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## Visual cues used by ball-rolling dung beetles for orientation

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**Abstract** Ball rolling by dung beetles is considered to be a derived behaviour that evolved under pressure for space, and from competitors at the dung pat. Straight-line orientation away from the pat using a celestial cue should be the most successful rolling strategy to move dung to an unknown burial site. We tested this hypothesis in the field and the laboratory by presenting five species of ball-rolling beetles with different orientation tasks, involving reaction to obstacles as well as to reflected sunlight and artificial light sources. Beetles were found to consistently orientate along a chosen route, usually in the direction of the sun. Beetles rolling dung balls successfully negotiated barriers and returned to the original path as did beetles falling from ramps, or rotated about a fixed point while rolling a ball. The sun was found to be the main orientation cue, which could be substituted by reflected or artificial light. However, beetles reoriented themselves less accurately in response to lights in the laboratory, than they did to the reflected sun in the field. It is probable that phototactic orientation using the sun, which is widespread amongst arthropods, has been incorporated in the straight-line foraging behaviour that has evolved in ball-rolling dung beetles.

**Keywords** Celestial cue · Foraging · Scarabaeidae · Scarabaeinae · Visual orientation

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### Introduction

Most dung beetles do not roll balls, but rather sequester dung in tunnels that they dig directly beneath the pat and into which they transport small lumps of the dropping, without ever exposing themselves on the soil surface. Ball rolling is considered to be a derived behaviour, that evolved in a few species in response to competition for food and space within the dung pat and below it (Bernon 1981; Cambefort and Hanski 1991). The ball has one of three fates: either as a food ball which is eaten over a period of days; a brood ball in which an egg is laid; or a nuptial ball which some species including *Kheper nigroaeneus*, use to attract mates (Tribe 1975). Dung is a valuable but patchy and ephemeral resource, therefore dung-rolling beetles construct the ball as a transportable resource unit, which can be rolled away for a long or short distance and usually buried.

The orientation of ball-rolling dung beetles is possibly one of the oldest recorded accounts of animal behaviour. Horapollo, a late Egyptian writer, described the scarab beetle “which rolls the ball from East to West, looking himself towards the East” (Brandon 1985). This early observation suggests that ball-rolling beetles use the sun to navigate their prize away from the dung pat. However, in the intervening 3,000 years, little has been done to examine this phenomenon in more depth (Matthews 1963). Amongst other animals, orientation with the aid of celestial cues is widespread (Waterman 1989), and well known in insects (Wehner 1984). However, such behaviour generally involves navigation between a fixed position, such as a nest, and a learned or novel position such as a feeding site (von Frisch 1967), or simply determination of an efficient escape direction using a sun compass, as shown by beach sandhoppers (Pardi and Papi 1953; Ugolini et al. 1993). Navigation by path integration is often achieved by orientating to celestial cues (Collett and Collett 2000a, 2000b). Ball rolling, on the other hand, is usually a one-way orientation, away from a food source over a novel terrain

towards an unknown destination where the ball is buried.

Competition, both inter- and intra-specific, at the pat can be intense (Heinrich and Bartholomew 1979; Ybarrondo and Heinrich 1996). Ball-making time and ball volume are reduced in *K. nigroaeneus* in the presence of competitors, and thoracic temperatures may be metabolically elevated to improve ball-making or rolling speed, or the chance of stealing a ball from another beetle (Bartholomew and Heinrich 1978; Ybarrondo and Heinrich 1996). A further potential cost of handling dung above the ground is the increased risk of predation, although this has not yet been quantified (Cambefort and Hanski 1991). Such selection pressures will therefore favour beetles that can remove dung balls swiftly and efficiently, which will presumably be in a straight line. A unique aspect of this foraging behaviour is that in most species, neither the food source nor the burial site are familiar to the beetle and are not returned to.

