

## Tracking the Namib Desert spider *Leucorchestris arenicola* — reading the story in the sand (Arachnida, Araneae, Sparassidae)

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### Abstract

Track reading and direct observations on the locomotory behaviour of the spider *Leucorchestris arenicola* showed distinct differences between the sexes and between the different stages of their life histories. Adult male spiders make much longer excursions than do adult females and immature spiders, and paths of males are characterised by far less inward retracing of the outward path. Observations with infrared cameras and geophone equipment gave new insights into the signalling behaviour of this spider species and revealed so far unknown possible male-female signalling performed by the male spiders.

**Key words:** Locomotory behaviour, homing, navigation, signalling

### Laufspuren der namibischen Wüstenspinne *Leucorchestris arenicola* — Geschichten, die der Sand erzählt (Arachnida, Araneae, Sparassidae)

**Zusammenfassung:** Die Auswertung von Spuren und direkte Beobachtungen des Laufverhaltens der Spinne *Leucorchestris arenicola* zeigten deutliche Unterschiede zwischen Geschlechtern und Entwicklungsstadien. Adulte männliche Spinnen unternehmen viel längere Ausflüge als adulte weibliche und immature Spinnen und rückverfolgen ihren wegführenden Pfad deutlich seltener. Untersuchungen mit einer Geophonausrüstung und Beobachtungen mit Infrarotkameras gaben neue Einblicke in das Signalverhalten dieser Spinnenart und enthüllten eine bisher unbekannt Signalgebung der männlichen Spinne bei der Balz.

### Introduction

Even relatively small animals, such as insects and spiders, leave footprints when they move around on the fine-grained dune sand of the central Namib Desert sand sea. This fact was utilised in the present study of the locomotory behaviour of the nocturnal *Leucorchestris arenicola* LAWRENCE 1962 (Araneae: Sparassidae) also known as the Dancing White Lady Spider (LAWRENCE 1962).

Observing animal behaviour without interfering with the same behaviour that one attempts to study can often be rather difficult, and this is indeed the case when observing *L. arenicola* in the Namib Desert. Contrary to the intuitive expectation that sand will deaden sound, it actually conducts sound vibrations remarkably well. This is the case both when the vibrations are in the form of sur-

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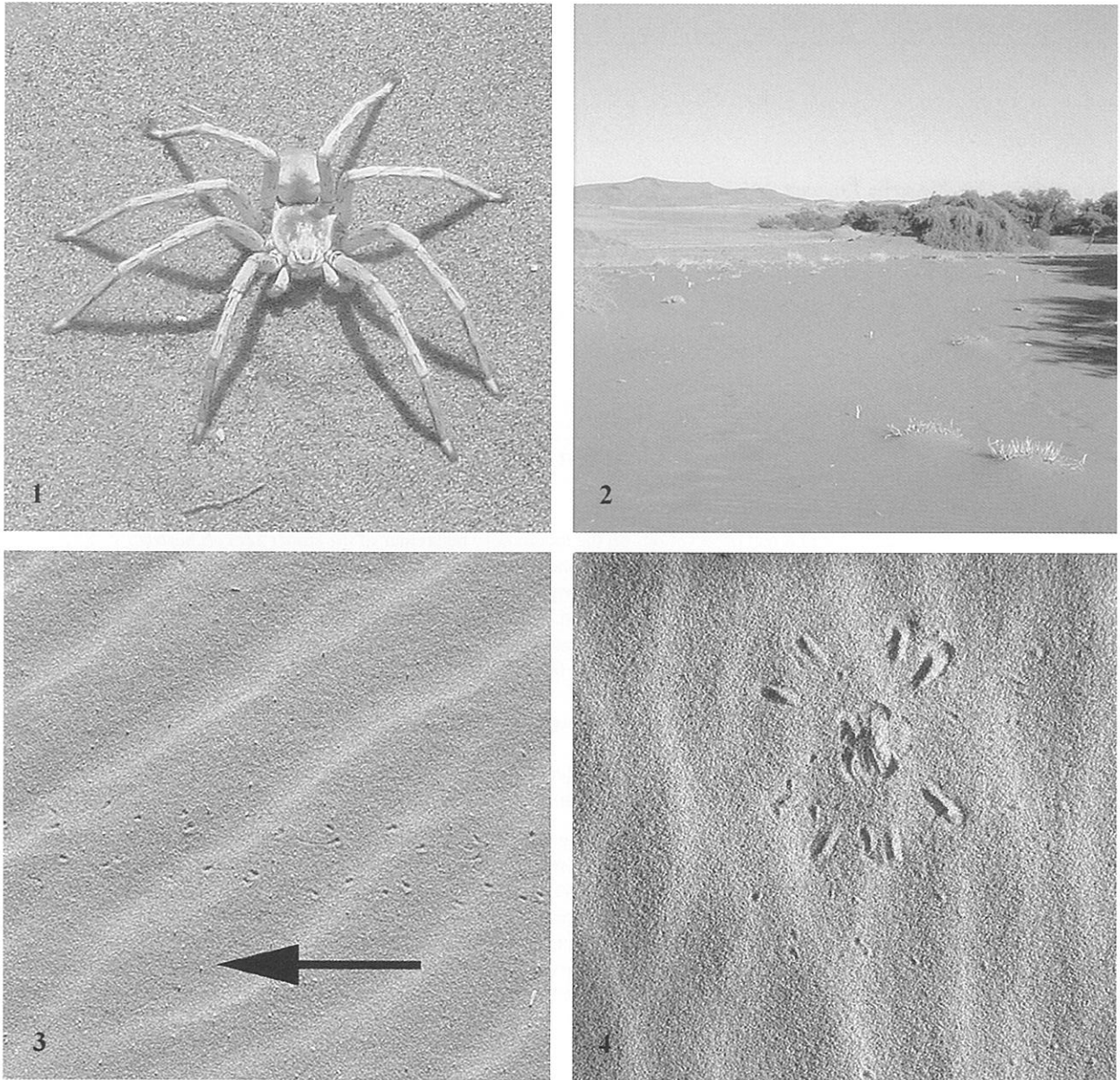


