

NOCTURNAL NAVIGATION IN *LEUCORCHESTRIS ARENICOLA* (ARANEAE, SPARASSIDAE)

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ABSTRACT. When the males of the Namib Desert spider *Leucorchestris arenicola* (Araneae, Sparassidae) reach the adult stage they undertake long nocturnal searches for females. From these searches they return to their home burrow often in a straight line only retracing a fraction of their outward path if at all. Distances of 40 m and 13 m are conservative estimates of the mean round trip length and maximum distance from the burrow. Returning to the starting point of a round trip of such length is theoretically only possible if the navigator uses external cues for positional reference. The possible involvement of a range of external cues in the male *L. arenicola* was investigated. The direction of gravity, the sun, polarized sunlight, olfaction, constant wind direction and vibrational beacons are ruled out or deemed unlikely to be involved in the spiders' homing.

Keywords: Homing, egocentric, geocentric navigation, path integration, dead reckoning

Complex long distance navigation by arthropods is usually associated with the formidable navigational capabilities of the eusocial hymenopterans such as bees and ants (e.g., von Frisch 1967; Wehner 1992). In spiders long distance traveling is most often done by ballooning involving extrusion of silk threads into the air (Suter 1991). This form of transportation is, however, only used by relatively small spiders. In large spiders such as the mygalomorph spider *Aphonopelma hentzi* Girard 1854 (Araneae, Theraphosidae) travels over long distances are by walking rather than ballooning. However, these spiders only do one-way excursions without returning to the starting point (Janowski-Bell & Horner 1999). Keeping a straight line so as not to end up at the starting point, which may represent an area where resources are overexploited or an area not well suited for a given life stage, might require actual navigation (Dacke et al. 2003). However, returning to the starting point of an excursion, i.e. showing homing behavior, is a far more demanding navigational task for an animal than a long walk in a chosen direction.

In spiders, studies of homing have so far been reported to occur over distances of less than a meter (Seyfarth & Barth 1972; Seyfarth

et al. 1982; Görner & Class 1985; Dacke et al. 2001). However, in the central Namib Desert a spider shows impressive skills of navigation. Henschel (1990, 2002) was the first to notice that the adult males of *Leucorchestris arenicola* Lawrence 1962 (Araneae, Sparassidae), like foraging bees or ants, also return to the starting point after excursions over distances of tens of meters on the desert floor.

The purpose of the present account is to outline the current state of knowledge about the mechanisms used or not used in the long distance homing navigation of *L. arenicola*, show new results concerning the role of vibrational beacons, and finally point out the most promising leads that will be followed in future experiments.

LEUCORCHESTRIS ARENICOLA AND ITS MOVEMENT PATTERNS

Leucorchestris arenicola is an endemic sparassid (Jäger 1999) of the Namib Desert. It is a large spider weighing up to 5 g (Henschel 1990), heavy enough to leave footprints in the sand (per. obs.). Adult males have standing leg spans often exceeding 10 cm (Fig. 1). Adult females have shorter legs but are usually slightly heavier than the males. Adult males comprise up to 12% of the population and occur only in the summer period (September–April) (Henschel 1990). The spiders dig 30–