Before rolling their ball away from the pat, dung beetles usually perform a quick orientation “dance”, by circling once on top of the ball with the head held out horizontally, coming down on the side of the ball opposite the direction of travel (Fig. 1a). The dance lasts about 2 s and then the ball is usually pushed away from the pat backwards, using the hind and middle legs to roll

and steer the ball, whilst pushing on the ground with the fore legs. The beetle therefore travels backwards, in a head-down position with both the ball and its body obscuring any view of the route (Fig. 1b). The eyes, which are divided horizontally to some extent by a pronounced canthus (which is a bar of chitin extending into the eye), are located at the back of the head between the gena and prothorax, where only the dorsal portion has a view of the whole sky (Fig. 1c).

Sun orientation in the Scarabaeoidea has been noted by several authors (Birukow 1953; Geisler 1961; Fraenkel and Gunn 1961). However, the subject of these investigations, *Geotrupes silvaticus* (*G. stercorosus*) (Geotrupidae), is a Palaearctic forest species, which does not roll dung balls. Astro-orientation between the nest and a food source during repeated foraging has been reported in the genus *Lethrus* (Scarabaeidae: Lethrinae) and is accomplished by the use of polarised light (Frantsevich et al. 1977). Observations of *Canthon pilularius* (Scarabaeinae) suggest a possible role for the sun in ball rolling orientation, when the effects of wind and slope are removed (Matthews 1963). Surprisingly, apart from some investigations of the effects of thermoregulation and body size on ball rolling (Heinrich and Bartholomew 1979; Tomkins et al. 1999), this unusual behaviour has remained unexplored with regard to orientation.

Here we report results of field and laboratory experiments on the ball rolling behaviour of five species of dung beetles (Scarabaeinae) and the role of the sun in this behaviour. Two questions are addressed: (1) do ball-rolling beetles roll dung balls in a straight line, and (2) do they use the sun as an orientation cue for this rolling behaviour?

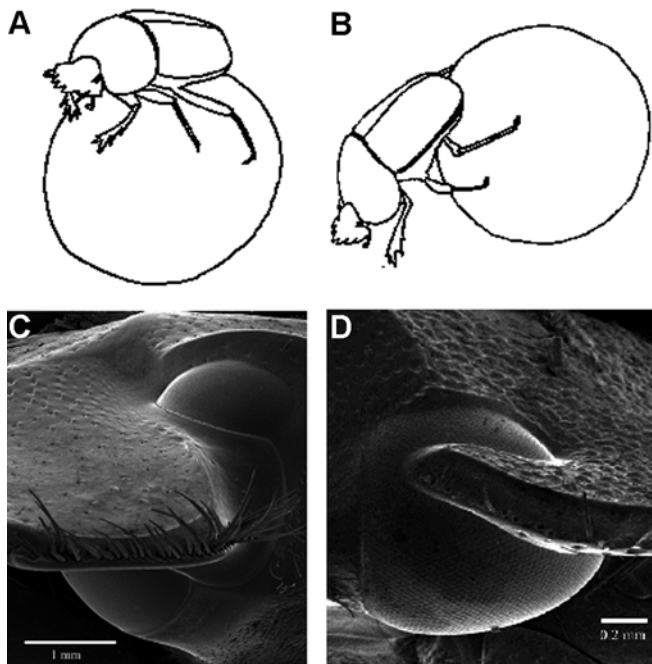
## Methods and materials

### Experimental species and sites

The following five species of beetles were used in a variety of experiments, depending upon their availability; *Scarabaeus rugosus* (Hausman), *S. rusticus* (Boheman), *K. nigroaeneus* (Boheman) and *Pachylomerus femoralis* (Kirby) are all in the tribe Scarabaeini, in which the dorsal and ventral eye is completely divided by a broad canthus (Fig. 1c). *Garreta unicolor* (Gymnopleurini) has an incomplete canthus which extends only part way across the eye (Fig. 1d). All are strictly diurnal.

All fieldwork was carried out during the day, during the austral summer, wet season in South Africa. *S. rusticus*, *K. nigroaeneus* and *G. unicolor* were studied at Pullen farm (25°57' S, 31°17' E), the University of the Witwatersrand's field station near Nelspruit, Mpumalanga Province, and *P. femoralis* was studied at Cinery Game Farm (24°38' S 28°45' E), near Nylstroom, Limpopo Province. *S. rugosus* was studied at Kleinzee, Namaqualand (29°39' 55 S 17°10' 34 E). Laboratory experiments were conducted on all species in Lund, Sweden within 2 weeks of capturing the beetles, as they were found to gradually lose their rolling behaviour after an extended period in captivity. When maintained at 25°C and supplied with fresh dung, recently captured beetles readily rolled balls in the laboratory.

