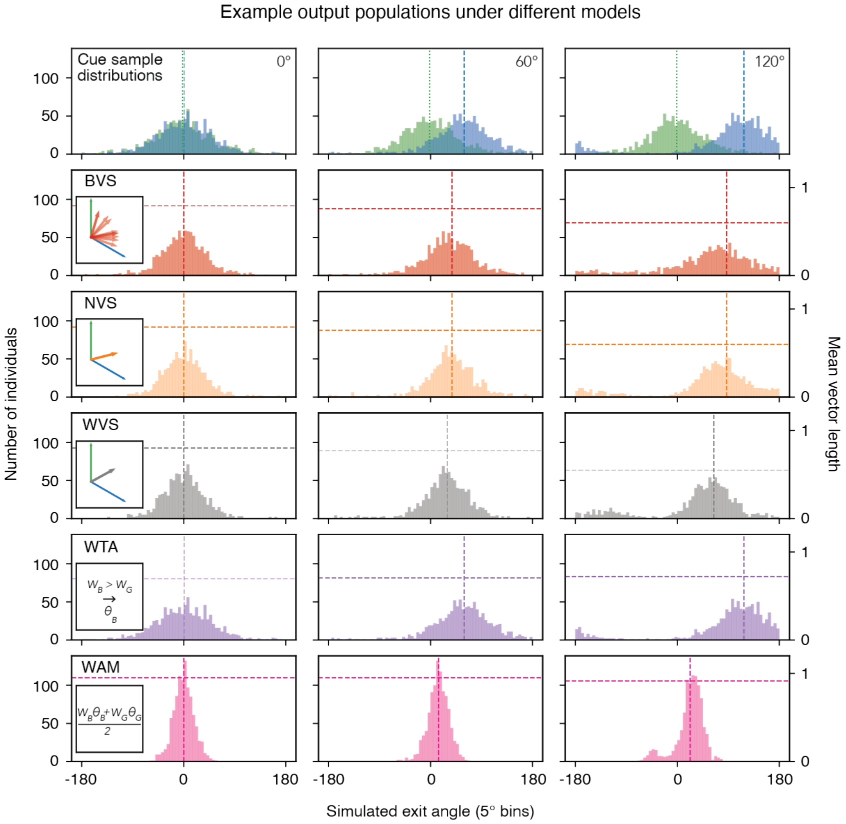

Figure 5.3: Output from different cue integration models based on input samples from behavioral data of beetles orienting to a simulated sun or simulated wind. Top row: The two sample distributions from beetles orienting in the presence of a simulated sun (green) or wind flow (blue) (from determining orientation precision in the presence of the cues in isolation, see **Figure 4.2**; **Paper II**), used as input to the models. Each cue is described by a von Mises noise distribution (knows as the "circular normal distribution") with $\kappa_{Green} = 2$, $\kappa_{Blue} = 2.05$, $\mu_{Green} = 0$, and $\mu_{Blue} \in \{0°, 60°, 120°\}$ (columns). From bottom: **WAM** (Weighted Arithmetic Mean): A simple weighted average of the angles. **WTA** (Winner-take all): Weights are compared and the cue with the greatest weight wins complete influence. **WVS** (Weighted Vector Sum): Angular samples are converted to vectors and then summed. **NVS** (Non-optimal weighted Vector Sum): Weights (vector magnitudes) are adjusted and then the vectors are summed. **BVS** (Biased non-optimal weighted Vector Sum): Noise is added to the weights. This strategy can generate different outputs for the same inputs due to the added noise, and best reflects the behavioral data in **Figure 5.2**. From **Paper II** (Shaverdian et al., 2022).

Most experiments on cue conflict in *K. lamarcki* discussed thus far have examined the changes in heading between consecutive runs. This means that a beetle always performs at least one rotation event in the presence of the original cue configuration before steering its ball along its straight-line travel, as well as *another* rotation event in the *conflicting scenario* (i.e., where the directional information from cues are conflicting compared to the previous configuration) before steering its ball anew. In this experimental paradigm, the beetles respond to changes in the azimuthal position of the sun under a range of solar elevations (Dacke et al., 2014; Khaldy et al., 2020; **Paper II**). If instead allowed to move continuously through a solar manipulation, i.e., without a rotation event in the conflicting