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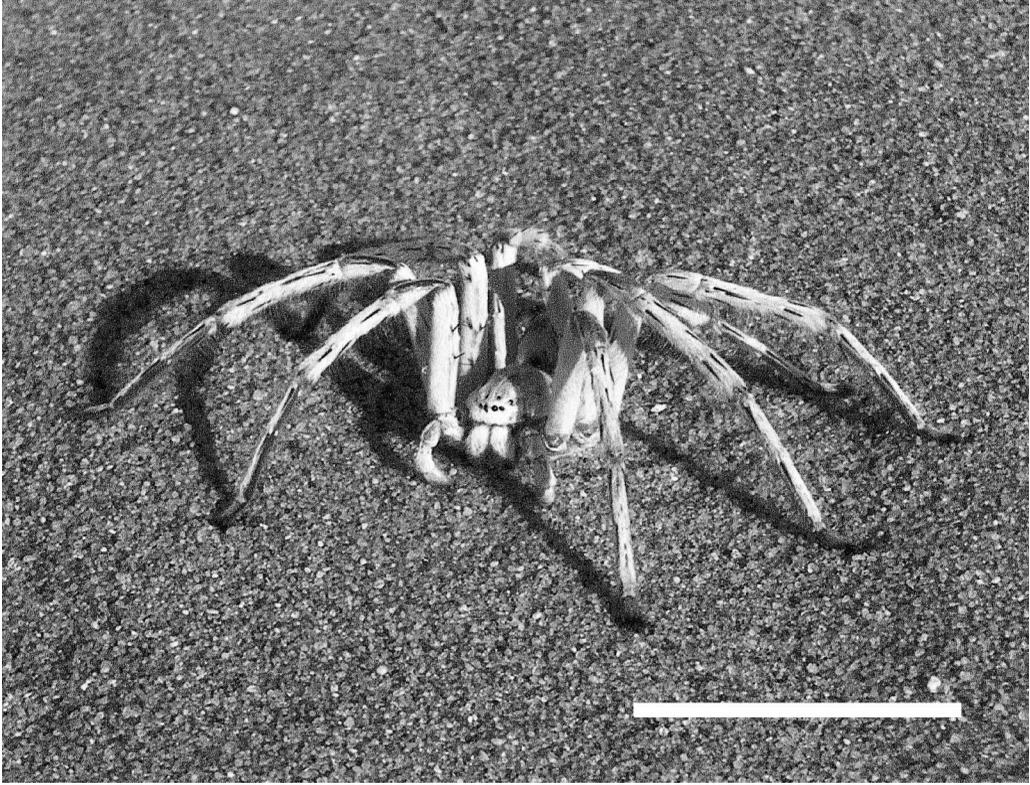


Figure 1.—Adult male *L. arenicola* showing protective coloration against the dune sand. Scale bar: 5 cm.

40 cm long burrows in the sand at an angle of ca. 30 degrees (Henschel 1990). This gets the spider to a depth of approximately 25 cm where climatic conditions are far more tolerable than on the desert surface (Henschel 1990). They are strictly nocturnal spiders, most frequently first becoming active an hour after sunset (Fig. 2). This was established using infrared beam sensors and time-event data loggers (TinyTag). The beams were placed so they crossed the entrance of the burrows. Thereby the time a spider left the burrow was recorded. This activity pattern is probably an adaptation to the high temperatures in the desert during the day and the relative absence of predators at night (Cloudsley-Thompson 1983; Henschel 1990). Like many nocturnal desert spiders they have a light color rendering them inconspicuous against the desert sand (Cloudsley-Thompson 1983; Dippenaar-Schoeman & Joqué 1997). In the desert, the spider is found at the dune base where the sand is more stable and less stony compared

to the slip face of the dunes and the gravel plains found between the dunes (for definitions of dune habitats see Robinson & Seely 1980). The spiders are highly territorial and defend an area with a radius of 3–4 m from their burrow (Henschel 1990; Birkhofer 2002). Especially burrow construction by another spider triggers strong aggressive behavior from a territory owner (Birkhofer 2002). Females and immature spiders mainly restrict their surface activity, e.g., prey capture, to within their territories. The main prey is tenebrionid beetles. The prey are killed on the desert surface and then dragged into the burrow (Henschel 1994). At the time the immature spiders disperse from their maternal burrow or when an adult female leaves her offspring, they may walk beyond their 3–4 m territory boundaries. However, these are one-way trips over distances far shorter than the roundtrip of the adult males. Observing the tracks of the spiders, it quickly becomes clear that adult males truly are the ones that regu-