Fig. 1: Adult male *L. arenicola*. Note the three dorsal spines visible on all tibia. — Fig. 2: Study area close to the Kuiseb River. White plastic markers show positions of *L. arenicola* burrows. — Fig. 3: Track of *L. arenicola*. The black arrow shows the direction of walking. — Fig. 4: Drum-mark on track of male spider facing to the left. Note the drop shape of the footprints.

face waves and when in the form of compression waves within the substratum (BROWNELL 1977, 2001). Because of this, most animals adapted to living in sandy habitats are well equipped to sense such vibrations (CLOUDSLEY-THOMPSON 1991, BROWNELL 2001). This ability can be useful both for the detection of prey, conspecifics and of potential predators. Spiders like *L. arenicola* use lyriform organs and trichobothria for detection of both vibrations conducted by the substratum and airborne sound (FOELIX 1996, BARTH 2001). They can detect prey, e.g. a moving beetle, at a distance of at least 3 m (BIRKHOFFER 2002). The spiders are therefore always aware of an approaching human observer, often long before the observer has even registered the spider's presence.

Despite its properties of conducting vibrations and the spiders' ability to detect them, the sand surface of the Namib Desert nevertheless provides a means of substantially minimising, if not eliminating, the impact of interference while studying these spiders. Their behaviour can be studied indirectly by reading their tracks left behind on the sand surface, and much can be learned by doing so. Reading the tracks left behind after a spider's nocturnal activities has previously been used to obtain information about hunting success, prey preference, mating frequency and territoriality (HENSCHER 1990, 1994, 1997, 2002, BIRKHOFFER 2002). Furthermore, the footprints also reveal information about the large distances travelled and the navigational abilities of ♂ *L. arenicola*.

These spiders set out from and return to the same burrow at the end of their excursion on the surface. Only occasionally do they change the location of their burrow. Immature spiders may change burrow location after moulting if the diameter of the burrow they occupy becomes too small, and adult ♀♀ do so when leaving their offspring. Male spiders walk for long distances in search of mating opportunities and return to their burrows from far away with remarkably high precision (HENSCHÉL 2002, NØRGAARD et al. 2003). In contrast, the movements of ♀ and immature spiders are most often confined to the limits of their territories (HENSCHÉL 1994, BIRKHOFFER 2002). In the present account we describe some of the features of the tracks made and differences between the walking patterns of the sexes and the instars of *L. arenicola*. Motivations for making the excursions and the apparent solutions to the associated problems with them, e.g. avoiding predators, are also discussed.