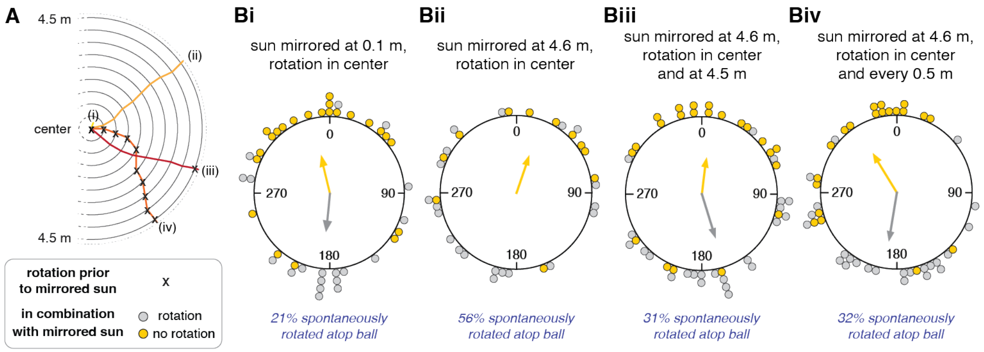

Figure 5.4: Responses to an apparent 180° azimuthal shift of the sun under a natural sky. A) Each beetle (*Kheper lamarcki*) was placed together with its dung ball at the center of a 5 m radius arena. It performed a rotation event at the center and then started rolling its dung ball along a set bearing. Beetles were exposed to an apparent 180° shift of the sun by the use of a mirror (see figure **Figure 1.3**) either after (i) 0.1 m of travel, or (ii-iv) 4.6 m of travel. Along its journey prior to the solar shift, a beetle could be prompted to perform an additional rotation event by holding its ball in place (indicated with **X**). Different groups of beetles were in this way prompted to rotate after (iii) 4.5 m of travel, or (iv) every 0.5 m radially from the center. B) The directional changes of beetles in response to the solar shift. In combination with the solar shift, beetles kept rolling their balls (directional changes: yellow data), or performed another rotation event (directional changes: gray data). In the latter group, beetles were either prompted to rotate atop their balls, or they did so ***spontaneously*** in response to the shifted sun. The proportion of undisturbed beetles that spontaneously rotated is indicated below each circular plot. The length of each arrow in the circular plots indicates the mean resultant vector length of the corresponding set of directional changes. Modified from **Paper III**.

scenario, beetles have been observed to continue along the same direction as before this solar shift (Baird et al., 2012). I further explored this in **Paper III**, and found that beetles that continuously rolled their dung balls throughout a 180° solar shift maintained their previous heading, irrespective of the distance traveled or the number of rotation events performed prior to the solar manipulation (see **Figure 5.4**B, yellow data points; **Paper III**). This makes sense in the context of their compass bump, considering that it is constructed to track rotational velocity (see **Chapter 3**); a smoothly shifting cue should be successfully tracked, whereas a sudden jump in directional input would not necessarily be tracked. If other external references remain available, the heading signal could be maintained by these stable inputs rather than follow the abrupt positional change of the sun. In nature, an external cue will never suddenly jump position, so from an ecological standpoint, maintaining a bearing relative to it should indeed result in robust steering.

In **Paper III**, I further demonstrate that a rotation event after a solar shift *restored* the beetles' bearing relative to the sun (see **Figure 5.4**B, gray data points). As it turns out, theoretical models (Cope et al., 2017; Mitchell, 2024) and functional imaging of the compass circuit of fruit flies (Fisher et al., 2019, 2022; Kim et al., 2019; Basnak et al., 2025) indicate that mapping of external information onto the internal compass occurs during rotations. This could explain the different influence that the shifted sun has on the dung beetles' orientation: *a*) without a dance, the beetles compass remain instructed by other unmanipulated cues while the sun's new position simply had not been learned and *b*) when dancing atop the ball, directional information from external cues are re-mapped, allowing for the new position of the sun to exert more influence again. Additionally, this re-mapping appears to be instructed by the dominant cue at a given moment (Basnak et al., 2025). In the case of beetles orienting at solar elevations between 30° and 60°, the sun should exert the greatest weight (as discussed above). This in turn would explain why beetles, in an attempt to steer along a set course, turn with the shift of the sun when performing a rotation event after the manipulation.

