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Long-distance navigation in the wandering desert spider *Leucorchestris arenicola*: can the slope of the dune surface provide a compass cue?

Abstract Males of the nocturnal spider *Leucorchestris arenicola* (Araneae: Sparassidae) wander long distances over seemingly featureless dune surfaces in the Namib Desert searching for females. The spiders live in burrows to which they return after nearly every such excursion. While the outward path of an excursion may be a meandering search, the return path is often a nearly straight line leading towards the burrow. This navigational behaviour resembles that of path integration known from other arthropods, though on a much larger scale (over tens to hundreds of meters). Theoretically, precise navigation by path integration over long distances requires an external compass in order to adjust for inevitable accumulation of navigational errors. As a first step towards identifying any nocturnal compass cues used by the male spiders, a method for detailed 3-D recordings of the spider's paths was developed. The 3-D reconstructions of the paths revealed details about the processes involved in the spiders' nocturnal way of navigation. Analyses of the reconstructed paths suggest that gravity (slope of the dune surface) is an unlikely parameter used in path integration by the *L. arenicola* spiders.

Keywords Arachnidae · Gravity · Homing · Path integration · Slope

Introduction

While well-studied central-place dwellers with long-distance navigation and homing capabilities such as honey

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bees (*Apis millifera*: e.g. von Frisch 1967; Dyer 1996; Srinivasan et al. 1996; Menzel et al. 1998) and desert ants (genus *Cataglyphis*: e.g. Wehner 1994, 1997) are diurnal, the spider *Leucorchestris arenicola* is nocturnal (Henschel 1990a). Nevertheless, the males of this large sparassid (Jäger 1999) also embark on long meandering excursions, and similar to honeybees and desert ants, the male spiders can return to their home burrow along a straight line without retracing their outward path (Henschel 2002). However, in contrast to foraging bees and ants it is the search for females and mating opportunities that motivates the male spiders to do these long excursions. Hence the journeys performed by the *Leucorchestris* males are neither foraging runs during which the animals search for food (Wehner et al. 1983) nor search paths employed in pinpointing the goal, i.e. searching for a place, after the path-integration vector has been run off (Müller and Wehner 1994). Besides this peculiar function (searching for mating possibilities) it is the time during which these journeys occur, in the darkest of all nights, that renders these runs an intriguing topic in the study of biological navigation.

Numerous arthropods have proved to have remarkable powers of navigation and homing (for a review see Wehner 1992). When *Cataglyphis* ants return home along a straight line rather than by retracing their outbound paths they do so by path integration (Wehner and Wehner 1986; Müller and Wehner 1988). While navigating by path integration the animal must continuously compute and update a vector pointing directly home (Mittelsteadt 1985; Benhamou and Séguinot 1995; Collett et al. 1999; Wehner et al. 2002). The necessary information about directions steered and distances covered can be obtained in two non-exclusive ways: either ideothetically by internally (e.g. proprioceptively) gained information, or allothetically by reference to external cues (Mittelsteadt and Mittelsteadt 1982; Mittelsteadt 1985). As path integration is highly sensitive to cumulative errors and as this problem is exacerbated if path integration is done by purely ideothetic means (Benhamou et al. 1990), successful long-distance navi-

gation by path integration requires one or more allothetic compass guides. In arthropods a number of such compass cues are known to be used in the context of path integration: the sun and/or polarised skylight (Wehner 1994; Wehner et al. 1996; Dacke et al. 1999), spectral gradients in the sky (Rossel and Wehner 1984; Wehner 1997), constant wind direction (Wehner and Duelli 1971), the direction of gravity (Bartels 1929; Hill 1979; Görner and Glass 1985) and, as has been claimed (Rickli and Leuthold 1988; Ugolini and Pezzani 1995; Frier et al. 1996), the earth's magnetic field.

In spiders, studies on homing by path integration have so far dealt only with short-range navigation over distances of less than one meter (Seyfarth and Barth 1972; Hill 1979; Seyfarth et al. 1982; Görner and Glass 1985; Vollrath et al. 2002). Both female and subadult *L. arenicola* spiders forage within, and defend, territories of up to 1–3 m in radial size (Henschel 1994), and thus are capable of returning to their burrow from distances that are larger than in previously studied spiders. Even more amazingly, however, the adult males of *L. arenicola* will readily leave their burrow for (bee-line) distances of 30 m or more by covering path lengths of more than 100 m on a single night excursion (Henschel 2002).

The *L. arenicola* spiders live in the Namib Desert dunes on the dune plinth and the upper dune base (Henschel 1990a). Robinson and Seely (1980) define these habitats and describe them as having slopes of substrate up to 10°. This habitat description lead us to speculate whether the presence of a constant slope could provide a compass cue that enables the spiders to perform their remarkable long-distance navigation. In addition the wheeling spiders, *Carparachne aureoflava* and *C. alba*, though on shorter distances, exhibit similar navigational behaviour. The wheeling spiders, close relatives of *L. arenicola*, live on the steep slip-faces of the dunes, i.e. in a habitat with a very constant slope of the substrate (Robinson and Seely 1980; Henschel 1990b).

