ORIGINAL PAPER

Thomas Nørgaard · Joh R. Henschel · Rüdiger Wehner

The night-time temporal window of locomotor activity in the Namib Desert long-distance wandering spider, *Leucorchestris arenicola*

Abstract Even though being active exclusively after sunset, the male *Leucorchestris arenicola* spiders are able to return to their point of departure by following bee-line routes of up to several hundreds of meters in length. While performing this kind of long-distance path integration they must rely on external cues to adjust for navigational errors. Many external cues which could be used by the spiders change dramatically or disappear altogether in the transition period from day to night. Hence, it is therefore imperative to know exactly when after sunset the spiders navigate in order to find out how they do it. To explore this question, we monitored their locomotor activity with data loggers equipped with infrared beam sensors. Our results show that the male spiders are most active in the period between the end and the beginning of the astronomical twilight period. Moreover, they prefer the moonless, i.e. darkest times at night. Hence, we conclude that the males are truly—and extremely—nocturnal. We further show that they are able to navigate under the very dim light conditions prevailing on moonless nights, and thus do not have to rely on the moon or on moon-related patterns of polarised light as potential compass cues.

Abbreviations LDE: Long-distance excursion · MDE: Medium-distance excursion · SDE: Short-distance excursion

T. Nørgaard (✉) · R. Wehner
Department of Zoology, University of Zuerich,
Winterthurerstrasse 190, 8057 Zuerich, Switzerland
E-mail: noergaard.thomas@gmail.com

J. R. Henschel
Gobabeb Training and Research Centre, P.O. Box 953,
Walvis Bay, Namibia

Introduction

Leucorchestris arenicola (Araneae: Sparassidae) is a large spider endemic to the Central Namib Desert (Lawrence 1962, 1965). During the day, the spiders occupy burrows dug into the desert sand and closed with trap doors. At night, the male *L. arenicola* often walks long excursions across the sand dunes (Henschel 2002; Nørgaard et al. 2003). These excursions are searches for females and may be several hundreds of meters long. Most frequently, the male returns to the burrow from which he started. Therefore, the excursions can generally be divided into two sections with distinct characteristics: a meandering outward search section and a relatively straight-line return section. This straight return section may be up to hundreds of meters long. Only adult males do these long excursions, whereas female and immature spiders normally do not wander beyond the boundaries of their 1–3 m territories (Henschel 1990).

During homing, the male *L. arenicola* spiders cover distances similar to the ones observed in diurnally foraging eusocial hymenopterans. The Saharan desert ants of the genus *Cataglyphis* provide an excellent example. Individually foraging ants will search for food items on the desert floor along circuitous paths up to several hundred meters (Wehner and Wehner 1986). After finding a food item, the foraging ant will immediately return to its nest by the shortest route possible, i.e. along a straight trajectory. *Cataglyphis* ants navigate by path integration implying that they keep track of distances covered and directions steered (Wehner 1982; Müller and Wehner 1988). Path integration based exclusively on ideothetic cues (Mittelstaedt 1985) gets extremely noisy when done over long distances (Benhamou et al. 1990). Hence, arthropods performing wide-ranging journeys employ a number of strategies to avoid the excessive accumulation of errors within the path integrator. They have been shown to use external compass cues as derived from the sun as well as from stray light patterns (polarization and spectral gradients) in the sky (Wehner

1982, 1997; Rossel and Wehner 1984; Dacke et al. 1999; for reviews see Wehner 1992; Wehner and Srinivasan 2003). Spiders have been shown to be able to detect polarised light and use it as a compass (Dacke et al. 1999; Ortego-Escobar and Muñoz-Cuevas 1999). In addition, ants and bees can use memorised images of the layout of the surrounding landmarks (e.g. Wehner and Räber 1979; Cartwright and Collett 1983; Åkesson and Wehner 1997; Kohler and Wehner 2005). If *L. arenicola* spiders also relied on visual cues for maintaining precision during their homing, they would be likely to use similar strategies. In addition to these visual cues, arthropod navigators have been demonstrated to use non-visual cues such as wind direction (Wehner and Duelli 1971; Wolf and Wehner 2000) and direction of gravity (Bartels 1929; Hill 1979) as navigational aids.