From my experiments outdoors, I could also conclude that a substantial proportion of beetles spontaneously rotate in response to a suddenly shifted solar position under a natural sky, i.e., in response to conflicting directional input (Baird et al., 2012; **Paper III**). In **Paper III**, I found that the proportion of beetles that do so varied with experimental condition: 21% when the conflict occurred after 0.1 m of travel (see **Figure 5.4**Bi), 31% and 32% when the conflict occurred after 4.6 m of travel while their preceding rotation event occurred 0.1 m prior (see **Figure 5.4**Biii-iv), and 56% when the conflict occurred after 4.6 m of *continuous* travel (see **Figure 5.4**Bii). In other words, a beetle was less likely to spontaneously rotate atop its ball in response to a shifted sun position after traveling a short distance or having recently performed a rotation event. I suggest that: *a*) a longer distance traveled decreases the strength of the beetle's directional signal, or degrades it, and *b*) a rotation event strengthens the directional signal (i.e., improves it if degraded). As a result, I also suggest that a spontaneous rotation event during cue manipulation reflects a need to improve the directional signal (as mentioned in ”b”) due to it having degraded during travel (as mentioned in ”a”)(**Paper III**). This interpretation is supported by the observation that rotations serve to map and re-map available information (Fisher et al., 2019, 2022; Kim et al., 2019), which would be necessary when directional signals are weak or degraded. Another result that follows the same logic is that the re-mapping under the conflicting scenario (sun's position suddenly shifted under a natural sky, see above) was clearly

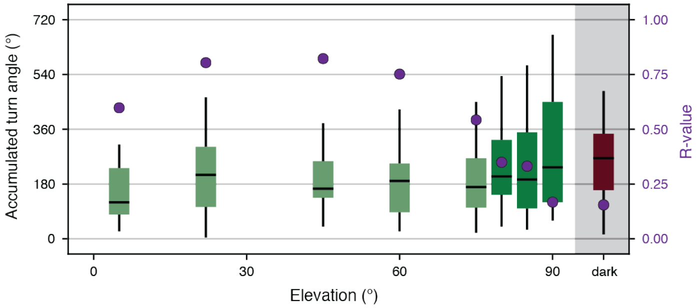

Figure 5.5: Rotation events performed under different simulated solar elevations and in darkness. The moment the beetle (*Kheper lamarcki*) started to climb its dung ball marked the start of a rotation event. It ended as the beetle descended the ball to continue its travel again. ***Left y-axis***: The absolute amount of rotation performed between the start and the end of the rotation event defined each beetle's accumulated turn angle (°) at different elevations of a green LED (green box-plots), and in darkness (red box-plot). Black horizontal lines indicate medians; whiskers extend to the minimum and maximum values (outliers are excluded for visualization purposes). ***Right y-axis***: Purple circles show the resultant mean vector length of the angular differences in bearing between two consecutive exits under the same simulated elevations and darkness. This shows that a decreased ability of the beetles to successfully maintain a bearing relative to the directional cue (or in the absence of it) coincides with an increase in accumulated turn angle. From **Paper I**.

instructed *primarily* by the position of the sun after a *recent* rotation event as the beetles turned according to its 180° shift (see Figure 5.4Bi, Biii, and Biv; Paper III). When instead having traveled a longer distance (or time) since the last rotation event, the beetles no longer clearly turned according to the position of the sun. In this case, the sun no longer appeared to instruct the re-mapping of cues under the conflicting scenario. Thus, the directional influence, or accuracy, of the sun on the compass signal appears to increase with a recent rotation event, highlighting the role of rotations in improving directional signals.

Additionally, in Paper I, I found that beetles performed longer rotations at higher simulated solar elevations (see Figure 5.5), meaning that longer rotations correlated with ambiguous directional information from the sun. This could reflect beetles struggling to determine when their heading aligns with their intended direction, or an attempt to strengthen the directional signal by sampling over a greater rotation angle Taken together, these findings suggest that rotation events serve to improve the directional signal from a cue whose coding accuracy is low or ambiguous.

Chapter 6

Dynamic collaborative steering

An interesting feature of straight-line ball-rolling dung beetles is that they perform their travels backward while transporting their dung balls along individually chosen intended directions of travel. Even more interesting is that, for some species, a pair of beetles can steer along a path together.