Detailed recordings of the animal's movements are imperative if these navigational performances are to be understood. Therefore, we started the investigation of the long-distance navigation as performed by *L. arenicola* males, and the possible use of allothetic directional guides, by developing a method for 3-D recordings of the spiders' paths. The present paper describes this method and shows how the 3-D recording technique can be used to gain more information about the allothetic cues used, or not used, during this spider's large-scale wanderings. It especially addresses the question whether the slope of the sand-dune surface can act as a reliable compass cue.

Materials and methods

The spider

L. arenicola is endemic to the Namib Desert (Lawrence 1962, 1965; Henschel 1990a). It is a large spider, with adult males weighing up to 3 g and having a standing leg span of up to 14 cm. They are long-lived, taking 2 years to reach the adult stage. As adults the males live an additional 2–3 months (Henschel 1990a). They are territorial spiders living in silk-lined burrows with trapdoors, excavated at an angle in the dune sand. From these burrows they hunt prey passing by on the sand surface (Henschel 1990a). Prey mainly consists of tenebrionid beetles (Henschel 1990a, 1994).

Experimental site

All tracks were recorded within a 27,000 m^2 area located approximately 1 km southwest of the Gobabeb Training and Research Centre in the Namib Desert (Namib-Naukluft Park; 23° 33' S; 15° 02' E). The area is a dune base bordered to the north by the ephemeral Kuiseb River and to the other sides by the quartz gravel of the inter-dune plains (Robinson and Seely 1980; Henschel 1990a). Larger landscape features in the area are a line of trees along the adjacent Kuiseb River and scattered groups of *Acanthosicyos horridus* (Cucurbitacae), *Salvadora persica* (Salvadoraceae) and *Tamarix usneoides* (Tamaricaceae).

Path-measuring procedure

Spider tracks were located in the morning hours just after sunrise, when the light from the low sun threw shadows inside the spider's small footprints. These shadows render the otherwise faint tracks more visible to the observer. Tracks made by males were mainly identified by the conspicuous drum-marks often produced by the spiders during their excursions (Henschel 1987). In addition, the sex of the tracked spider was verified by using a mirror to direct sunlight into the burrow occupied by the tracked spider. When within its burrow the spider is hanging in its preferred sideways upside down position, its sex can be determined by counting the number of spines on the tibia (Henschel 1990a).

The location of all occupied burrows found at the experimental site were marked. Male excursions were measured by placing markers along the entire lengths of the paths wherever the spider's course deviated from its previous direction by more than the width of its leg span. The positions of all distinct features of the path such as drum-marks, mating places, etc. were also marked and noted. A tape measure was laid down along the marked path and the distance from the burrow to each marker was recorded. The shape of the footprints and drum-marks along the track showed the direction the spider had been moving. Based on these measurements individual length of each path segment (distance between two adjacent markers) was calculated.

Finally the compass direction and the inclination of each path segment were measured by using a compass for the X, Y coordinates and a digital inclinometer (Bosch DNM 60 L) for the Z coordinate. Along the path fix points were established in order to later estimate and minimize the effect of cumulative errors inherent in the measurements. A fix point was established by recording the direct distance and compass direction from the burrow to a point on the spider's path chosen as the fix point.

Data processing procedures

The data on the length, direction, and inclination of each path segment represent a vector in 3-D space. Drawing on this information one can compute the spatial position of the end point of each segment relative to the starting point of the path (the spider's burrow). These 3-D coordinates of the segment end points can be exported to most available 3-D plotting computer programs. Then, by interlacing the end points the spider's 3-D paths can be completely reconstructed.

As minor errors in the field measurements are inevitable, the plotting of a path consisting of n segments does not end up at the starting point. Thus, $(X_n, Y_n, Z_n) \neq (X_{start}, Y_{start}, Z_{start})$, where $(X_{start}, Y_{start}, Z_{start})$ are the coordinates of the position of the burrow, i.e. the starting and the end point of the spider's entire

excursion. The coordinates (X_n, Y_n, Z_n) denote the position of the end point of a measured path consisting of n segments. The total individual errors in the X, Y and Z planes, being the direct distance between starting point and measured end point in 3-D space, can be calculated simply as $(E_x, E_y, E_z) = (X_n-X_{start}, Y_n-Y_{start}, Z_n-Z_{start})$. Further assuming that the measuring error of any given segment is proportional to the length l of that segment, the following method can be used to fit the end point of the recorded path to the starting point: If the total distance the spider has walked is $L = \sum_{j=1}^{n} l_j$, the error e per unit of L is $(e_x, e_y, e_z) = ((X_n-X_{start})/L, (Y_n-Y_{start})/L, (Z_n-Z_{start})/L)$, and then the fitted coordinates (X_{fi}, Y_{fi}, Z_{fi}) are:

$$\left(X_{fi}, Y_{fi}, Z_{fi}\right) = \left(X_i - e_x \cdot \sum_{j=1}^{i} l_j, Y_i - e_y \cdot \sum_{j=1}^{i} l_j, Z_i - e_z \cdot \sum_{j=1}^{i} l_j\right)$$

Thus, in the case where $i=n$, the end point is:

$$\left(X_{fn}, Y_{fn}, Z_{fn}\right) = \left(X_n - e_x \cdot \sum_{j=1}^{n} l_j, Y_n - e_y \cdot \sum_{j=1}^{n} l_j, Z_n - e_z \cdot \sum_{j=1}^{n} l_j\right)$$
$$= (X_{start}, Y_{start}, Z_{start})$$

A detailed analysis of the measuring errors will be presented in the Results.