Field experiments were run on level earth arenas (approx. 3 m diameter) that had been cleared of vegetation and rolled flat to remove any potential source of path deviation. A 2-l pat of cattle



**Fig. 1A–D** Head posture and eye position during ball rolling by dung beetles. **A** Orientation “dance” on the ball; note the head held out, allowing the dorsal eyes to scan the sky as the beetle rotates on the ball. **B** Rolling position, in which the dorsal eyes cannot see the intended route, and the ventral eyes can only see the ball and the ground. **C** Lateral view of the head of *Pachylomerus femoralis*, showing the dorsal and ventral eyes, at the back of the head, divided by the canthus. **D** Lateral view of the head of *Garreta unicolor*, showing the incomplete canthus

dung was placed at the centre of the arena and trials were run in one of two ways. At Cinergy and Kleinzee, beetles arriving at the dung naturally, were allowed to fly or walk onto the central dung pat, where they constructed a dung ball and rolled it away. Various manipulations (see below) were then performed when the beetles were about 1 m from the dung pat. To ensure a continual supply of beetles at Pullen farm, they were collected in dung-baited pitfall traps, then held in 10-l plastic bins with dung and soil, where they constructed and rolled balls. Rolling beetles were removed from the bins with their balls and placed on the central dung pat, then manipulated and observed as they rolled balls out of the arena. The observers took care not to block the beetle's view of the sky or the sun, and minimised movement around the test subjects, which are generally oblivious to the slow movement of large objects in the vicinity of fresh dung. Once a beetle had exited the arena, it was removed from the experiment. Orientation angles were measured with either a magnetic compass or a draughtsman's protractor, and used without modification in the analyses, but are presented in 5° categories for the figures. Reorientation trajectories were measured over about 30 cm, and the beetles were usually alone on the dung pat, therefore competitive interactions are assumed not to have influenced the results. We assumed that all the ball rolling observed was of food balls, which are usually smaller and less well constructed than brood balls and rolled by a solitary beetle (Cambefort and Hanski 1991).

### Beetle's response to manipulation of the route

#### Response to an obstacle

The orientation behaviour by beetles rolling balls away from the dung pat was tested by measuring the angle of deviation from the original direction of departure caused by an obstacle placed in the path of the beetle. *P. femoralis* and *S. rugosus* were allowed to roll balls away from the pat, where a transparent Perspex barrier (30 cm wide × 10 cm high), was placed perpendicular to their path of departure (Fig. 2a). Differences between the original and final angles of rolling were measured using a magnetic compass. All angular deviations from the original path were given the same sign (+), and subjected to statistical analysis.