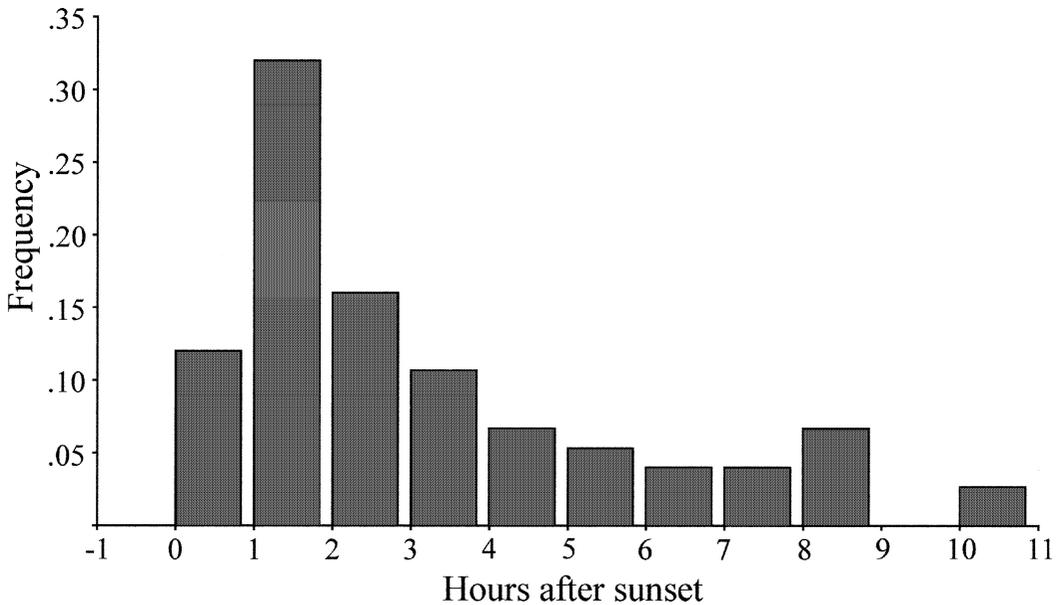


Figure 2.—Frequency of appearances from the burrows on the desert surface by male *L. arenicola* ($n = 75$) in relation to sunset (0 = sunset). Activity recordings were made with infrared beam sensors and time-event data-loggers.

larly wander far. The adult male spiders' tracks can easily be identified by the size of the leg span and the conspicuous drum and scrape marks often seen on the paths (pers. obs.).

When reaching the adult stage the male *L. arenicola* begins making long excursions searching for mating opportunities. These searches for the burrows of adult females are trips several orders of magnitude larger than the spiders' body size and over far longer distances than their average territory size and were, therefore, described as long-distance excursions (Henschel 2002). The general layout of the male spiders' excursions can be divided into two sections: an outward path and a return or homing path. The outward path is characterized by a meandering and occasionally very tortuous searching walk, while the return often is a straight line walk heading towards the burrow across ground not covered on the way out (Fig. 3).

By examining the general movement pattern of the male *L. arenicola* and drawing upon information from other navigating arthropods, especially spiders, we can list the probable methods male *L. arenicola* uses for homing.

HOMING NAVIGATION

Theoretically, a male *L. arenicola* could navigate to and from his burrow using two principally different methods. The spider could use either a geocentric or an egocentric system of references for determining his position. If navigating by geocentric cues, the male spider must determine his position relative to his burrow using landmarks in the surroundings. This requires memorization of a topographic map of the surroundings, also known as a cognitive map (Tolman 1948). The use of such a map has been suggested for honey bees (Gould 1986). So far however, the evidence for this has not been conclusive and the behavior of navigating arthropods studied has been explained by simpler mechanisms than a memorized topographic map (Wehner & Menzel 1990). In such a non-map fashion, landmarks in the surroundings and the contour they present against the horizon are used in homing by wood ants (*Formica japonica*) (Fukushi 2001; Fukushi & Wehner 2004).

If doing egocentric navigation the spider should assess his position in relation to his burrow by using information collected while he is walking. Therefore, instead of having a

map, the navigator continuously keeps track of all distances and directions traveled using this information to “calculate” the direction towards the burrow. This form of navigation is called dead reckoning or path integration (Mittelstaedt 1985).