Statistical procedures

Normality and homogeneity of the data were tested with the Kolmogorov-Smirnoff analysis and the Barthlett's test. In all analyses of correlations Pearson product-moment correlations were used. Comparisons between measuring errors in fix-point-adjusted measurements of the tracks and non-fix-point-adjusted measurements as well as comparisons between errors in the X, Y and Z planes (non-fix-point-adjusted data) were done by using one-way ANOVA statistics. The least significant difference test (LSD) was used for post hoc testing. The mean square successive difference test (Zar 1999) was applied to test for randomness in the degree of slopes encountered by the spiders along their paths. In all cases confidence levels were $P < 0.05$.

Results

3-D reconstruction of the spiders' paths

In total 22 complete round-trip paths of male spiders were recorded within the experimental area. The recorded paths were up to 13,676 cm long having a maximal (bee-line) distance to the burrow of 4,014 cm (Table 1). There was a strong positive correlation between path length and maximal distance to the burrow ($n=22$; $r=0.91$; $P=0.0001$). Figures 1, 2, 3, and 4 present examples of reconstructed male excursions and details about the topography of the paths.

Table 1 Descriptive analyses of the 22 measured paths showing some spatial characteristics of the walking behaviour exhibited by wandering male spiders. For definition of segment see Materials and methods

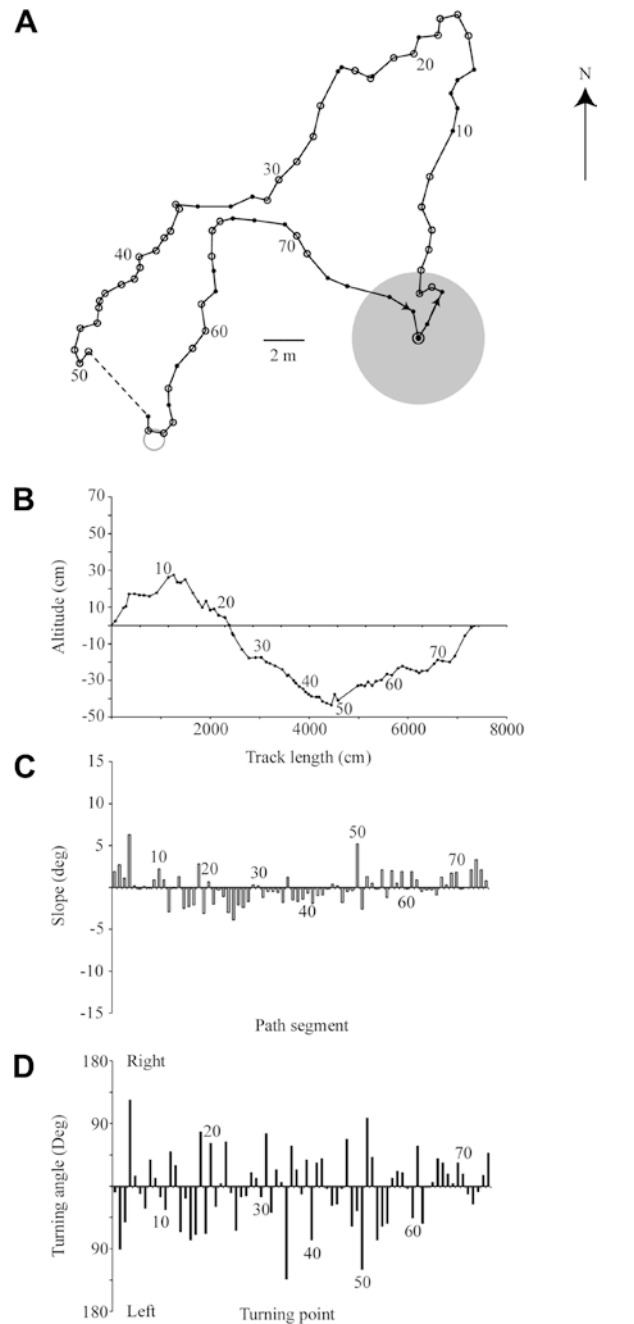|	n	Mean	SE	Min	Max
Path length (cm)	22	4091.77	663.83	338	13676
Segments per path	22	51.27	6.68	11	138
Segment length (cm)	1129	79.86	1.23	9	446
Max. distance to burrow (cm)	22	1313.23	222.67	145	4014
Turns ≥60° per path	22	11.45	1.46	3	27