1 Cooperative transportation

Cooperative transportation is in itself a rare occurrence across the animal kingdom, observed primarily in humans and ants (reviewed in Czaczkes and Ratnieks, 2013). Ants are regularly observed to transport food items many times heavier than themselves back to their nest in unison with other individuals, though the efficiency of this behavior varies considerably between species (Czaczkes and Ratnieks, 2013; McCreery and Breed, 2014). Recent studies in ants have revealed how efficient cooperative transport can emerge simply through collective motion based on the forces that individuals exert onto an object (Feinerman et al., 2018; Dreyer et al., 2025). This type of strategy also proves effective for transporting an object through a spatial puzzle, for ants as well as for humans (Dreyer et al., 2025). Beyond ants, social spiders sharing a web structure are known to collectively attack large prey (see for example Nentwig, 1985) and have been observed to cooperatively transport captured prey from the capture site to their shelters (Vakanas and Krafft, 2004). What these animals typically have in common is their social nature, to which cooperation may have collective benefits. In addition to this, the location to which they need to bring their bounty is known by the individuals beforehand. It is intriguing then that ball-rolling dung beetles, which *a*) do not live in communities like social humans, ants, or spiders, and *b*) do not have a predefined goal for their dung balls, nonetheless can be observed to move them away from

Figure 6.1: A pair of *Sisyphus schaefferi* transporting their brood ball horizontally over a flat surface (left) or vertically over an obstacle (right). The beetle dragging the ball with its hind legs in contact with the substrate (left photo, right photo), is the male and the beetle pushing the ball, with its hind legs placed on the ball (left photo, right photo), is the female. The female in the right image (closest to the ground) is performing a 'headstand'; a move that is part of the climb initiation sequence. Courtesy of Claudia Tocco.

a dung pat in pairs (see Figure 6.1).

2 Dung beetle nesting and brood ball transportation

Dung beetles are typically solitary but come together in pairs for reproductive purposes. For ball-rollers, this involves shaping a piece of dung into a brood ball, copulation, oviposition into the ball, transportation of it, burying it in the ground, and potential maintenance of the brood ball once in the ground, though not necessarily in that order (Hanski and Cambefort, 1991). In the process of collaborative ball-making, there is often an active and a passive partner, and whether the male or female takes the active role appears to differ between species. Similarly, while some species roll their brood ball together (Hanski and Cambefort, 1991; Paschalidis, 1974; Davis et al., 2020), the female of other species climbs onto the ball and holds on while the male pushes the ball alone (Hanski and Cambefort, 1991; Halffter et al., 2011; Davis et al., 2020). In the latter case, one of the participants (the male) clearly takes on a "leading" role and maintains an arbitrary heading without input from a second, potentially directionally conflicting, navigator.

When it comes to the cooperative transportation and steering of the brood ball, females of most African species of dung beetles, including *Kheper lamarcki*, appear to have a passive role (Halffter et al., 2011). This stands in contrast to what has been observed for other dung beetles, including species of the genus *Sisyphus*, where both partners actively cooperate in transporting the brood ball without a predefined goal (Fabre, 1918; Paschalidis, 1974; Davis et al., 2020).

3 Cooperative brood ball transportation

Over 100 years ago, the cooperative brood ball transportation was described for pairs of the species *Sisyphus schaefferi*, including how they repeatedly climbed obstacles along their