The necessary information about distances and directions steered can be obtained either ideothetically or allothetically (Mittelstaedt 1985). These two methods may be employed simultaneously. Ideothetic path integration implies that the spider navigates based entirely on internally gained information (Mittelstaedt 1985). This has been shown to be the case in the homing of the ctenid spider *Cuppiennius salei* Keyserling 1877 which can return to its refuge using only information gathered from the lyriform organs (Seyfarth & Barth 1972). Pure ideothetic navigation is, however, susceptible to accumulation of errors ultimately leading to severe loss of precision. It is, therefore, only usable when navigating over shorter distances (Benhamou et al. 1990). When traveling the distances navigated by the male *L. arenicola*, external cues are, therefore, supposedly necessary. Doing path integration and using external cues is called allothetic navigation (Mittelstaedt 1985). A number of external cues are known to be used by several arthropods when they are navigating by use of path integration. The sun and the moon are well-known sources of directional information, used directly or indirectly via the polarized light patterns and spectral gradients they produce in the sky (Tongiorgi 1969; Rossel & Wehner 1986; Wehner 1994, 1997; Wehner et al. 1996; Dacke et al. 1999; Gal et al. 2001; Dacke et al. 2003). The direction of gravity (Bartels 1929; Hill 1979), constant wind direction (Wehner & Duelli 1971) and perhaps magnetism (Ugolini & Pezzani 1995) are also cues used by arthropod navigators. Often more than one of these external cues are used in order to achieve better precision.

THE HOMING OF *L. ARENICOLA*

Based on empirical and theoretical grounds several experiments were designed and carried out in search of the external cues used in the navigation of *L. arenicola*. To begin unraveling the mechanisms of homing navigation for male *L. arenicola* it is important to record and analyze paths in detail. A method to record the paths in all three dimensions was therefore

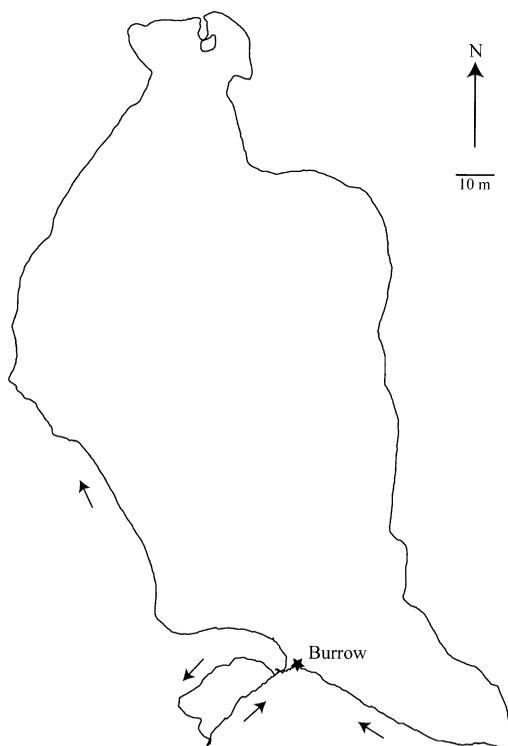


Figure 3.—Trajectory of a single night excursion of a male *L. arenicola* projected onto a 2 dimensional plane viewed from above. Total path length was 810 m.

developed (Nørgaard et al. 2003). A marker was placed along the paths each time the direction of the walk changed by more than the spiders leg span (approx. 5°). This divided the path into segments. The length of each segment was measured using a tape measure, the direction with a compass and the slope with a digital inclinometer (Bosch DNM 60 L). These recordings found a path length (mean \pm s.e.) of $4092 \text{ cm} \pm 664 \text{ cm}$ and a maximum distance to the burrow of $1313 \text{ cm} \pm 223 \text{ cm}$ (Nørgaard et al. 2003). The longer the path, the more difficult complete tracking becomes. These path measurements were therefore biased towards shorter distances as focus was solely on recording complete round trips. The area in which the recordings took place was densely populated by spiders and naturally bordered by interdune gravel plains and riparian vegetation of the ephemeral Kuseib river. Recent path recordings in another more open and less densely populated area have found far longer distances traveled by the spiders. An

approximately 810 m long path is the longest detailed round trip excursion recorded to date of any spider (Fig. 3). The ability to record the paths in all three dimensions allowed for an analysis of the slopes encountered by the spiders during their excursions. A constant slope of the substrate, i.e. direction of gravity, could potentially provide the spider with a usable compass during its navigation. However, the sand surface of the desert is corrugated by the wind and no even slope existed, and use of the direction of gravity in the spiders' navigation was therefore ruled out (Nørgaard et al. 2003) (Figs. 4–6).