Fig. 1 A Example of a typical nocturnal path (projected on to the X-Y plane) of a male *L. arenicola* spider. The *shaded grey circle* represents the male spider's average territory size (average radius 3 m). The burrow (*large black dot*) is located at the centre of the depicted territory, and is surrounded by an area with a radius of 0.5 m (*open circle*) normally densely covered with the spider's footprints. The *arrowheads* indicate the direction in which the spider had walked. The *small black dots* mark the positions of the markers used in reconstructing the paths. The *small circles* along the path represent drum-marks made by the male. The *large open circle* shows the position of a mating track (approximately 1 m in diameter) around a female's burrow. The *stippled line* indicates where the spider crossed a harder stony surface, on which details of the path could not be recorded. **B** Altitude profile (Z coordinate) of the spider's path. The burrow is positioned at the zero altitude line. **C** Histogram shows the degree of slope of each segment of the spider's path. **D** Histogram shows the size of the turning angle at each turning point along the spider's path
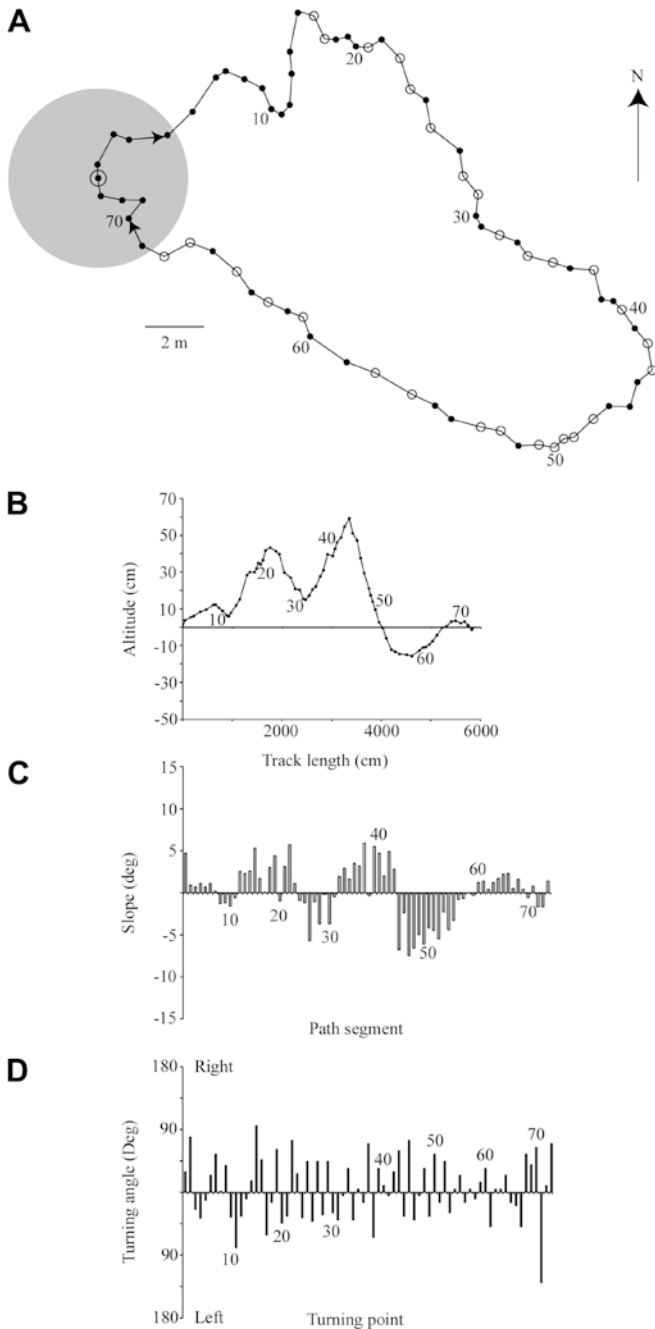
Fig. 2 A Example of a spider's path and B its altitude profile. C Slope histogram, and D turning-angle histogram. For conventions see Fig. 1

Due to small errors of measurement, plotting the paths using the raw field data (before adjustments have been made using fix-point measurements) resulted in round-trip trajectories that did not end up at the starting points. There was a significant positive association between track length and the measuring error when the data had not been adjusted by using fix-points ($n = 22$; $r = 0.60$; $P = 0.003$). The total measuring error after adjusting the data by using the fix-point coordinates was significantly smaller than the error in the non-adjusted data (one-way ANOVA, $F = 5.28$; $P = 0.028$). Further-

more no correlation was found between path lengths and measuring errors, when data were fix-point-adjusted ($n = 18$, $r = -0.0046$, $P = 0.99$).

The measuring errors differed significantly in the X, Y and Z plane (one-way ANOVA; $F = 9.41$; $P = 0.0002$) (Table 2). A following LSD post hoc test reveals that the Z error is significantly smaller than the X and Y errors, whereas no significant differences exist between the latter two. This indicates that the compass readings provide a larger source of error than the slope measurements. This finding is further supported when comparing the results of correlations between measuring error and number of turns ≥60°. A significant correlation was found between the number of large turns and the measuring error in the non-adjusted data ($n = 22$; $r = 0.58$; $P = 0.0048$). No significant correlation was found when the fix-point data were used ($n = 18$; $r = -0.018$; $P = 0.94$). This again shows that the fix points ensure that measuring errors do not accumulate during the recordings of the paths.

As the measuring error is positively correlated with the path length and as the number of segments per path is also positively correlated with the path length ($n = 22$; $r = 0.95$; $P < 0.0001$), it is obvious that in the unadjusted data set the measuring error is positively correlated with the number of segments per path ($n = 22$; $r = 0.62$; $P = 0.002$). The number of segments is equivalent to the number of readings of instruments carried out during the recordings, and each of these measurements is a potential source of error. By frequently recording fix points during the recording of a path error accumulation is avoided, because the number of consecutive measurements between "recalibrating" the recording is kept low. This frequent recalibration procedure results in the lack of any correlation between the number of segments per path and the measuring error ($N = 18$; $r = 0.04$; $P = 0.87$). Taken together, the results from the 22 round-trip paths presented here show that using fix-points kept accuracy within 70 cm (Table 1). Applying the data of the error per centimetre in each of the X, Y and Z planes (Table 2) and again assuming a linear correlation between error and path length, one can arrive at a rule of thumb for the necessary number of path segments between fix point recordings (assuming a precision of ± 50 cm): In future measurements the number of segments or, more precisely, the number of measurements between fix-points should not exceed 25.