In contrast to most of the examples mentioned above the *L. arenicola* spiders are nocturnal (Henschel 1990). When the sun sets and day turns into night, the conditions under which an arthropod navigator must operate change dramatically. The sun itself becomes gradually unavailable as a means of navigation, but will influence the optical skylight parameters until it has reached an elevation of 18° below the horizon (Rozenberg 1966). During the astronomical twilight period, the light intensity gradients in the sky caused by the sun could potentially still be used as a directional cue. Sunset patterns of polarized light another and very conspicuous cue that could be used as a directional guide as well. However, if active after astronomical twilight the navigator will not be able to use either polarization or intensity gradients produced by the sun. The moon has been demonstrated as being a source of polarised light equal to the one produced by the sun albeit a thousand times less intense (Gal et al. 2001). This lunar polarised light pattern is used as a compass by African dung beetles (Dacke et al. 2003). During most nights except for the days around full moon, there will be periods where the moon is not present in the night sky. This situation culminates on new moon nights where the moon is never present. At these times, the only available celestial cues would be the stars.

Navigation by the use of stars has been suggested by Doujak (1985) for crabs. If these crustaceans with their apposition compound eye can perceive a sufficient number of stars to navigate by, the single-lens eyes of the *L. arenicola* spiders are likely to be able to do the same. From sunset until the end of astronomical twilight, the ambient light intensities also decrease by several orders of magnitude (Lythgoe 1979). Navigation by use of landmarks at this time would therefore require optical adaptations to cope with these dim light conditions (Warrant 2004) and, the visual system of *L. arenicola* might well be equipped with neural mechanisms that boost light sensitivity. Visual landmarks, especially the silhouette of the horizon skyline as provided by the ridges of the surrounding dunes might then be used as a navigational aid.

Hence, it is of utmost importance to obtain detailed information about the times of night, during both the circadian and the lunar cycle, at which the male spiders are active. By mapping the spiders' footprints in the sand surface (Henschel 2002; Nørgaard et al. 2003), we have already a means at hand to record the spatial layout of the spiders' journeys. However, the traces obtained this way do not reveal any information about the times at which the spiders have been active. This information, however, is crucially important, if one wants to correlate the spiders' activities with the presence (or absence) of particular visual cues. The present account deals with this very correlation, by which we hope to be able to narrow down the potential cues used by the males of *L. arenicola* in night-time long-distance navigation.

Materials and methods

Spider

The *L. arenicola* spider is a large sparassid (Lawrence 1962; Jäger 1999) also known as the Dancing White Lady spider. Adult males can weigh up to 4 g and have standing leg spans that can exceed 10 cm. The spiders reach the adult stage after 2 years. Thereafter, the male spiders may live for an additional 6 months (Henschel 1990). More often than not, however, due to high rate of predation during their long excursions on the sand surface, the adult males only survive a few months. The spiders' main predators are the gerbils, but the list of other predators is long (Henschel 1990). The spiders live in burrows dug into the sand surface at an angle of about 30° extending down to approximately 20 cm below the surface (Henschel 1990). The burrows are closed by a well-camouflaged trap door made up of sand particles interwoven with silk.

Field site

All spiders were monitored in a fenced-off area of approximately 7,500 m² (Fig. 1a) positioned close to the Gobabeb Training and Research Centre in the Namib Desert (23°33′S; 15°02′E). The fence prevents livestock, mostly goats and donkeys, to enter the research area. However, it does not prevent the male spiders from moving in and out of the area. The fenced area is a flat inter-dune section adjacent to the ephemeral Kuiseb river. The riparian vegetation of the Kuiseb river, which predominantly consists of *Salvadora persica* (Salvadoraceae) shrubs and *Acacia erioloba* (Acacieae) trees, borders the area to the North and North-West. A low !Nara plant *Acanthosicyos horridus* (Cucurbitacae) grows in the middle of the area, and a large !Nara forms a hummock of approximately 3 m in height in the South-west corner of the area (Fig. 1a).
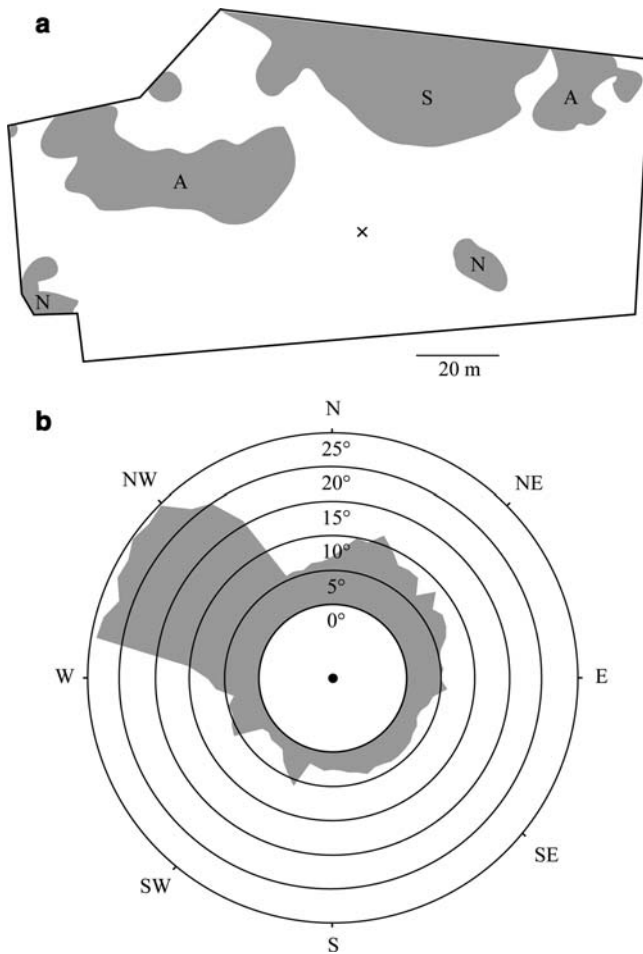
Fig. 1 a Map of the research area. The *polygon line* depicts the fence surrounding the area. Areas covered by vegetation are shown in *dark grey*. The *letters* refer to the type of vegetation: *A, Acacia* trees; *S, Salvadora* shrubs; *N, !Nara* shrubs. The *cross* (×) indicates the position at which the data shown in (**b**) were collected. **b** Horizontogram of the research area depicting the contour of the horizon skyline. The elevation of the skyline is given in degrees

