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ORIGINAL PAPER

Use of local cues in the night-time navigation of the wandering desert spider *Leucorchestris arenicola* (Araneae, Sparassidae)

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Abstract Adult male *Leucorchestris arenicola* can walk round-trips of several tens of meters in search of females. Most excursions end with the spiders returning to their burrow. For small animals homing over distances of several meters is theoretically impossible without the aid of external cues. It was investigated, whether the spiders use local cues or they rely solely on global cues. Individually marked male spiders were captured during their excursions and displaced several meters inside an opaque box. Ten out of twelve displaced spiders returned to their burrows. This shows that the male *L. arenicola* are using local cues during their homing, as the comparatively small displacement distances could not be detected by means of global, e.g. celestial cues. In order to test whether the spiders could be using olfactory guidance, the burrows were displaced by 2 m while the spiders were out on their journeys. In 12 out of 15 experiments, the spiders did not find their burrows. These results show that the burrows do not function as olfactory beacons for the homing spiders.

Keywords Sparassidae · Homing · External cues · Landmarks · Olfaction

Introduction

Leucorchestris arenicola Lawrence 1962 (Araneae: Sparassidae) is a large wandering spider endemic to the Namib Desert. The spiders live in burrows dug into the desert sand. They stay in the burrows during the day and are only active on the surface at night (Nørgaard et al. 2006a). This strict nocturnal lifestyle is likely a consequence of the high risk of predation and the lethal daytime temperatures on the desert sand surface (Henschel 1990). The reasons for the spiders to venture out from the relative safety of their burrows at night include hunting, mating and chasing away other *L. arenicola* spiders from the vicinity of their burrows (Henschel 1990, 1994). The spiders uphold and vigorously defend a small territory around the burrow entrance (radius ca. 3–4 m, Henschel 1990; Birkhofer et al. 2006). Intruding spiders and prey was detected by vibrations carried through the substrate. Adult females and immature spiders mainly confine their surface activities to the boundaries of their territory (Henschel 1990). Therefore, when searching for mating opportunities, the adult male *L. arenicola* spiders must naturally leave their own territories to find the adult females. When doing so, they are capable of wandering long distances and yet still manage to return to their home burrow (Henschel 2002; Nørgaard et al. 2003; Nørgaard 2006). The excursions are usually 40–60 m long round-trips (Nørgaard et al. 2003), but paths of several hundreds of meters have been observed (Nørgaard et al. 2006b). Striking features of the paths are a meandering outward journey and a return to the starting point, the burrow, during which the spider does not retrace its outward path. Often the paths show signs of bee-line returns, but as the question always is where

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and when the spider decided to return, any bee-line is difficult to define.

This ability to take a short-cut route home crossing unfamiliar terrain appears similar to the returns from foraging trips studied most intensively in desert ants of the genus *Cataglyphis* (e.g. Wehner 1992). The *Cataglyphis* ants navigate using path integration (Müller and Wehner 1988, 1994; Wehner and Wehner 1986, 1990; Wehner 2003). Path integration implies that the navigating animal continuously computes its current position in relation to its starting point from its past trajectory. To do this, the navigator must obtain information about all distances and directions travelled. This information can then be integrated into a vector pointing home at any particular time. This information can be gathered either ideothetically or allothetically (Mittelstaedt 1985). In ideothetic navigation the animal relies entirely on internally gathered information, e.g. on proprioceptive cues conveyed by the lyriform organs (Seyfarth et al. 1982), whereas in allothetic navigation, the animal relies on external cues. The two different mechanisms often complement each other. However, as pure ideothetic navigation is subject to the accumulation of errors (e.g. Benhamou et al. 1990), it is not reliable as a method for homing over longer distances as it occurs in *L. arenicola* males. When returning to their burrows the male spiders are therefore likely to employ an allothetic navigational strategy and are thus expected to use external cues.