### Materials and methods

*Leucorchestris arenicola* is a large species belonging to the family Sparassidae (JÄGER 1999). It is endemic to sandy environments in the southern-central Namib Desert (LAWRENCE 1966, DIPPENAAR-SCHOEMANN & JOQUÉ 1997). Adult ♂♂ (Fig. 1) can have a standing leg span of 10–15 cm and weigh 2–4 g. Adult ♀♀ have slightly shorter legs but are more heavily built and normally weigh 3–5 g (HENSCHÉL 1990). The ♂ of *L. arenicola* has yet to be formally described, but is very likely to be the ♂ described as *Leucorchestris kochi* LAWRENCE 1965. *L. kochi* shares the same distribution area and there have been numerous observations of ♂ *L. kochi* mating with ♀ *L. arenicola* (HENSCHÉL 1990). In the present account the name *L. arenicola* is used throughout. The spiders live in silk-lined burrows excavated at an angle into the sand. They stay in their burrows during the day and, in this way, avoid potentially lethal temperatures on the surface of the sand (CLOUDSLEY-THOMPSON 1991, HENSCHÉL 1997). The burrows are closed with a lid consisting of silk and sand, which provides the burrows with excellent camouflage. The sex and the instar of the spiders can be determined by directing sunlight into the burrows with a small mirror. In the burrows the spiders are always situated upside down and with the body's axis perpendicular to the axis of the burrow. In this position the number of spines on the tibia can be counted. As only ♂♂ have three dorsal tibial spines, the sex can be determined (Fig. 1). Because the diameter of the burrow lid is correlated with the size of the inhabitant it can be used as an indicator of life stage (HENSCHÉL 1990). In the following ac-

count all spiders not positively identified as either adult ♂♂ or ♀♀ and having a lid diameter equal to or less than 20 mm are treated as immature spiders.

All the observations and data presented here were made and collected at a site where large numbers of spiders were found. The site is positioned approximately 1 km south west of the Gobabeb Training and Research Centre in the Namib Naukluft Park (23°33' S, 15°2' E). All occupied spider burrows found were marked with white plastic markers. The area is best described as a sand-covered inter-dune section but appears much like an extended dune base (ROBINSON & SEELY 1980). It is bordered to the North by the riparian vegetation of the ephemeral Kuiseb River and by inter-dune gravelly plain in the other directions. The open sand surface in the area is only interrupted by a few patches of vegetation (Fig. 2).

Tracking of *L. arenicola* is most easily carried out in the early morning when the sun is still near the horizon and therefore casts shadows in the footprints of the spiders. Alternatively, tracking can be undertaken at night with the aid of a strong artificial light source held close to the sand surface thereby creating the same shadow effect. The spiders walk almost always in a slightly undulating fashion and the paths of ♂♂ were recorded by placing a marker in the sand every time the spider changed direction from its previous course by more than the width of its leg span corresponding to approximately 5°. The distances between each marker and the compass direction were recorded (for a detailed description of path recording procedures, see NØRGAARD et al. 2003). The direction in which the spiders had been moving can be determined from the tracks by the shape of the footprints (Fig. 3). The moving spider tends to drag its feet out of the sand and by doing so creates a drop-shaped depression with the pointed end in the direction of walking. In the case of adult ♂♂ the direction can also be determined from the shape of the drum marks and scrape marks often found along their paths (Fig. 4). When measuring the paths of adult ♀ and immature spiders the total length of the path and the part retraced by the spider was recorded. Retracing occurred when the spider's outward and inward tracks were overlaid. Furthermore, the distance to the furthest point of the track from the burrow was recorded using a tape measure. Direct observations of the spiders behaviour without disturbing the animals were done with infra-red cameras (CBLL20 Sony Exview) and recorded on video tape. The cameras were overlooking a ♂ burrow and parts of the experimental area. In addition geophone equipment (Input/Output SM-4/PE-3/C) hidden in the sand was simultaneously used to record any audible activity.

The collected data was tested for normality with the Kolmogorov-Smirnoff test and homogeneity with Barthlett's test. Following this, analysis using 1-way Anova statistics were carried out (ZAR 1999). The standard deviation (*s.d.*) is used throughout to indicate the dispersal of the data.