#### Response to a fall and loss of contact with the ball

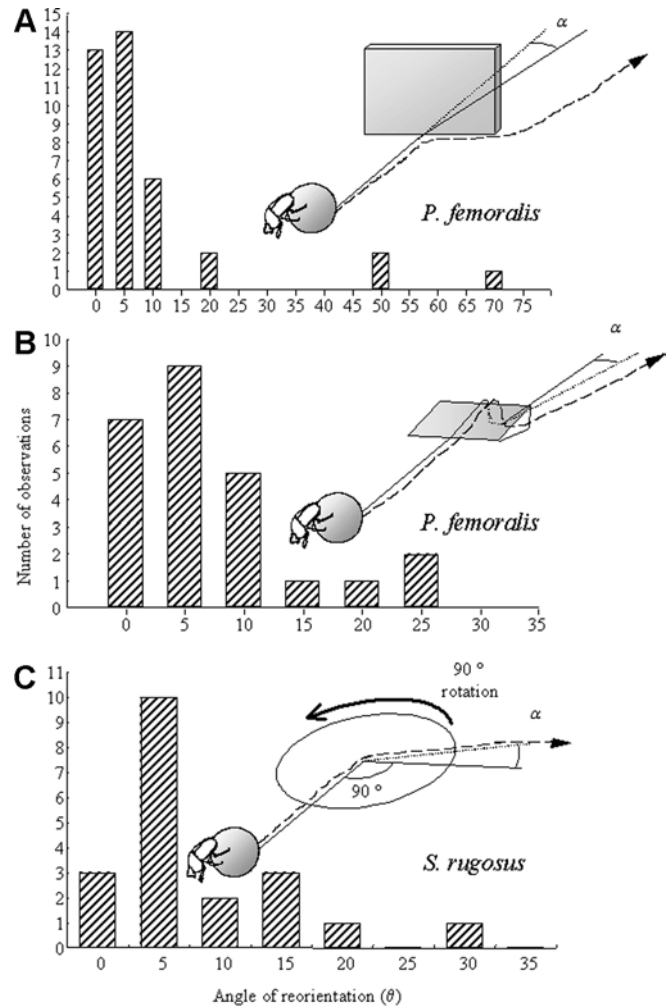
All five species were tested by placing a Perspex ramp (12 cm wide × 20 cm long; 5 cm drop) in the path of a beetle rolling a ball (Fig. 2b). Beetles rolled up the ramp and fell off the end, losing control of their ball. This caused the beetle to perform an orientation dance on top of the ball before resumption of rolling. Differences between the original and final angles of rolling were measured using a protractor, and subjected to statistical analysis.

#### Response to induced rotation

Beetles rolling balls were placed on a wooden disc (42 cm diameter) that could be rotated either clockwise or anti-clockwise. As the beetle reached the centre of the disc, the entire set-up was rapidly rotated through 90°, in less than 1 s (Fig. 2c). *P. femoralis* and *S. rugosus* were tested to determine their ability to correct for this rotation. The angular deviation from the expected reorientation of 90° was measured with a protractor from the path left on the disc, and subjected to statistical analysis.

#### Statistical analysis

Statistical analysis was carried out with the methods reported by Zar (1996). The mean resultant vector ( $\alpha$ ) was calculated for each distribution. Rayleigh's test was used to ascertain whether the



**Fig. 2A–C** Angles of course correction by beetles in response to a variety of obstacles placed in the path of the beetle while rolling a ball. All turning angles were treated as positive. **A** Response to a barrier (*P. femoralis*). **B** Response to falling from a ramp (*P. femoralis*). **C** Response to rotation on a disc (*Scarabaeus rugosus*). Summary statistics are presented in Table 1. Dotted lines: ideal orientation direction (perfect correction); dashed lines with arrows: actual orientation direction.  $\alpha$  = angle between actual and ideal orientations

distributions differed from uniformity. In trials where there was an expectation of particular orientation angle, the data were subjected to a modified Rayleigh test (Zar 1996). Depending on the type of data, *t*-tests or ANOVA were used for comparisons between species.

### Orientation in response to the sun

#### Response to reflected sunlight

The influence of the sun on the orientation behaviour of *P. femoralis* was tested by allowing individual beetles to roll balls in full afternoon sunlight. After 1 m of travel, the disc of the sun was shielded by a board (75 cm<sup>2</sup>), from the direct view of the beetle, and reflected 180° from the opposite side using a mirror. The angular difference between the two paths, before and after reflection, was measured using a protractor, and analysed as above. A mean

deviation of 180° between the two paths is expected if the beetles use the sun as an orientation cue.

#### Orientation to artificial lights

A single tungsten lamp (Osram Concentra R50; 40 W; 45° elevation) was used to replace the sun, in the laboratory. Beetles rolled balls in an indoor arena (60 cm×100 cm), where the position of the light source was switched instantaneously to a second light at either 90° or 180° from the original position. The angle of deviation from the original path was measured with a protractor and tested as above, with the expected deviation being the angle between the first and second light.

#### Orientation towards the sun

To test whether beetles showed a phototactic response to the sun, *P. femoralis* individuals were allowed to roll balls away from a dung pat at the centre of the arena between 1400 and 1600 hours on the same day, when the sun azimuth moved between 272° and 260°, respectively. The bearing of their direction of departure was recorded as they left the arena.