due to spiders sitting long periods of time in the beam path unlikely. Logged events were summed up and subsequently recorded in 1-min bins. One-minute bins with logged events were termed activity records. Activity records caused by other nocturnal animals, e.g. tenebrionid beetles was not a frequent problem, and when occurring the interfering animals could be identified by the spoors left in the sand.

In addition to the automatic monitoring by the IR beams, the spiders were monitored every morning. In all cases in which their tracks could be detected, the trajectories were measured as described by Nørgaard et al. (2003). Due to environmental conditions such as wind or fog, it is often impossible to map out long-distance paths. In order to ensure reliable datasets, the paths were divided into three groups by using the largest bee-line distance between the spiders' positions and the burrow entrance. The excursions that were less than 20 cm away were termed short-distance excursions (SDE). These tracks occur when the spiders only emerge from their burrows and remain at the entrance. Excursions that were more than 20 cm and less than 300 cm away from the burrow were termed medium-distance excursions (MDE). The 300 cm limit of this group was based on the average size of an adult spider's territory. Any excursions where the spiders ventured more than 300 cm from the burrow, i.e. were outside their foraging territory were termed long-distance excursions (LDE). An average LDE distance exceeding 40 m has previously been established (Nørgaard et al. 2003).

Statistical procedures

In all statistical calculations, the Kolmogorov–Smirnoff test was used to check for normality of the data distributions. When appropriate, the Bartlett's test was applied to test for differences in standard deviations. The Mann–Whitney test and the Kruskal–Wallis test followed by Dunn's multiple comparison post test were used for analysing non-parametric data. Where applicable, data were log transformed to fit a Gaussian distribution in order to allow for parametric One-way ANOVA analysis. In the latter case, post testing was done by using the Tukey–Kramer multiple comparison test.

Data collection

During each night, the temporal activities of five spiders were recorded by using TinyTag time-event data loggers with custom-built infrared (IR) beam sensors. The data loggers were buried in the sand with the IR beams placed in a way that they passed across the trap doors of the spiders' burrows. Hence, the spiders could not leave their burrows without breaking the IR beam. Every time the beam was broken, an "event" was logged when the beam reconnected. The beams of the loggers were so narrow that a leg of the spiders were sufficient to break them. Surveillance of male spiders with IR camera done on another occasion, but in the same area, have shown that the spiders very rarely linger on the surface and even less so when they are in the vicinity of the burrow. This is probably to minimise exposure to predators when near the safety of the burrow. This behaviour and the long legs of the spiders made erroneous timings of events

Results

Using data loggers and IR beam sensors, LDEs by 26 spiders taking place during 18 nights were successfully recorded (Fig. 2a). Likewise, MDEs by 24 spiders from 20 nights (Fig. 2b) and SDEs by 25 spiders from 18 nights were recorded (Fig. 2c) (Table 1). During four nights both LDEs and MDEs, and during four other nights both LDEs and SDEs could be detected. It happened five times that MDEs and SDEs took place during