### Results

Data from 71 spider paths that had been tracked and measured were used in the following account. These tracks consisted of 22 paths recorded from adult ♂ spiders and 49 paths recorded from adult ♀♀ and immature

spiders. Analysis of lid size (mm categories) and corresponding life stage, and distance walked showed no significant difference between adult ♀♀ and immature spiders (1-way Anova;  $F = 0.60$ ;  $p = 0.44$ ). Nor was any

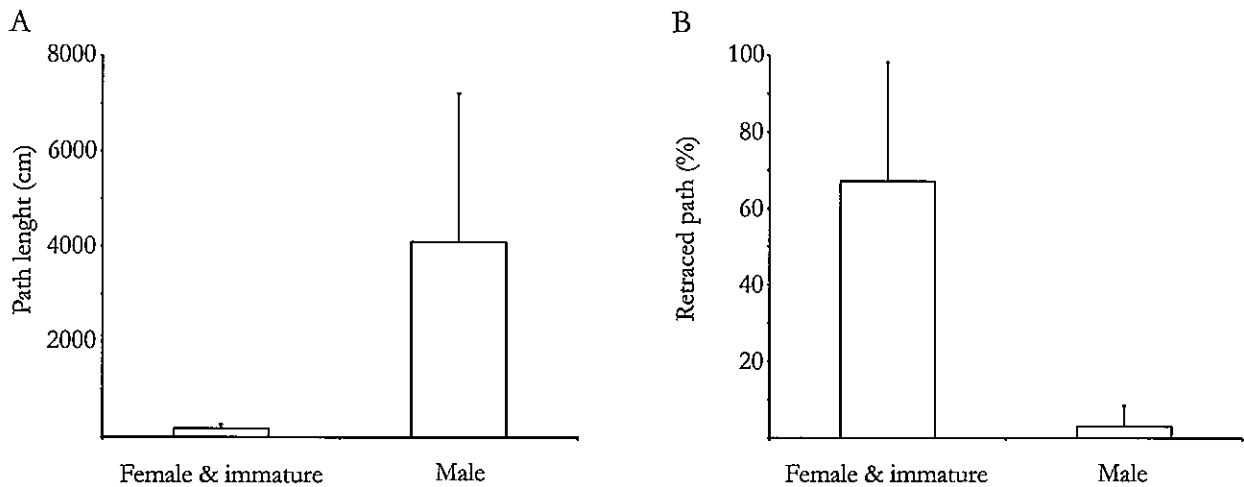


Fig. 5: A. Mean path lengths (+ *s.d.*) of adult female and immature spiders compared to those of adult males. — B. Mean percentage of retraced path (+ *s.d.*) of female and immature spiders and of adult males

significant difference found between these two groups in terms of the percentage of each of the paths retraced (1-way Anova;  $F = 0.32$ ;  $p = 0.57$ ). The two groups are therefore treated as one in the following analysis. The average distance walked by ♂♂ and by ♀♀ plus immature spiders was found to be  $4094.14 \pm 3115.18$  cm (mean  $\pm$  *s.d.*) and  $183.69 \pm 86.27$  cm (mean  $\pm$  *s.d.*), respectively (Fig. 5 A). Not surprisingly, a significant difference was found between the distances that the ♂♂ walked and the distance walked by the combined group of ♀ and immature spiders (1-way Anova;  $F = 78.47$ ;  $p < 0.05$ ). On average, ♂♂ retraced only 3.05 % of their paths while ♀♀ and immature spiders showed a much higher degree (67.10 %) of retracing (Fig. 5 B) (1-way Anova;  $F = 91.48$ ;  $p < 0.05$ ). Fig. 6 shows examples of recorded paths from a ♂ and a ♀ spider that illustrate these differences. Tracks of hunting spiders do not always show high retracing percentages. Handling captured prey may result in more complicated tracks. In such cases the straight-line return path is often a notable feature (Fig. 9).

Only complete records of adult ♂ roundtrip paths were used in the calculations ( $n = 22$ ), but in three cases “incomplete” paths from extremely long distances walked by adult ♂♂ were also observed and measured. On one of these a large ♂ (leg span 14 cm) was traced over ca. 500 m. The track was straight and step size constant. This indicates a fairly even walking speed and no apparent searching for ♀♀. Only when the spider entered an area in which other *L. arenicola* burrows occurred did the path become meandering and drum-marks appeared. The other two instances were similar in basic layout but the tracks were shorter (ca. 250 and 350 m). Although the end-points of these three excursions were

found, none of them seems to have been a round trip as no return track was found at the burrows from which the ♂♂ set out.