In analysing the geometrical structures of the paths, we first determined the turning angles made by the spiders between successive segments of their paths (Fig. 5A) as well as the angles between the directions indicated by the current states of the spider's path integrator (after the spider has completed its step n) and the direction of the next path segment (step $n + 1$; see Wehner and Wehner 1990) (Fig. 5B). The histograms show that the spiders during their excursions make as many turns of a particular angular size to the left as they do to the right (Fig. 5A, B). We further asked whether the spiders' turning angles were

Fig. 3 A Example of a spider's path and **B** its altitude profile. **C** Slope histogram, and **D** turning-angle histogram. For conventions see Fig. 1
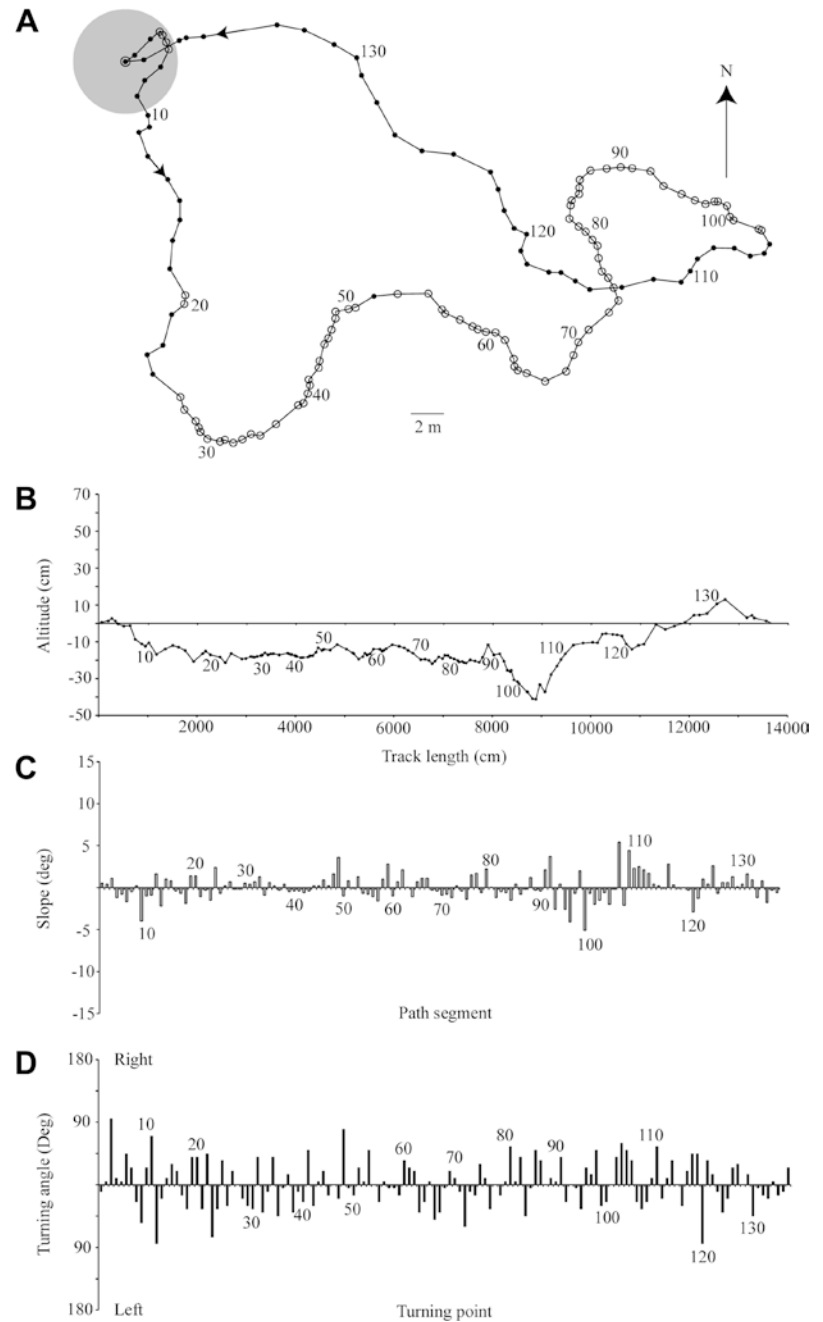
correlated, in one way or another, with (1) the slope of the terrain where these turns had occurred, (2) the azimuthal direction of the path integration vector, and (3) the distance from the start. The Pearson product moment test (Zar 1999) did not reveal any correlation in the first two cases (1: $r = 0.0316$, 2: $r = -0.0031$; $P > 0.05$ and $n = 1068$ in 1 and 2). In the third case only a very weak correlation occurred (3: $r = -0.12$; $P < 0.05$; $n = 1068$). In cases with large sample sizes (n) the correlation (r) required to yield a significant P value in the Pearson product moment procedure is low, and the weakly significant outcome of the latter comparison (3) must be seen in this light.