Long distance homing over ground which was not covered during the outward trip immediately excludes the use of pheromone trails. Direct homing by olfactory means is unlikely to function over the long distances the spiders travel; this is corroborated by observations of spiders having different homing directions on the same night and the occurrence of changing wind directions. Directly using constant wind direction as a compass cue is unlikely for the same reason and because of the turbulence at the surface caused by the sand ripples. Olfactory cues may however still be involved in the final pinpointing of the burrow.

Sand is the major component of the spiders' habitat and one of the physical properties of this substrate is its ability to conduct vibrations as surface waves in the range between 300–500 Hz (Brownell 2001). These frequencies have wavelengths of 9–15 cm (Brownell 2001), and the leg span of *L. arenicola* falls into this range. Some spiders are highly sensitive to vibrations detected by the lyriform organs on their legs (Foelix 1996), raising the possibility that the spiders could derive directional information from a vibration source.

With a geophone one can hear such sand vibrations. If vegetation hummocks have a distinct sound this might create a "sound landscape" with unique "landmarks" or sound beacons usable in the spiders' navigation, in the same way as a visual landmark possibly could. Therefore, an experiment was carried out to investigate whether or not the spiders could be using such sound beacons. Two speakers were buried in the sand as beacons. Beacon A was placed at a distance of 5 m from a male spider's burrow and beacon B was placed 10 m away in the same direction.

An amplifier (Star sound SSA-2040) and a MP3 player (Loomax 300 M), both powered by a 12 V battery, supplied the audio signal for the beacons. A continuous 300 Hz tone audible in the sand from a distance of at least 20 m was emitted from beacon A starting before sunset. At night when the spider had left his burrow beacon A was switched off and beacon B switched on. In this way the position of the beacon was virtually shifted. In nine experiments, each with different males, no effect of switching the position of a sound beacon was found. All spiders behaved as if undisturbed, searching for females, mating, and returning to their burrows as normal. Thus, while these spiders are likely to depend heavily on vibration sensing for prey detection, this sensitivity does not appear to be important for navigation.

Of the celestial cues available to the spiders, only the moon and the polarized light it produces need be considered here as they are strictly nocturnal. Individual bright stars, star constellations or perhaps the band formed by the Milky Way might also be used by the spiders as a compass cue.

CONCLUDING REMARKS

Many possible external cues are available to the navigating male *L. arenicola* and, as described above, a number of these have by now been ruled out entirely or must be considered highly unlikely to be involved in the process. Of the possible non-visual external cues, magnetism remains to be tested. Magnetism used for bipolar positional reference may be used by lobsters to return to a specific area (Boles & Lohmann 2003). This is not sufficiently precise to locate a tiny burrow entrance in the desert floor. Moreover, the distances over which *L. arenicola* wanders are probably too short to allow for magnetic navigation. Recent experiment has shown that vision plays a role in the navigation done by *L. arenicola* (unpub. data). Thus, with our current knowledge, a visually based navigation system appears to be the most promising explanation of the remarkable homing behavior of *L. arenicola*. The necessity of visual cues has been shown in the wolf spider *Lycosa tarantula* (Linnaeus 1758) (Ortega-Escobar 2002), even though it is navigating over distances far shorter than what is seen in *L. arenicola*.