The recordings of spider paths presented here show that in general the spiders’ locomotory patterns can be divided into 4 categories:

- 1) female and immature spiders foraging;
- 2) female and immature spiders moving to a new site;
- 3) males searching for mates; and
- 4) males relocating to a new area of potential mates.

The tracks made by ♂♂ are distinguished from tracks made by ♀♀ and immature spiders in other ways than merely the greater distance generally travelled. The so-called drum-marks are a feature unique to the ♂ spider tracks (Fig. 4). These marks are made when a ♂ spider taps its feet on the ground in rapid succession from the hind to the front legs. This makes a drumming sound audible even to the human ear. HENSCHER (1990, 2002) suggested that these marks might be generated during signalling behaviour between two ♂♂. This notion has now been substantiated by simultaneously using infrared cameras and geophones to observe a ♂ spider drumming. Immediately afterwards, a similar drumming was heard through the geophone. This was clearly an answer to the observed male’s first signalling and this male responded by retreating into its burrow.

Infrared camera observations of ♂♂ also revealed another type of signalling behaviour not previously described. Marks on the tracks that previously were believed to be signs of especially intense drumming may actually be signs of an entirely different type of signalling behaviour. Instead of drumming with the legs, these

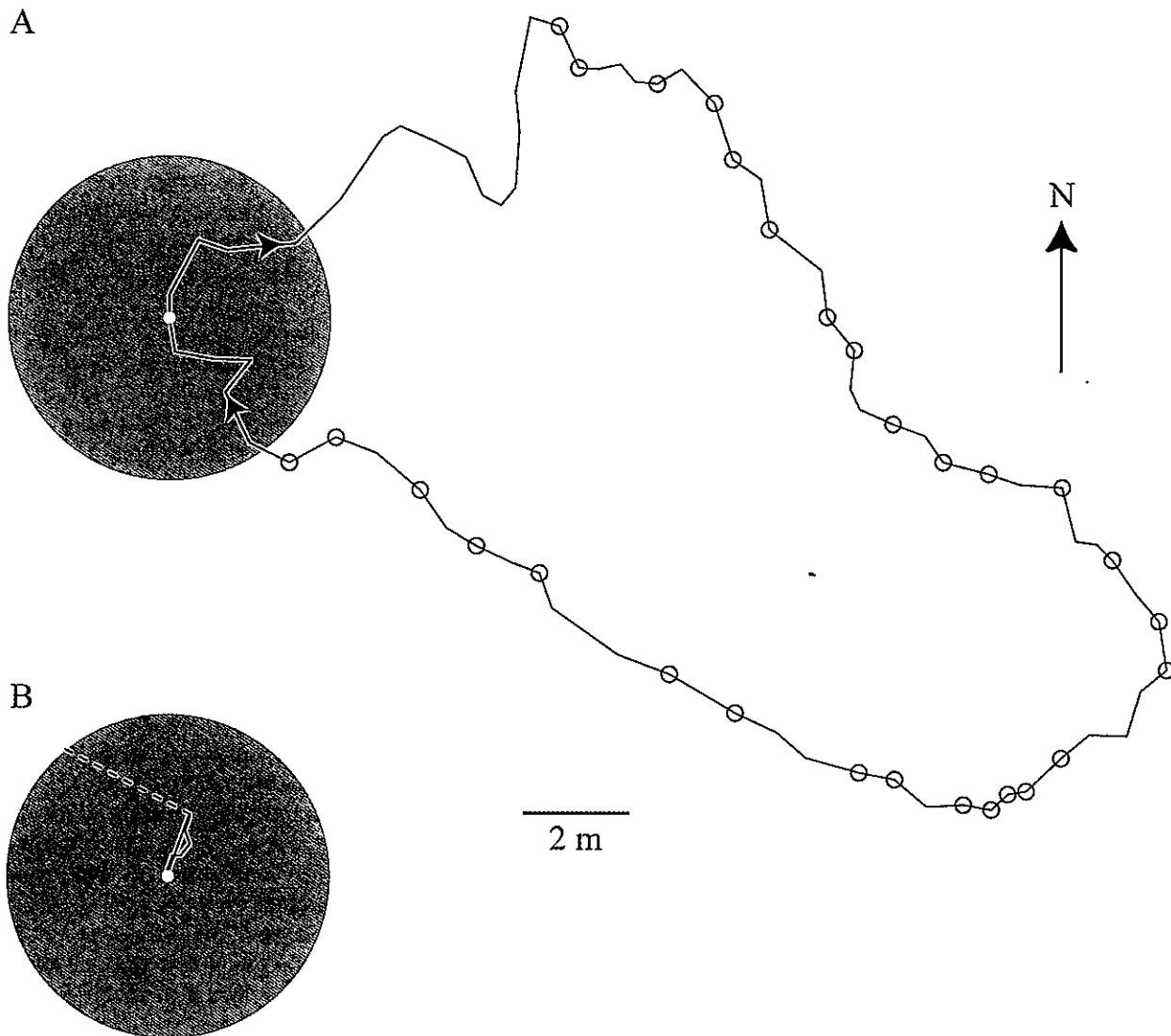


Fig. 6: A. Recorded path of an adult male. Note that there is no retracing of the path (modified from NØRGAARD et al. 2003). — B. Recorded path of an adult female hunting successfully. The grey circles indicate the average territory size and the white dots mark the spiders' burrows. In A the open circles along the path show the position of drum-marks and the dashed line in B shows the trajectory of the prey (in this case a lepidopteran larva).

marks are made by a sideways motion of the spider's body while the animal is standing up. It is carried out with the coxae and opisthosoma pressed onto the sand surface. Sideways scraping creates marks clearly different from drum-marks (Fig. 7). A ♂ spider was observed to make these movements near a ♀ spider's burrow. This was immediately followed by the ♀ coming out onto the sand surface. Scraping movements are thus very possibly a way in which ♂ spiders lure ♀♀ from their burrows for mating. Males were also observed occasionally to enter the burrows of ♀♀ which also resulted in the ♀♀ exiting