Fig. 2 a Activity records of long-distance (>300 cm) excursions (LDEs). The *white areas* at the top and bottom of the graph indicate the times when the sun was above the horizon. The areas between the *solid* and *dashed lines* mark the astronomical twilight periods. The *light grey* areas between sunset and sunrise indicate that the moon was present in the night sky, and *dark grey* areas show the time when the moon was not present. The *white columns* mark the time spans between the first and the last activity records per night. The *horizontal stripes within the white columns* mark the times when activity records were logged at the burrow entrance. **b** Activity records of medium-distance (>20 cm, <300 cm) excursions (MDEs). **c** Activity records of short-distance (<20 cm) excursions (SDEs)
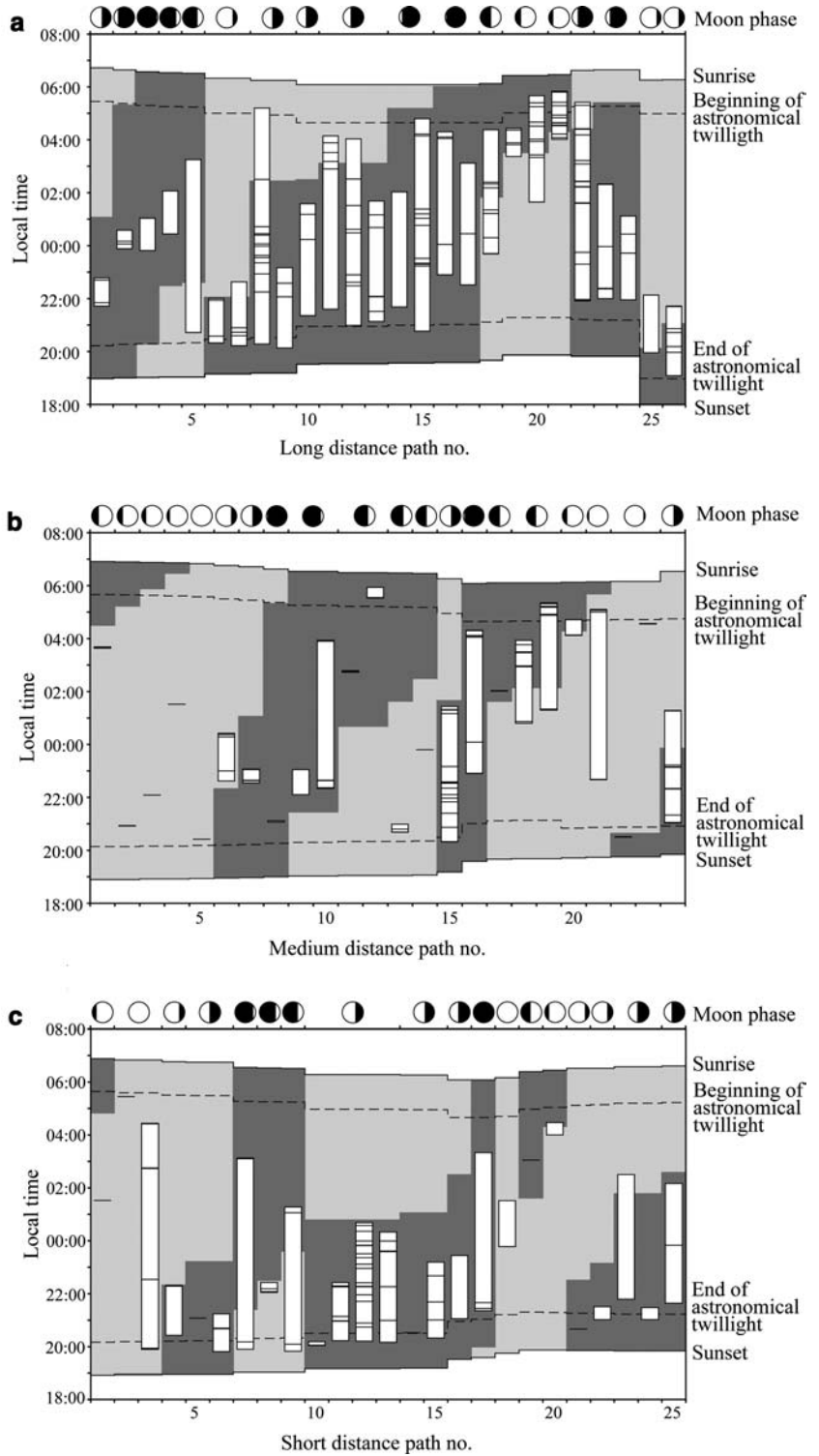
the same night, but we have never been able to observe that all three groups of excursions had taken place during the same night.