## Results

### Straight-line orientation

Despite orientating backwards, facing away from the direction of travel, in all of the cases we examined, beetles were able to maintain an accurate, straight-line, ball-rolling path in the direction in which they had started when leaving the dung pat.

#### Response to an obstacle

Beetles encountering the barrier, rolled to either the one or the other end, and then resumed rolling in the original direction, usually without performing an orientation dance. Angles of reorientation were not significantly different from 0° for either species (Table 1, *P* values). *P. femoralis* maintained a mean angle within 13.4° of its original path, but individuals deviated up to 73° (Fig. 2a). *S. rugosus* showed a mean deviation of 16.8° from its original direction, with individuals ranging up to 50° off course. There was no significant difference between the performance of the two species (Table 1).

#### Response to a fall and loss of contact with the ball

*P. femoralis* reoriented with a mean angle of 7.2° to its original path, but individuals deviated up to 25° (Fig. 2b). The mean deviation from the original direction of travel for all species fell within a range of 7.2–13.8°, and was not significantly different from zero for any of the species (Table 1, *P* values). *S. rugosus* reoriented least successfully of the five species tested, but there were no significant differences between the species (Table 1).

#### Correction for rotation

All of the beetles of both species, corrected for rotation by turning in the opposite direction to the direction of

**Table 1** Mean angles of reorientation ( $\alpha$ ), of ball-rolling beetles to a straight-line path after encountering an obstacle (*r* length of the mean vector, *n* sample size, *u* value of the modified Rayleigh test; *P* level of significance of the modified Rayleigh result). The Rayleigh test was used to compare the mean angular correction obtained for each species, with that expected if the course correction was perfect. Statistical comparisons were used to compare results from different species and refer to data in the same columns. A *t*-test was used for two species comparisons, or ANOVA was used for several species

Parameters	Obstacle		
	Barrier	Ramp	Rotation
<i>Pachylomerus femoralis</i>			
$\alpha$ (°)	13.4	7.2	21.6 <sup>a</sup>
<i>r</i>	0.966	0.992	0.99
<i>u</i>	8.299	6.960	5.82
<i>P</i>	<0.001	<0.005	<0.001
<i>n</i>	39	25	20
<i>Scarabaeus rugosus</i>			
$\alpha$ (°)	16.8	13.8	8.7 <sup>a</sup>
<i>r</i>	0.966	0.977	0.99
<i>u</i>	7.30	7.100	6.191
<i>P</i>	<0.001	<0.005	<0.001
<i>n</i>	32	28	20
<i>Scarabaeus rusticus</i>			
$\alpha$ (°)	–	9.6	–
<i>r</i>		0.993	
<i>u</i>		4.379	
<i>P</i>		<0.005	
<i>n</i>		10	
<i>Garreta unicolor</i>			
$\alpha$ (°)	–	6.4	–
<i>r</i>		0.995	
<i>u</i>		4.420	
<i>P</i>		<0.005	
<i>n</i>		10	
<i>Kheper nigroaeneus</i>			
$\alpha$ (°)	–	11.9	–
<i>r</i>		0.974	
<i>u</i>		4.669	
<i>P</i>		<0.005	
<i>n</i>		12	
Statistical comparisons	<i>t</i> -Test <i>df</i> =69 <i>t</i> =0.820 <i>P</i> =0.45	ANOVA <i>df</i> =4,80 <i>F</i> =1.93 <i>P</i> =0.11	<i>t</i> -Test <i>df</i> =38 <i>t</i> =5.174 <i>P</i> <0.001

<sup>a</sup>Means in the same column followed by the same letter are statistically different at *P*=0.05

turning, without performing an orientation dance. *S. rugosus* maintained a mean angle within 8.7° of its original path, but individuals deviated up to 30° (Fig. 2c) The angle of correction did not differ significantly from 0° for either species, but *S. rugosus* reoriented itself significantly better than *P. femoralis* (Table 1).

### Orientation in response to the sun

All of the beetles showed a response to the sun in the field and to lights in the laboratory. This indicates that the sun is an important visual cue, which beetles use as a reference to orient away from the dung pat.