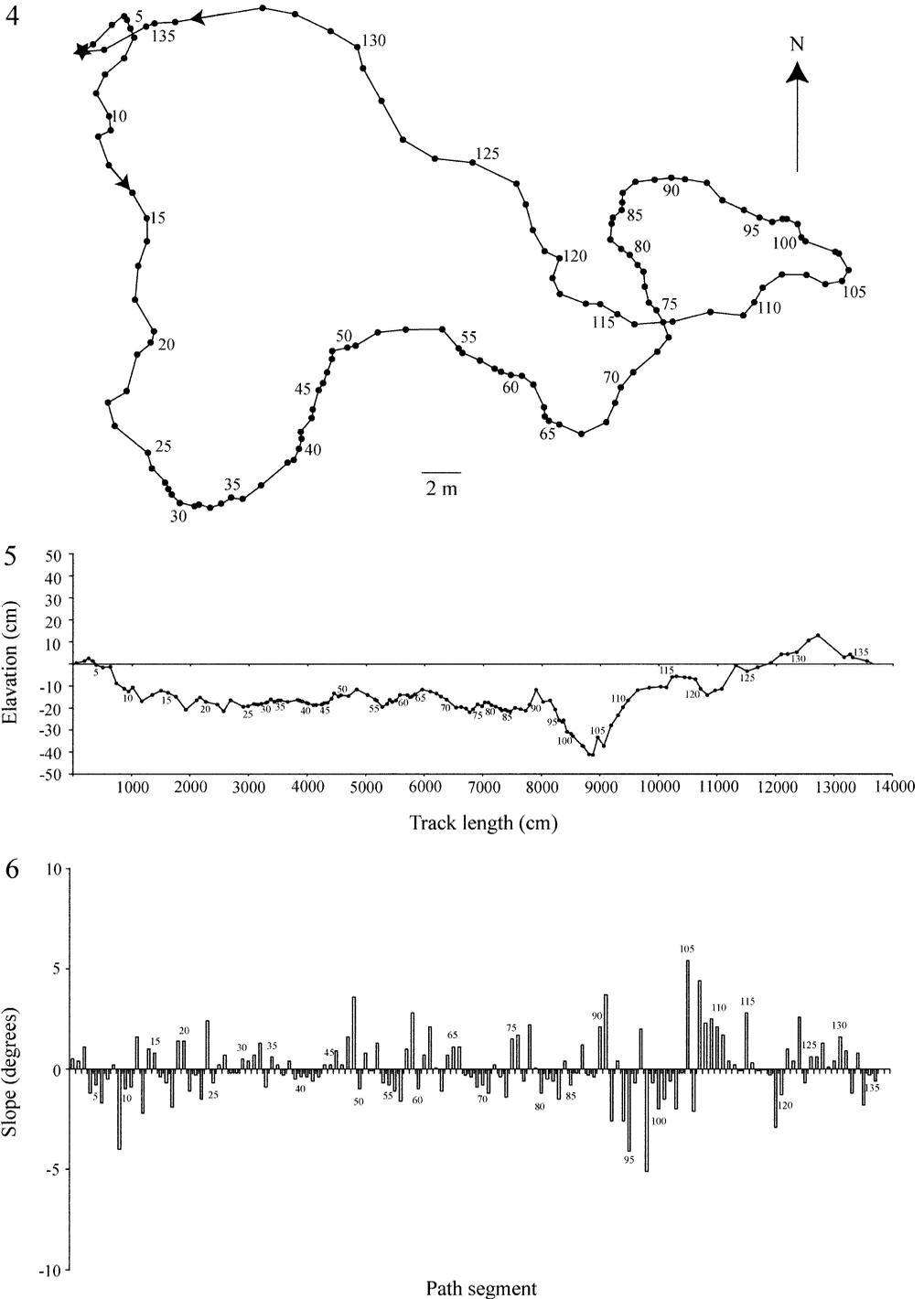


Figure 4–6.—4. Path of a male *L. arenicola* spider projected on to a flat plane. The black star marks the burrow and the arrowheads indicate the direction in which the spider had walked. The small dots along the path each represents a marker put down for the path measurement. The numbers denote every fifth marker and thus path segment. 5. Elevation profile of the spider path illustrated in Fig. 4. The burrow is positioned at the zero elevation line. 6. Histogram showing the slope of each segment of the spider path illustrated in Fig. 4. The 0° line is horizontal. (Adapted from Nørsgaard et al. 2003).

The experiments so far have been focused on the compass component of the spiders' navigation mechanism, but path integration also requires an odometer. Many other questions call for investigation. For example, why do the males return to the burrow from which they started out? Is the energy cost of building a new burrow too high because it is necessary to have a deep burrow to survive high day-time temperatures? Or is it simply too risky to build a new burrow because of cannibalism (Henschel 1990; Birkhofer 2002)?

Due to the scale of the excursions, most of the experiments with male *L. arenicola* can only take place in the field. The collection of data is, therefore, subjected to the constraints of the climate of the Namib Desert and the seasonal availability of adult males. These are conditions that may slow down, but not stop, the progress in gaining knowledge about the astounding homing navigation of *L. arenicola* males.

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