During 3 years with very frequent visits to the research area and other areas occupied by *L. arenicola* spiders in the Namib Desert, no adult male spider was ever observed to be walking on the surface before sunset or after sunrise. These observations were corroborated quantitatively by the records of the male spiders' activity. Moreover, from the activity records, an even finer detailed pattern emerges. Not only are the spiders exclusively active between sunset and sunrise, but by far the most activity records obtained for all three excursion distance groups fall within the boundaries between the

Table 1 Activity parameters recorded for the spiders' long-, medium- and short-distance excursions

	Excursion type	N	Mean	SE	Min	Max
Duration of excursion (min)	Long	26	237.88	27.82	42.00	535.00
	Medium	24	103.13	31.82	1.00	545.00
	Short	25	149.80	31.43	1.00	512.00
Number of activity records per night	Long	26	6.15	0.81	2.00	18.00
	Medium	24	4.33	0.72	1.00	15.00
	Short	25	4.00	0.73	1.00	18.00
Number of events per activity record	Long	159*	17.80	1.05	2.00	95.00
	Medium	103*	13.12	0.80	2.00	40.00
	Short	100*	14.00	1.29	2.00	83.00
Number of records per night with the moon absent	Long	26	5.12	0.67	1.00	14.00
	Medium	24	2.96	0.77	0.00	15.00
	Short	25	3.16	0.77	0.00	18.00
Number of records per night with the moon present	Long	26	1.04	0.28	0.00	4.00
	Medium	24	1.38	0.36	0.00	7.00
	Short	25	0.84	0.33	0.00	7.00

N denotes number of excursion nights, except for the values marked * were it is total number of activity records. See Sect. "Materials and methods" for the definitions of activity records and events

evening end and the morning beginning of astronomical twilight (Fig. 2a–c). The spiders are thus active at times when the light from the sun does no longer influence skylight optics. The spiders' preference for darkness is further supported by the temporal occurrence of the activity records. On those nights that were characterized by the largest amounts of logged LDE records the moon was not present ($P < 0.0001$, Mann–Whitney test). Hence, the LDEs occurred at the very darkest times of the night (Fig. 2a). Similarly, during nights with SDEs significantly more activity was recorded, when the moon was absent than when it was present ($P < 0.0012$, Mann–Whitney test) (Fig. 2c). Only on the nights during which MDEs were recorded did the difference between the numbers of events in nights with and without the moon not reach significance levels ($P = 0.2581$, Mann–Whitney test) (Fig. 2b). Intergroup—rather than intragroup—comparisons also revealed marked differences ($P = 0.0073$, Kruskal–Wallis test). On nights with LDEs, the number of no-moon activity records was significantly higher than in the two other groups (in both cases $P < 0.05$, Dunn's multiple comparison test). On the other hand, the difference between the number of no-moon activity records on MDE and SDE nights was not significant ($P > 0.05$, Dunn's multiple comparison test). Nor was there any statistically significant difference between any of the groups when the numbers of activity records obtained under moonlight conditions were compared ($P = 0.2812$, Kruskal–Wallis test). The contour of the horizon in the research area might explain some of the activity records obtained shortly before the end of astronomical twilight and in the period between moonrise and moonset. High shrubs (see Sect. "Materials and methods") would cast shadows and hence extend the period where the spiders prefer to be active (Fig. 1b).

The time interval between the first and the last activity records on a given night was regarded as the longest possible duration of the spiders' surface (outdoor) activity during that night. This parameter was found to differ significantly among the three groups of excursion distances ($P = 0.0014$, Kruskal–Wallis test). The maximal duration of surface activity was found to be longer on LDE nights than on MDE nights ($P < 0.01$, Dunn's multiple comparison test) (Fig. 2a, b). Although the duration between the first and last activity records was absolutely longer on LDE nights than it was on SDE nights, this difference was not significant in the post hoc testing procedure ($P > 0.05$, Dunn's multiple comparison test) (Fig. 2a, c). The same comparison made between the maximal durations of surface activity of MDEs and SDEs did not show significant differences either ($P > 0.05$, Dunn's multiple comparison test) (Fig. 2b, c).

The duration between the activity records obtained during the excursion nights is a measure of the time the spiders could have been away from the safety of the burrow. This parameter was found to differ highly significantly ($P = 0.0001$, Kruskal–Wallis test) between the excursion groups. The number of minutes passing between activity records during LDE nights is found to be equal to that of SDE nights ($P > 0.05$, Dunn's multiple comparison test). These two groups were both having a significantly longer time span between records than seen on MDE nights (in both cases: $P < 0.01$, Dunn's multiple comparison test).