their burrows. However, the ♂♂ always tapped on the edges of the ♀ burrow entrance gently with their front pair of legs before cautiously entering. Shortly after a ♂ entered a female's burrow both spiders would emerge and if the ♀ was receptive mating took place on the surface of the sand. This tapping signal also leaves detectable marks around the ♀ burrow entrance. Good evidence for a mating that has taken place is the track it leaves on the sand surface. These mating tracks consist of dense amount of footprints in a constricted area around the ♀ burrow (Fig. 8).

## Discussion

The observations and recordings of spider tracks described here show that there are major differences in the locomotory behaviour between the sexes and instars of *L. arenicola*. These differences are most probably correlated with the different motivations of adult male, female and immature spiders for making their excursions from their burrows.

Measurements of the furthest distance from the burrow support the notion that ♀♀ and immature spiders restrict their movements to an area of about 3 m radius from the burrow. Their trips tend often to be straight lines in and out with high degrees of retracing the outward paths while returning. The reason why ♀♀ and immature spiders are active on the sand surface is mainly for hunting. The spiders appear to be capable of sensing approaching prey while in their burrows. They dart out and intercept prey on their territory (Fig. 6 B & Fig. 9). Prey is killed on the surface and dragged into the burrow where it is eaten. Females and immature spiders are likely trying to minimise their time outside the relative safety of the burrow and the optimal way of doing so is to move in a straight line from the burrow to the prey and to follow the same straight line back. This behaviour minimises exposure to potential predators. Not only do White Lady spiders have a large number of predators (see HENSCHEL 1990), but they are also highly cannibalistic. Crossing into a neighbour's territory is therefore dangerous.

Adult ♂♂ on the other hand do not restrict their movements to their own territory. When they become adult, ♂♂ cease hunting and instead invest all their remaining energy in making long distance excursions in search of mating opportunities (HENSCHEL 1990, 2002). The spiders are promiscuous (HENSCHEL 2002) and in order to find as many different ♀♀ as possible ♂♂ need to venture far from the safety of their burrows. Consequently they cannot stay within the borders of their territories, as ♀ and immature spiders do. Males therefore face high exposure to visual predators, and minimise this threat by being most active on the darkest nights i.e. the fortnight around new moon or at times when the moon is not present in the night sky (NØRGAARD et al. 2006). When a ♂ spider reaches the reproductive stage it switches from comparatively short-distance navigational tasks within its 3 m territory to long excursions requiring the ability to home over great distances.