3-D structure of the terrain covered by the spiders' paths

The slopes of the segments measured along the spiders' paths represent the only information about direction and degree of slope available to the navigating animal. From the profiles and distribution of slopes (e.g. Figs. 1B, C; 2B, C; 3B, C; 4B, C and Fig. 6A–E) of the topography of the terrain, over which the spiders navigated, it is evident that the small-scale topography consists of irregular up-and-down inclinations rather than a continuous slope. The measurements of slopes do not show any consistent patterns in the uphill and downhill trends of the paths (Figs. 1B, C; 2B, C; 3B, C;
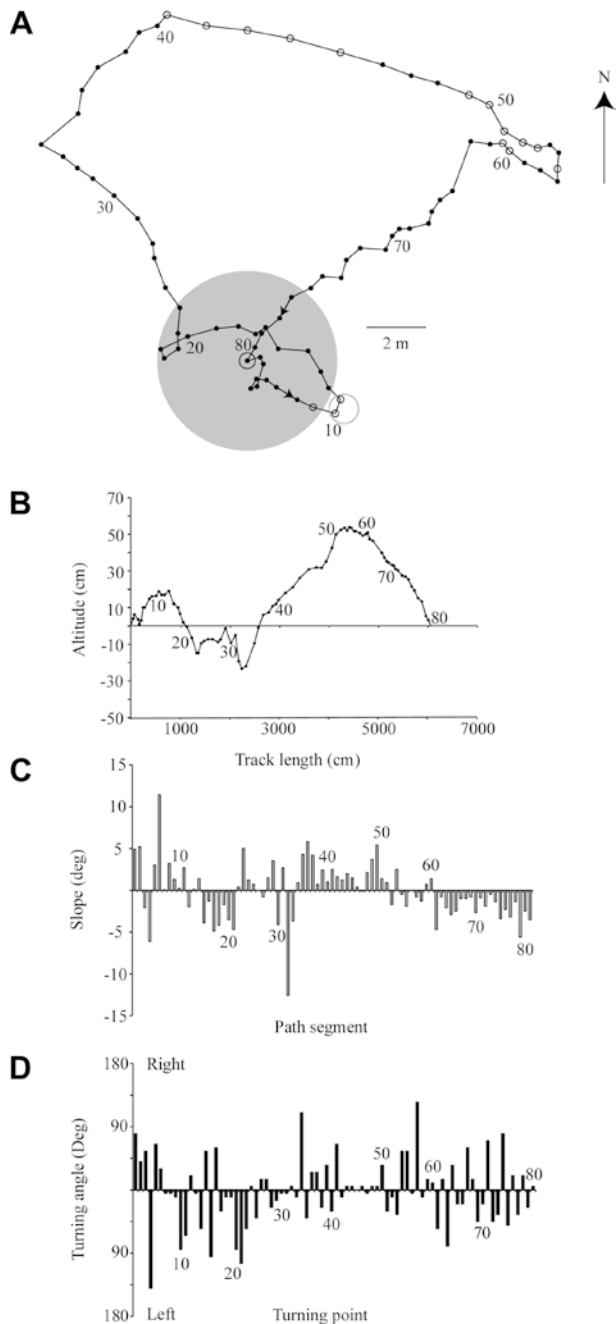
Fig. 4 A Example of a spider's path and **B** its altitude profile. **C** Slope histogram, and **D** turning-angle histogram. For conventions see Fig. 1

Table 2 Total measuring errors in non-fix-point-adjusted data (NFA), fix-point-adjusted data (FA), and the measuring errors in the X, Y and Z planes of 3-D space (NFA data)

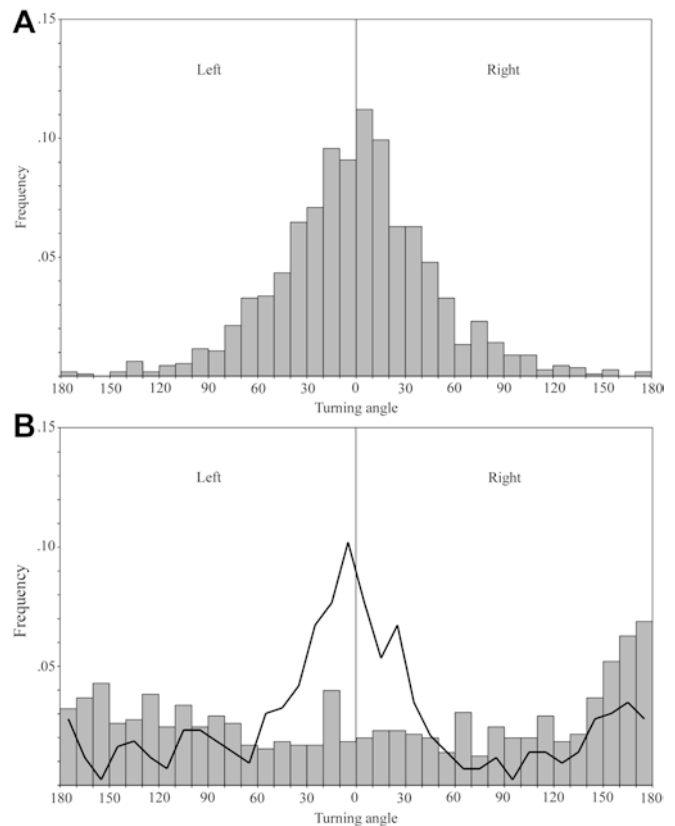|	n	Mean	SE	Min	Max
Total NFA error (cm)	22	117.93	15.92	14.28	221.30
Total FA error (cm)	18	68.94	11.68	4.59	199.38
Total X error (cm)	22	54.61	11.86	0.10	219.43
Total Y error (cm)	22	67.95	12.02	6.56	214.72
Total Z error (cm)	22	8.50	1.72	0.15	0.49
X error per cm path (%)	22	1.6239	0.358	0.0057	7.0446
Y error per cm path (%)	22	1.8747	0.2834	0.4499	5.1270
Z error per cm path (%)	22	0.2285	0.0396	0.0218	0.8454