If one assumes, as one certainly can, that the more the spiders had been moving around the more activity records had occurred, then the number of activity records, and also the number of events, i.e. the number of times the beam was broken, can be regarded as a measure of the level of activity by the spiders during any particular night under consideration. There was a significant difference in the number of activity records per night, if LDE, MDE and SDE nights were (one-way ANOVA, $F = 3.899$, $P = 0.0303$). More activity records occurred on LDE than on SDE ($P < 0.05$, Tukey–Kramer multiple comparison test), while no significant differences were found between either LDE nights as compared to MDE nights, or MDE nights as compared to SDE

nights (in both cases: $P > 0.05$, Tukey–Kramer multiple comparison test). In addition, there are significant differences between the excursion groups, if the numbers of events, i.e. the number of times the spiders broke the IR beam of the logger, were compared ($P = 0.0003$, Kruskal–Wallis test). Activity records on LDE nights comprised more events than the activity records on MDE and SDE nights (in both cases: $P < 0.01$, Dunn's multiple comparison test). The number of events per activity record on MDE and SDE nights did not differ significantly ($P > 0.05$, Dunn's multiple comparison test).

We can obtain more direct information about the spiders' outdoor behaviour, if we combine the records of the spiders' activities with the track readings in combination with the observations done with IR cameras. The lack of significant difference in the maximum duration between LDEs and SDEs appears to result from the fact that on SDE nights the spiders often check whether the conditions are favourable enough for venturing out on an excursion. When doing so, they repeatedly break the IR recording beam. This conclusion is further emphasised by the observation that the average time intervals between the activity records are similar in the LDE and SDE groups. The notion that the activity records on SDE nights are indeed such brief surface checks is supported by the fewer events recorded on SDE nights.

Examining the excursion data on a larger (seasonal) scale by examining the distribution of excursion types taking place over the period from full moon to full moon show that the highest numbers of LDEs took place between the last quarter of the moon and new moon (Fig. 3). MDEs appear to have the most even distribution occurring throughout the full-moon-to-full-moon period with a rather constant rate. SDEs on the other hand seem to be more frequent on the nights with a brighter moon albeit also often occurring in the period immediately after new moon. At full moon, the moon rises approximately at the same time as the sun sets, but then rises later each following night at a rate of

approximately 50 min per day (Fig. 3). Therefore, the nights begin to have longer periods of darkness, which favours excursions to take place from a few days after full moon onwards.

Discussion

A great number of spiders are nocturnal (e.g. Cloudsley-Thompson 1985). Furthermore in the Namib Desert, the heat and dryness of the air prevailing during the day has caused many animals to be active at night when ambient temperatures and humidity are far more tolerable. It is therefore not surprising that our results obtained by monitoring the activity of male *L. arenicola* spiders with IR beam data loggers clearly show that the spiders are nocturnal to the extreme. Henschel (2002) already reported that the activity of the adult male spiders was concentrated around new moon nights. Here, we show when exactly during the nights of a lunar cycle the spiders are active (Fig. 3).

The experimental set-up employing IR beams and data loggers does not have the resolution to show whether the spiders ventured out on the surface or simply opened the burrow lid to assess, whether the conditions were suitable for performing an excursion. Yet, the overall picture that can be drawn from Figs. 2a–c and 3 is clear-cut: the spiders prefer moonless conditions between the end of the evening and beginning of the morning astronomical twilight period. This observation is verified by the higher number of activity records logged when the moon is not present. Another indication of the apparently more favourable conditions on those dark nights, at which the most LDEs occurred, is that the number of activity records at these times was higher than in the other two groups of excursion distances (the MDEs and the SDEs). Furthermore, the individual records consisted of more events on LDE nights rather than on MDE or SDE nights. This also indicates a