In our ongoing study, the recorded paths and navigational processes during these excursions on moonless nights are being compared with the navigational methods known from many other arthropods (WEHNER 1992). The impressive distances covered by ♂ *L. arenicola* spiders are far longer than those recorded in any other species of

spider. Their ability to return to their burrows in straight lines from distances of tens of meters on dark moonless nights is truly remarkable, but the straight-line returns from hunting excursions undertaken by ♀ and immature spiders indicates that they also continuously keep track of their position relative to the location of the entrance of their burrow.

Extremely long and straight spider paths without search patterns or return paths suggest that ♂♂ may occasionally look for new sites. They may be in search of an area where more ♀♀ are to be found. This does not happen often. The cost of energy associated with digging and silk lining a burrow (PETERS 1992) is probably a limiting factor while the risk of accidentally settling in another spider's territory and thereby provoking an attack also is high.

Vibration-conducting properties of the substratum are actively utilised by spiders for communication (KOTIAHO et al. 2000). The *L. arenicola* ♂♂ seem to avoid fighting with each other by communicating through drumming. It is likely that they can determine the size and/or strength of an opponent from its drumming signals as seen in other spiders (RIECHERT 1978, SUTER & KEILEY 1984). The sideways scraping movements (Fig. 7) on the sand surface, which was observed near a ♀ spider's burrow, may have been employed by the ♂ to lure the ♀ onto the sand surface for mating. Yet another form of signalling by ♂ spiders is gentle tapping on the lid of a ♀ burrow before entering it. This may inform the ♀ that a ♂ and not a predator or prey is approaching. It is functionally similar to the rhythmic tapping on ♀ webs by ♂♂ of many web building species. On the whole, the signalling behaviour of *L. arenicola* appears to be quite diverse, with different approaches being applied depending on the situation.

Reading tracks has one major disadvantage compared with direct observations. The time spent in walking cannot be inferred from tracks alone. This problem can, however, to a large extent be solved by combining track reading with direct observation and by using data loggers that record the time of activity. Still, in situations such as the dunes of the Namib Desert, where a vibration-conduction substratum dominates the physical environment, the reading of tracks is often preferable to direct observation. Knowledge of the tracks left behind by a spider in undisturbed conditions can often show whether or not direct observation interferes with its behaviour. Studying animal tracks can be employed to investigate the behavioural patterns of many other animals that live in areas with soft surface. However, results obtained from reading of tracks should always be interpreted in context with direct observations.



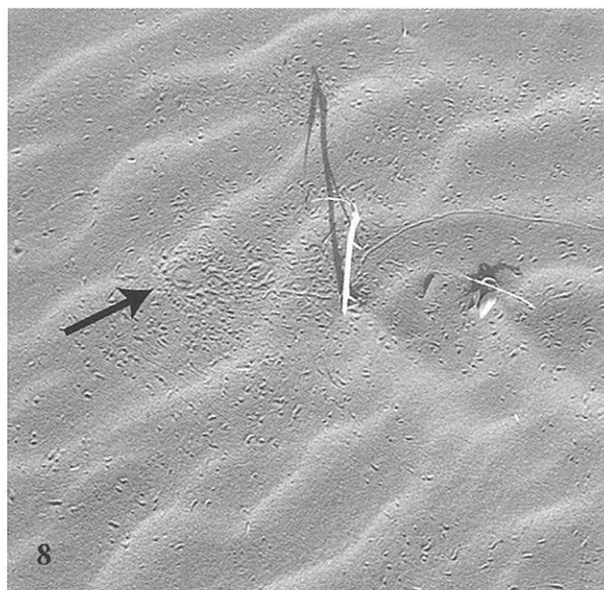


Fig. 7: Scrape-mark on track of a male spider facing towards the top. Scraping with the coxae and ventral opisthosoma leaves the sand heaped up around a central depression. The scrape-mark was found approximately 75 cm from the entrance of a female burrow. — Fig. 8: Track made by mating spiders showing the many footprints that make these tracks different from those of a single spider. The arrow shows the position of the female's burrow entrance. — Fig. 9: Track of an immature *L. arenicola* that successfully captured a beetle. The beetle passed below the spider's burrow entrance from right to left on the photo. Note the spider's straight-line return path.