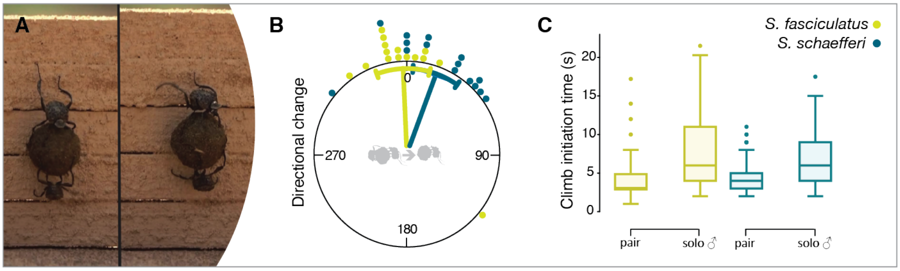

Figure 6.2: Coordinated travel by pairs of Sisyphus fasciculatus and Sisyphus schaefferi. A) Pair of ***S. fasciculatus*** climbing a 6.5 cm obstacle; male in dragging position on the top and female in pushing position with the right mesoleg and head in contact with the obstacle. B) Change in bearing between a pair of beetles (male and female) and the solo male, traveling from the center of a circular arena to its perimeter (***S. fasciculatus***: green data; ***S. schaefferi***: blue data). For both species, a V-test showed that the changes in bearing between the pairs and the respective males significantly cluster around 0°. C) Duration of the climb initiations (i.e., from the moment when the beetle first made contact with the obstacle until the dung ball had been lifted from the ground and the leading male had reached a height of 2.6 cm high with the metatarsal claws of one leg) of both successful and failed climbs for pairs and solo males of both species. Generalized linear mixed models show significant differences between pairs and solo males in climb initiation time (displayed here) and entire climb time (not displayed here). Horizontal bars show the median and the boxes show the quantiles. The female facilitated the climb over obstacles placed in the beetles' path, but did not contribute to the travel across flat ground. Adapted from **Paper IV** (Tocco et al., 2024).

path to remain along their intended course (Fabre, 1918). The two members of the pair also employ separate roles during transport, where one places its long "spider-like" hind legs on the ball and pushes it backward while the other, from the other side of the ball, is dragging the ball with its front legs, also walking backward (see **Figure 6.1**). More recent field work on this species has revealed that one individual starts the construction of the ball and the other one joins the effort, after which the pushing and dragging of the ball can be carried out by either sex (Paschalidis, 1974; Rizzotto et al., 2021).

It is interesting to consider how these pairs maintain a single bearing *without a predefined goal location* while coordinating the transport of their brood ball away from the dung pat, as well as managing to climb obstacles. In **Paper IV**, my colleagues and I set out to further our understanding of how orientation can be sustained by a dung beetle pair through such challenges by studying the cooperative transport of *Sisyphus fasciculatus* and *S. schaefferi*. In contrast to previous studies (Paschalidis, 1974; Rizzotto et al., 2021), we found that the male of each pair always dragged the brood ball while the female always pushed it. In Rizzotto et al. (2021) the authors highlighted the difficulty of determining the beetles' sex while performing field work, whereas the determination of sex was done post-experiment in our study, leading to high precision.

We also found that *a*) males maintained the bearing if their partner was removed whereas females stopped moving (see **Figure 6.2**), and *b*) solo males and couples performed their straight-line orientation equally well (**Paper IV**). In other words, the male of both species appeared to be controlling the steering, while the female only passively contributed to ball transportation while moving across flat ground. By having one of the participants (the male) occupying a "leading" role while maintaining an arbitrary heading, the beetles can ensure that there is no conflict in which way to travel. This strategy indeed appears beneficial when traveling together without a predefined, and agreed upon, destination. The females, however, played an active role in clearing obstacles placed in the couples' path. In particular, a female contributed with a ”headstand”, pushing the ball off the ground while the male was pulling it from a higher point of the vertical obstacle, as part of the couple's *initiation* of their climb (see **Figure 6.1**B; **Paper IV**). The help from a female resulted in a greater likelihood to initiate a climb as well as faster clearance of obstacles compared to a male traveling solo (see **Figure 6.2**C). By increasing its contribution under challenging conditions, the more passive participant helps in moments of need, while simply not imposing a hindrance to the straight-line travel otherwise.

Taken together, the results from **Paper IV** demonstrate how a dung beetle pair can efficiently and dynamically steer along a straight-line path while transporting a brood ball, even in the absence of a predefined destination.

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Papers

For the purpose of investigating aspects of oriented behavior among dung beetles, I have mainly focused on the straight-line orientation performed by the South African diurnal species *Kheper lamarcki* and its orientation dance; yaw rotations performed atop its dung ball. I defined triggering factors of these ”dances” (or *rotation events*), characterized their angular components (**Paper I**, **Chapter 2**), and identified how repeated rotation events affect their their orientation (**Paper III**, **Chapter 5**). I further described the controlling factors behind the dynamic weighting of directional information that guides the beetle's straight line travel (**Paper II**, **Chapter 5**), as well as discussed the challenges of steering by idiothetic cues in the absence of external references (**Paper III**, **Chapter 4**).

Straight-line orienting beetles maintain their bearings while actively transporting their dung balls. Normally, beetles that are about to mate can be identified by the male rolling a massive brood ball with a female that holds on to the side of the ball; simply following along for the ride. In contrast to this, couples of the species *Sisyphus fasciculatus* and *Sisyphus schaefferi* steer their dung ball together. Together with colleagues I described how they overcome this challenge in an elegantly simple way (**Paper IV**, **Chapter 6**).