### Response to reflected sunlight

All individuals of *P. femoralis* corrected for a 180° reflection of the sun's position, by interrupting the rolling behaviour as soon as the manipulation occurred, and performing an orientation dance on top of the ball. The beetles then resumed rolling, sometimes back along exactly the opposite path they had just rolled prior to reflection of the sun. For all beetles together, the mean reorientation angle was 160.5°. The majority of beetles under-compensated for the correction required (Fig. 3a). But the change in direction did not differ significantly from 180° (*P* value, Table 2), implying that the beetles use the sun as an orientation cue. It is important to note that the original direction in which a beetle was rolling was not necessarily towards, or away, from the sun. Nevertheless, this result shows they were using the sun to maintain a particular bearing to orientate away from the dung pat (photomenotaxis).

### Orientation to artificial lights

All species responded to a change in the position of the light, selecting a new rolling direction, as expected on the

basis of the manipulation. The majority of individuals under-compensated by turning less than the angle by which the light was displaced, in both the 90° and 180° turns (e.g. Fig. 3b). However, in neither case did the actual correction differ significantly from the expected one (90° or 180°) (*P* values, Table 2). None of the four species performed significantly differently in either trial (Table 2).

### Orientation towards the sun

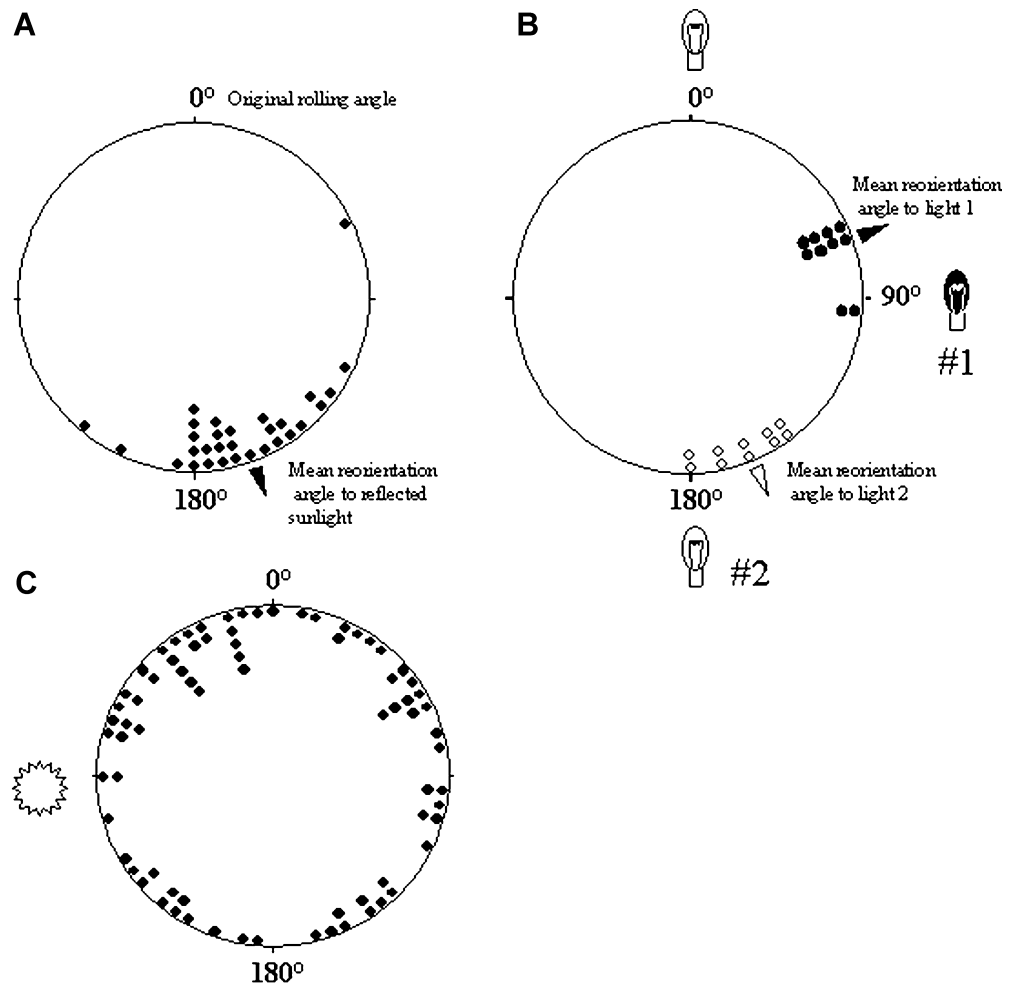
During a 2-h period of observation beetles were found to roll balls at all angles away from the dung (Fig. 3c), supporting the conclusion that their orientation is mainly menotactic, not phototactic.