Fig. 3 Histogram exhibiting the distribution of occurrences of the different excursion types (averages of observation periods, *Y*-axis to the *left*). For definitions of SDE, MDE and LDE see Fig. 2a–c. The *stippled thick grey line* depicts the time of moonrise in relation to sunset (marked by the *solid line*) over an entire full-moon-to-full-moon period. The line is derived from an average of ten full-moon-to-full-moon periods (*Y*-axis to the *right*)
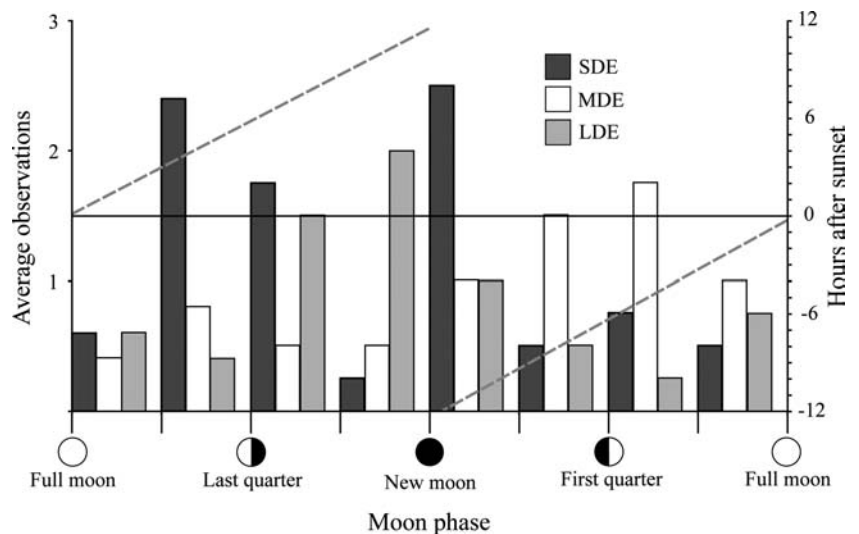
higher amount of surface activity during these nights. Locomotor activity, and most intriguingly, the LDEs are framed by the end and the onset of astronomical twilight, i.e. are restricted to the period during which the sun has no influence on optical skylight parameters. Most LDEs take place around new moon, when the moonless period of time present after astronomical twilight is the longest. In conclusion, the ambient light intensity levels appear to be an important factor determining the temporal window of the spiders' locomotor activity.

The ecological reason why the males choose the darkest times at night for being active on the desert surface could be the high pressure exerted by visually hunting predators, e.g. gerbils (Henschel 1990). In predator avoidance, the spiders are far more likely to rely on their prominent ability to sense substrate-conducted vibrations caused by approaching enemies (Barth 2001; Nørgaard et al. 2003). This possibility would give them an advantage over their visually guided predators under the dim light conditions of moonless nights, when the detection of prey targets against the terrestrial background of the desert floor gets increasingly difficult.

What can be inferred from the results reported here about possible ways of navigation employed by the spiders? As the spiders are active in the time span between the end of the evening astronomical twilight period and the beginning of the morning astronomical twilight period, potentially powerful compass cues such as the sun and/or sun related patterns of polarised light can be ruled out. This conclusion underlines the power of experiments conducted in the field. In contrast to experiments performed under laboratory conditions recordings done in the field allow for testing the effect of fading ambient light intensity levels. In laboratory tests, the effect of the astronomical twilight period shown here to be important would have easily gone unnoticed.

Nevertheless, the fact that the spiders' nocturnal activity window is confined to the darkest times at night does not completely dismiss any mean of skylight navigation. As recent studies have shown, the compound eyes of insects are sensitive enough to enable their owners to navigate under very dim light conditions (Warrant 2004). Theoretically, the spider's single-lens camera types of eyes would have much higher intrinsic light-capturing capacities than insect compound eyes have (Nilsson 1990). Therefore, stars and star patterns can possibly be detected. Current investigations of the optics and retinal structures of the various types of Leucorchestris's eyes aim at substantiating this claim.

Furthermore, and even more importantly, vision might be involved in detecting landmark-based cues even in moonless nights. For example, the horizon skyline provides a conspicuous, though coarse-grain, optical feature in the spiders' habitat. We are presently investigating what role this borderline between the spiders' terrestrial and celestial visual world might play in nighttime navigation. If this role turns out to be decisive, the navigation strategies employed by long-distance wanderers such as the nocturnal desert spiders, Leucorchestris, and the diurnal desert ants, Cataglyphis, could be quite different indeed. Given the large distances covered by the spiders during their far-ranging excursions, the spiders' horizon skyline might not provide sufficiently accurate compass information, as motion parallax would heavily interfere. To what extent, then, does the wandering Leucorchestris depend on path integration at all? Does it employ a rather noisy path integrator exploiting distant landmark cues, and then zoom in on close-range goal-detecting navigational strategies? These are questions that can be phrased that sharply only after we have fully established, as done in the present account, that the wandering Leucorchestris spiders restrict their nocturnal activities to the really dark moonless nights well beyond astronomical twilight periods.