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## References

- BARTH, F. G. (2001): A spider's world, senses and behavior. — Berlin, Heidelberg, New York (Springer); 394 pp.
- BIRKHOFER, K. (2002): Territorial behaviour of *Leucorchestris arenicola* (Araneae: Sparassidae). — M.Sc. thesis, Technische Universität Darmstadt, 99 pp.
- BROWNELL, P. H. (1977): Compressional and surface waves in the sand: used by desert scorpions to locate prey. — *Science*, **197**: 479–482.
- (2001): Chapter 6. Sensory ecology and orientational behaviours — Pp. 159–183 in: BROWNELL, P. H., & POLIS, G. A. (eds.), *Scorpion biology and research*. — New York (Oxford Univ. Pr.).
- CLOUDSLEY-THOMPSON, J. L. (1991): *Ecophysiology of desert arthropods and reptiles*. — Berlin, Heidelberg, New York (Springer); 203 pp.
- DIPPENNAAR-SCHOEMAN, A., & JOCQUÉ, R. (1997): *African spiders. An identification manual*. — Pretoria (Agricultural Research Council), 392 pp.
- FOELIX, R. F. (1996): *Biology of spiders*. 2nd edition. — Cambridge, Massachusetts, London (Harvard Univ. Pr.), 306 pp.
- HENSCHEL, J. R. (1990): The biology of *Leucorchestris arenicola* (Araneae: Heteropodidae), a burrowing spider of the Namib Desert. — Pp. 115–127 in: SEELY, M. K. (ed.), *Namib ecology: 25 years of Namib research*. — Transvaal Museum Monograph no. 7; Pretoria (Transvaal Museum).
- (1994): Diet and foraging behaviour of huntsman spiders in the Namib dunes (Araneae: Heteropodidae). — *Journal of Zoology*, **234**: 239–251.
- (1997): Psammophily in Namib Desert spiders. — *Journal of Arid Environments*, **37**: 695–707.
- (2002): Long distance wandering and mating by the Dancing White Lady Spider (*Leucorchestris arenicola*) (Araneae, Sparassidae) across Namib dunes. — *Journal of Arachnology*, **30**: 321–330.
- JÄGER, P. (1999): Sparassidae — the valid scientific name for the huntsman spiders (Arachnida: Araneae). — *Arachnologische Mitteilungen*, **17**: 1–10.
- KOTIAHO, J., ALATALO, R. V., MAPPES, J., & PARRI, S. (2000): Microhabitat selection and audible sexual signalling in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). — *Acta Ethologica*, **2**: 123–128.
- LAWRENCE, R. F. (1962): Spiders of the Namib Desert. — *Annals of the Transvaal Museum*, **10**: 197–211.
- (1966): New dune spiders (*Sparassidae*) from the Namib Desert, South West Africa. — *Cimbebasia*, **17**: 3–15.
- NØRGAARD, T., HENSCHEL, J. R., & WEHNER, R. (2003): Long distance navigation in the wandering desert spider *Leucorchestris arenicola*: can the slope of the dune surface provide a compass cue? — *Journal of Comparative Physiology*, **A189**: 801–809.
- NØRGAARD, T., HENSCHEL, J., & WEHNER, R. (2006): The nighttime temporal window of locomotor activity in the Namib Desert long-distance wandering spider, *Leucorchestris arenicola*. — *Journal of Comparative Physiology*, **A192**: 365–372.
- PETERS, H. M. (1992): On the burrowing behaviour and the production and use of silk in *Seothyra*, a sand-inhabiting spider from the Namib Desert (Arachnida, Araneae, Erisidae). — *Verhandlungen des naturwissenschaftlichen Vereins Hamburg*, **33**: 191–211.
- RIECHERT, S. E. (1978): Games spiders play: behavioural variability in territorial disputes. — *Behavioral Ecology and Sociobiology*, **3**: 135–162.
- ROBINSON, M. D., & SEELY, M. K. (1980): Physical and biotic environments of the southern Namib dune ecosystem. — *Journal of Arid Environments*, **3**: 183–203.
- SUTER, R. B., & KEILEY, M. (1984): Agonistic interactions between male *Frontinella pyramitela* (Araneae, Linyphidae). — *Behavioral Ecology and Sociobiology*, **15**: 1–7.
- WEHNER, R. (1992): Chapter 3. Homing in arthropods. — Pp. 45–144 in: PAPI, F. (ed.), *Animal homing*. — London (Chapman and Hall).
- ZAR, J. H. (1999): *Biostatistical analysis*. 4th edition. — London (Prentice-Hall), pp. I–XII, 1–663.

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