## Discussion

### Straight-line orientation

Dung beetles are food-caching foragers that hoard dung for deferred consumption by either themselves or their offspring, and most species are nomadic in that they are

**Fig. 3A–C** Bearings taken by ball rolling beetles in response to visual orientation cues. Each symbol denotes the direction selected by one individual. Summary statistics are presented in Table 2.  
**A** Response to reflected sunlight by *P. femoralis*. 0° represents the original rolling direction. **B** Response to an artificial light source by *S. rusticus* that is switched either 90° (#1), or 180° (#2), from the original direction of rolling. **C** Response to afternoon sunlight by *P. femoralis*. The sun symbol indicates the azimuth of the sun during the experiment



**Table 2** Orientation of ball-rolling beetles in response to the sun, or a light substitute ( $\alpha$  mean angle of reorientation,  $r$  length of the mean vector,  $n$  sample size,  $u$  value of the modified Rayleigh test;  $P$  level of significance of the modified Rayleigh result). The Rayleigh test was used to compare the mean angular correction obtained for each species, with that expected if the course correction was perfect. Statistical comparisons were used to compare results from different species and refer to data in the same columns. A  $t$ -test was used for two species comparisons, or ANOVA was used for several species

Parameters	Light source		
	Mirror reflecting sunlight 180°	Lights switched 90°	Lights switched 180°
<i>Pachylomerus femoralis</i>			
$\alpha$ (°)	160.5	–	–
$r$	0.889		
$u$	6.4929		
$P$	<0.001		
$n$	30		
<i>Scarabaeus rugosus</i>			
$\alpha$ (°)	–	70.7	143.9
$r$		0.977	0.801
$u$		4.51	3.99
$P$		<0.001	<0.001
$n$		12	19
<i>Scarabaeus rusticus</i>			
$\alpha$ (°)	–	72.9	160.6
$r$		0.980	0.974
$u$		4.19	4.11
$P$		<0.005	<0.001
$n$		10	10
<i>Garreta unicolor</i>			
$\alpha$ (°)	–	77.5	167.2
$r$		0.996	0.978
$u$		3.88	3.816
$P$		<0.005	0.001
$n$		10	8
<i>Kheper nigroaeneus</i>			
$\alpha$ (°)	–	62.9	–
$r$		0.978	
$u$		3.854	
$P$		<0.005	
$n$		10	
Statistical comparisons	NA	ANOVA $df=3, 37$ $F=2.153$ $P=0.109$	ANOVA $df=2, 34$ $F=2.565$ $P=0.085$

not known to live permanently in one area. In this regard their orientation during provisioning is very different to hymenopteran foragers which have received most attention to date. The beetles can perform their orientation tasks while travelling backwards. We have shown here, in five different species from two tribes with different eye morphologies, that ball rolling beetles travel in a straight line away from the food source, on a bearing which they maintain in the face of a variety of obstacles, and which may involve loss of contact with the ball. Ball rolling is accomplished by orientation to a fixed angle of departure from the dung source. This angle is maintained with reference to at least one celestial cue, the sun.

The “zigzag” path described by Matthews (1963) for *C. pilularius*, rolling a ball over rough terrain eventually

results in a straight path being taken from the dung. In our experiments, on smooth ground, beetles selected a straight departure path and accurately compensated for a forced 90° turn without climbing onto the ball to scan the sky or landscape (Fig. 2a). Straight-line orientation is seen in a variety of animals and has obvious value in preventing accidental return to a starting point, and ensuring that the maximum distance is covered in the minimum time. Because the beetle has no particular goal, it does not run the risk of arriving at the wrong place, but by orientation to a reference direction, it achieves a rapid departure, which is an advantageous strategy.