References

Åkesson S, Wehner R (1997) Visual snapshot memory of desert ants, Cataglyphis fortis. Proc Neurobiol Conf Göttingen 25:482

Bartels M (1929) Sinnesphysiologische und physiologische untersuchungen an der trichterspinne Agelena labyrinthica (Cl.). Z Vergl Physiol 10:527–591

Barth FG (2001) A spiders world, senses and behavior. Springer, Berlin Heidelberg New York

Benhamou S, Sauvé JP, Bovet P (1990) Spatial memory in large scale movements: efficiency and limitations of the egocentric coding process. J Theor Biol 145:1–12

Cartwright BA, Collett TS (1983) Landmark learning in bees. Experiments and models. J Comp Physiol 151:521–543

Cloudsley-Thompson JL (1985) The biorythms of spiders. In: Nentwig W (ed) Ecophysiology of spiders. Springer, Berlin Heidelberg New York, pp 371–379

Dacke M, Nilsson D-E, Warrant EJ, Blest AD, Land MF, O'Carroll DC (1999) Built-in polarizers form part of a compass organ in spiders. Nature 401:470–473

Dacke M, Nordström P, Sholtz CH (2003) Twilight orientation to polarised light in the crepuscular dung beetle Scarabaeus zambesianus. J Exp Biol 206:1535–1543

Doujak FP (1985) Can a shore crap see a star? J Exp Biol 116:385–393

Gal J, Horvath G, Barta A, Wehner R (2001) Polarization of the moonlit clear night sky measured by full-sky imaging polarimetry at full moon: comparison of the polarization of moonlit and sunlit skies. J Geophys Res 106(D19):22647–22653

Henschel JR (1990) The biology of Leucorchestris arenicola (Areneae: Heteropodidae), a burrowing spider of the Namib desert. In: Seely MK (ed) Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No. 7. Transvaal Museum, Pretoria, pp 115–127

Henschel JR (2002) Long distance wandering and mating by the dancing white lady spider (Leucorchestris arenicola) (Araneae, Sparassidae) across Namib dunes. J Arachnol 30:321–330

Hill DE (1979) Orientation by jumping spiders of the genus Phidippus (Arenae: Salticidae). Behav Ecol Sociobiol 5:301–322

Jäger P (1999) Sparassidae—the valid scientific name for the huntsman spiders (Arachnida: Areneae). Arachnol Mitt 17:1–10

Kohler M, Wehner R (2005) Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path-integration vectors? Neurobiol Learn Mem 83:1–12

Lawrence RF (1962) Spiders of the Namib desert. Ann Transvaal Mus 10:197–211

Lawrence RF (1965) New and little known arachnida from the Namib Desert, South West Africa. Scientific papers of the Namib Desert research station, vol. 27, pp 1–12

Lythgoe JN (1979) The ecology of vision. Oxford University Press, New York

Mittelstaedt H (1985) Analytical cybernetics of spider navigation. In: Barth FG (ed) Neurobiology of arachnids. Springer, Berlin Heidelberg New York, pp 298–316

Müller M, Wehner R (1988) Path integration in desert ants, *Cataglyphis fortis*. Proc Natl Acad Sci USA 85:5278–5290

Nilsson D-E (1990) From cornea to retinal image in invertebrate eyes. Trends Neurosci 13:55–64

Nørgaard T, Henschel JR, Wehner R (2003) Long-distance navigation in the wandering desert spider *Leucorchestris arenicola*: can the slope of the dune surface provide a compass cue. J Comp Physiol A 189:801–809

Ortego-Escobar J, Muñoz-Cuevas A (1999) Anterior median eyes of *Lycosa tarantula* (Araneae, Lycosidae) detect polarised light: behavioural experiments and electroretinographic analysis. J Arachnol 27:663–671

Rossel S, Wehner R (1984) Celestial orientation in bees: the use of spectral cues. J Comp Physiol A 155:605–613

Rozenberg GV (1966) Twilight: a study in atmospheric optics. Plenum Press, New York

Warrant EJ (2004) Vision in the dimmest habitats on earth. J Comp Physiol A 190:765–789

Wehner R (1982) Himmelsnavigation bei insekten. Neurophysiologie und verhalten. Neujahrsbl Naturforsch Ges Zürich 184:1–132

Wehner R (1992) Arthropods. In: Papi F (ed) Animal homing. Chapman & Hall, London, pp 45–144

Wehner R (1997) The ant's celestial compass system: spectral and polarization channels. In: Lehrer M (ed) Orientation and communication in arthropods. Birkhäuser Verlag, Basel, pp 145–185

Wehner R, Duelli P (1971) The spatial orientation of desert ants, *Cataglyphis bicolor*, before sunrise and after sunset. Experientia 27:1364–1366

Wehner R, Räber F (1979) Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). Experientia 35:1569–1571

Wehner R, Srinivasan MV (2003) Path integration in insects. In: Jeffery KJ (ed) The neurobiology of spatial behaviour. Oxford University Press, Oxford, pp 9–30

Wehner R, Wehner S (1986) Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. Monitore Zool Ital 20:309–331

Wolf H, Wehner R (2000) Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. J Exp Biol 203:857–868