Fig. 5 A Frequency distribution (in 10° bins) of left/right turning angles, i.e. of the changes in direction between adjacent segments of the paths. **B** Frequency distribution (in 10° bins) of left/right turning angles relative to the path integration vector at each of the turning points along the spiders' paths. *Bars*: outward paths (from burrow to maximal distance from burrow); *heavy black line*: inward paths

4B, C). The mean square successive test applied to the sequence of slopes of each of the 22 measured paths confirm this and shows that the sequences of slopes encountered by the spiders are indeed random (in all but one cases $P > 0.05$). Nor do the results from all the 22 recorded spider paths suggest any constant slope underlying the apparent corrugated sand surface within the experimental area. Thus, no uniformity was found in either the direction or the degree of the slope of the substrate over which the spiders navigated.

Discussion

The main question addressed in this account is whether the slope of the desert terrain inhabited by *L. arenicola*—the dune plinth and upper dune base—provides a consistent and reliable compass cue. To answer this question, we had to record the distribution of the local slopes encountered by the spiders while navigating. This had to be done exactly along the paths taken by the wandering spiders, because this is the only information

Fig. 6 Frequency distribution of the slopes (in 1° bins) of the terrain along the spiders' paths illustrated in Fig. 1 (histogram **A**), Fig. 2 (histogram **B**), Fig. 3 (histogram **C**) and Fig. 4 (histogram **D**). **E** The total frequency distribution of the slopes (in 1° bins) of the terrain along all the 22 recorded paths
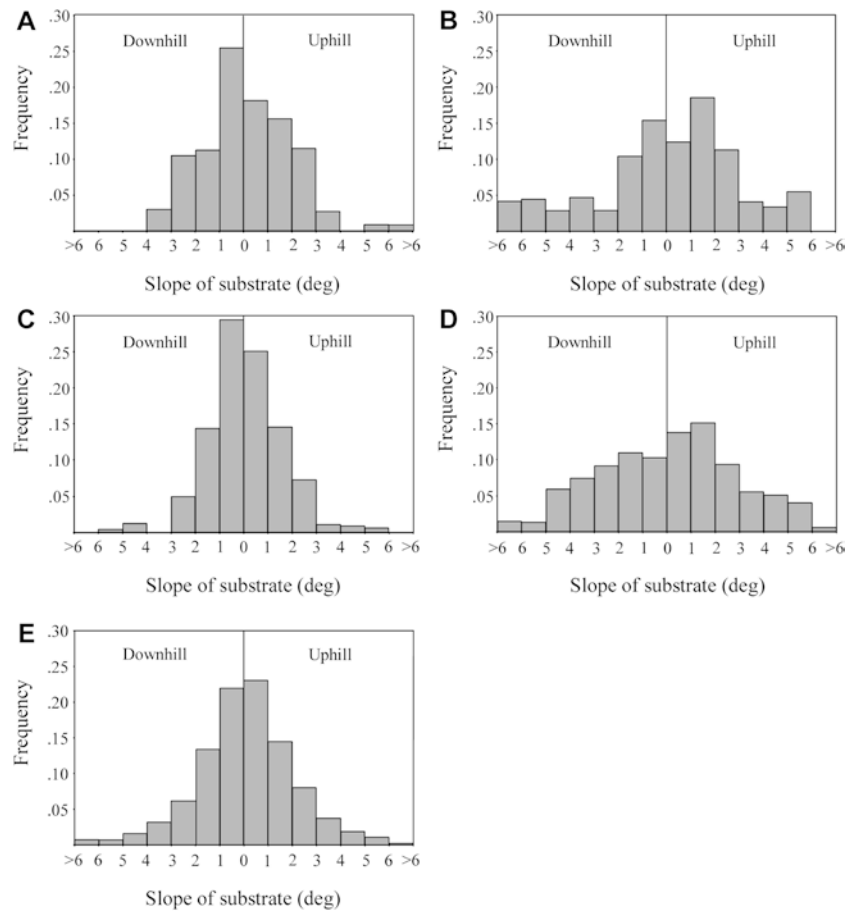
available to the animals. Hence, we first had to develop a technique to record the spiders' paths three-dimensionally. We did so by measuring the paths the morning after the spiders had completed their nocturnal round-trips. This recording technique provided a means of studying the spider's behaviour without any interference. Spiders, like many other desert arthropods, are extremely sensitive to vibrations travelling in the sand and on its surface (Brownell 1977, 2001; Barth 2002). In fact, the walking behaviour of *L. arenicola* males was disturbed when the observer was present during the spiders' excursions.