### Response to obstacles

Involuntary deviations from a straight course of locomotion are usually corrected by the innate optomotor responses that cause an insect to turn in the direction of the motion perceived from the visual panorama. Optic flow has been shown to evoke a turning response in bees (Srinivasan et al. 1999), even if it is induced by flying in a straight tunnel with differently patterned walls (Lehrer 1996). The relative motion of the ground passing below the large ventral eyes of ball-rolling beetles could provide optic flow to correct for deviations from a straight course. However, beetles rotated on a disc were able to compensate for rotation, without visual information from the ground. Beetles falling from ramps reoriented by scanning the sky (or possibly the horizon) during an orientation “dance” on top of the ball. This suggests that visual cues, such as celestial cues or landmarks, are used for orientation rather than kinetic or optomotor orientation mechanisms, and provides the most satisfactory explanation for the accurate straight-line orientation recorded here.

The experimental arenas used in these trials were free of nearby landmarks, in fairly uniform clearings in mixed vegetation. When considered with the fact that beetles travel backwards away from the dung, and that they respond to lights and the sun as directional cues, we conclude that landmarks are of minor importance during dung beetle orientation.

The dung ball itself, weighing up to 79 times the weight of the beetle (Sato and Imamori 1987), offers the potential for inertial orientation, but can be rejected along with the optomotor response as the main orientation information source, because this information flow is also interrupted when contact is lost with the ball during a fall, after which beetles were shown to resume their original course.

### Phototaxis or menotaxis?

Foraging Hymenoptera use a hierarchy of cues to orient over long and short distances (Lehrer 1998). Our results suggest that the sun is dominant over other orientation cues available to dung beetles, because they react

immediately to reflected sunlight (Fig. 3a). Even when the polarised sky is still visible they turn approximately 180° while viewing a full rotating skylight polarisation pattern, which they ignore in favour of the sun. When polarised light is absent, beetles reoriented to a moved light source (Fig. 3b). Nevertheless, because they maintain a variety of angles to the sun in the field, their response to the sun is considered to be menotactic (Fig. 3c).

Geisler (1961), found individuals of *Geotrupes silvaticus* (Scarabaeidae) to consistently select a particular angle when walking on a sphere towards a light source. This suggests that sun orientation is a basic and widely shared trait within the Scarabaeidae, and one that has been incorporated into different behaviours within the family. Opposite turning responses were found in *Geotrupes* depending on which portion of the eye was illuminated, suggesting that a particular portion of the eye must be stimulated to maintain a fixed angle to the sun (Fraenkel and Gunn 1961). However, some species, such as *Garreta unicolor* can change their rolling position by turning around and pulling the ball backwards towards themselves, which moves the sun to a completely new position on the eye. *G. unicolor* did not perform significantly differently to the other species in any of these trials, in its ability to orient along a chosen bearing. Even though innate orientation responses may be hardwired into the small brains of invertebrates, they are nevertheless capable of modification or suppression within individuals to allow for improvisation (Lehrer 1997).

## Conclusion

Ball rolling is considered to be a derived behaviour (Cambefort 1991), performed by only about 10% of mainly tropical and subtropical dung beetle species (Bernon 1981). The sun has been shown here to be an important orientation cue for ball-rolling dung beetles, and is almost sufficient on its own for accurate orientation. However, under certain circumstances it emerges that orientation is also influenced by polarised light (M. Dacke, P. Nordström and C. Scholtz, unpublished observations). A synergy between these and other different responses, with flexibility allowing for improvisation (Campan 1997) will result in a biologically meaningful orientation for dung beetles. We predict that a hierarchy of celestial and terrestrial cues can be used by Scarabaeinae for straight line ball rolling, and propose that the orientation behaviours, and the underlying morphological features found in all Scarabaeidae, have been incorporated into the unique ball-rolling behaviour of the Scarabaeinae to orientate efficiently away from a food source.

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