The method of 3-D mapping developed and presented in this study proved to be of high accuracy. By using a 10×10-m² reference grid Henschel (2002) reports a spatial accuracy of approximately 1 m. Although the path-recording procedure described in the present account is a more time-consuming process than measurements done with the aid of a grid, it has the considerable advantage that it can be applied wherever a male track is encountered. In addition, it provides a simple method using only reliable equipment that continues to function even when the environmental conditions are harsh, as is the case in the Namib Desert.

The corrections necessary to make the graphic reconstructions end up at the starting points yield detailed information on the nature of the errors in each of the measuring planes. The results show that the major

recording errors in tracing out the spiders' paths occur within the horizontal plane (*X–Y*) and mainly refer to the directional information as provided by compass cues. The measurement of distance, i.e. the measurement of the length of a path segment, contributes less to the total measuring error.

Note that the method by which the tracks were recorded can by itself be regarded as an example of navigation by path integration. In particular, it shows how navigation by path integration is prone to the accumulation of errors, and is especially so in the directional (compass) component. This has been predicted theoretically by Benhamou et al. (1990). Only by repeatedly taking fix-points could the precision of the measurements be improved and the total error per round trip be kept lower than 1 m. In order to achieve this kind of precision fix-points should be established at least at every 25th measuring point (marker). The difference between the fix-point-adjusted and non-fix-point-adjusted data provides a nice example of how cumulative errors affect precision. Furthermore, the positive correlation between track length and error is indicative of the accumulation of errors characterising navigation by path integration.

In order to utilize gravity, or more specifically the slope of the substrate, as a directional cue for homing, a regular and predictable slope is required. The

3-D measurements show the near absence of such even slopes of the substrate in the spiders' terrain. Considering the evident irregular corrugation in the small-scale topography of the habitat, the spiders are apparently able to compensate for the up and down movements in the total integration of their paths. This ability has been demonstrated in ants (Wohlgemuth et al. 2001, 2002). Employing a memory map of the micro-topography would not be a secure way of navigating in the Namib Desert either. This is due to the considerable changes in micro-topography that a few days of strong wind can cause. Therefore, information about the micro-topography gained during an excursion on one night cannot provide the spider with a memory map usable for navigation at subsequent nights. In conclusion, the current study does not support the notion that substrate slope and thereby gravity is necessary as a compass in the spider's navigational process.

What other sensory cues could provide the nocturnal spider with compass information? Even though it has been reported for isopods (Ugolini and Pezzani 1995), termites (Rickli and Leuthold 1988), and honey bees (Frier et al. 1996) that arthropods can derive directional information from the horizontal component of the earth's magnetic field, the use of this cue in a path integration task has not been demonstrated so far in any arthropod species. In fact, a recent study on tethered flying monarch butterflies, *Danaus plexipus*, did not provide any evidence of the use of magnetic information in determining or maintaining migratory directions (Mouritsen and Frost 2002). On the other hand, the results of recent displacement experiments in spiny lobsters, *Panulirus argus*, are compatible with the hypothesis that these marine crustaceans possess a magnetic map, i.e. are able to derive positional (bicoordinate) information from two different magnetic field components (Boles and Lohmann 2003). However, over the relatively short distances travelled by the *Leucorchestris* males the "magnetic topography" is much too small to be exploited in taking positional fixes. Furthermore, as in the desert night sky at new moon a reliable pattern of polarisation is not available, as it is on full-moon nights (Gal et al. 2001), the use of a polarised-light compass is unlikely as well. This apparent lack of a usable "genuine" compass cue leads us to assume that the spiders could be relying instead on other means of reducing their navigational errors. Distant landscape features—provided they can be seen along the entire path walked by the spider—could function as a directional guide (Fukushi 2001). Arthropods may have efficient means to detect horizon skylines (Wehner et al. 1996) especially by exploiting the marked contrast between long- and short-wavelength radiation.

In long-distance navigation a male spider might only need a homing accuracy of about 3 m. This accuracy would ensure that it reached its home territory (territorial range: Henschel 2002). Within this territory the spider might switch to alternative ways of homing.

Henschel (2002) describes search-like behaviour if the male misses its burrow entrance upon returning to its territory. Perception of and orientation by pheromones is well documented in spiders (Pollard et al. 1987; Papke et al. 2001). Although olfactory cues are unlikely to operate over larger distances due to the high risk of changes in wind direction during such excursion, the spiders might use such cues on the final stage of their homing process. In any case, the finishing few meters of the spiders' return paths needs further examination. Wind direction as a potential cue in the orientation is not discussed in detail in the present account as this parameter is currently being measured and will be presented in a forthcoming paper.

The main result gained from the 3-D reconstructions of the spiders' paths presented here is that the slope of the sand-dune surface over which the spiders walk is an unlikely candidate for providing the animal with compass information. Having excluded this possibility, we are left with the following hypotheses of how the male spiders could accomplish their navigational task: (1) they could use hitherto undetected compass mechanisms; (2) they could employ a completely ideothetic path-integration mechanism of exceptionally high accuracy; or (3) they could rely on a path integration system supplemented by geocentric navigational information. Work is currently in progress to further narrow down these possibilities, especially to define the roles that visual and olfactory cues could play in the spider's new-moon nocturnal navigation.

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