The possible external cues available to the navigating spider can be either global or local. These two groups of external cues differ in fundamental ways. Celestial cues, for instance, are virtually at infinity in relation to the navigator, and thus provide only directional information, i.e. has a compass function. In contrast, local cues, which are in the vicinity of the navigator, can potentially provide positional information as well. Compasses known to be involved in arthropod navigation are the earth's magnetic field (Boles and Lohmann 2003), the direction of gravity (Bartels 1929; Hill 1979; Vollrath 1986), constant wind direction (Wehner and Duelli 1971) or celestial cues such as the sun (Santschi 1911; von Frisch 1967), polarised light (Wehner 1976, 1994; Dacke et al. 1999), spectral gradients in the sky (Rossel and Wehner 1986; Wehner 1997), the moon (Tongiorgi 1969), and possibly bright stars (Doujak 1985). Possible local cues could be landscape features such as the horizon skyline (Wehner et al. 1996; Fukushi 2001; Fukushi and Wehner 2004).

The aim of the two experiments presented in the present account was to investigate whether or not local cues are involved in the remarkable homing abilities shown by the wandering male *L. arenicola* spiders.

Materials and methods

Research site

All experiments were carried out in the Namib Desert close to the Gobabeb Training and Research Centre (Namib–Naukluft Park 23°33'S; 15°02'E). The two, nearly connected, research areas are flat sandy interdune sections or dune bases as defined by Robinson and Seely (1980). To the north, the areas are bordered by a line of trees and bushes growing along the banks of the ephemeral Kuiseb River (Fig. 1). To the south, the areas turn into quartz gravel plains which are not inhabited by *L. arenicola*. This border in area 1 corresponds approximately to the position of an east–west going car track (Fig. 1).

Spider displacement experiment

Male spiders were found by searching for their telltale tracks in the sand in the early hours after sunrise (Henschel 2002; Nørgaard et al. 2003). Spiders identified as adult males (Henschel 1990; Nørgaard et al. 2006b) were dug up and marked with individual colour codes (small dots of non-toxic paint applied to the

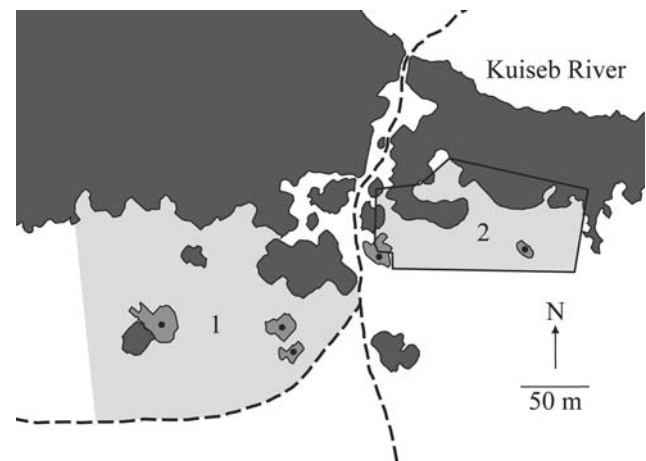


Fig. 1 Map showing the spatial layout of the major landmarks in and close around the experimental areas. The *light grey* areas show the experimental areas themselves. Area 1 is where the spider displacements took place. The *black polygon* shows the fence surrounding area 2 where the burrow displacements took place. The four *medium grey* areas are hummocks formed by *Acanthosicyos horridus* with heights approximately between 1 and 3 m. *Dark grey* areas are trees and shrubs, mainly *Acacia erioloba*, *Faidherbia albida*, *Tamarix usneoides*, and *Salvadora persica* with heights approximately between 3 and 10 m. The *stippled lines* are car tracks. The male spiders used in the experiments were found throughout the areas. In the well-populated research areas the distance to the nearest neighbour was almost between 3 and 8 m. The sex ratio is roughly 1 male to 3 females

cephalothorax). The marked spiders were released at the same location where they were caught. Spiders can be induced to build a burrow at any chosen location by releasing them under a cage during daytime. In our case, the cage was a large, white, upside-down bucket fitted with a wire mesh bottom. The spiders thus exposed to light and unable to escape built a new burrow inside the cage. After a spider had built its burrow, the cage was removed. Every night the burrows of all known adult males were checked. If a male was found to be out of his burrow, his tracks were followed. When the spider was found on the surface, he was caught in an opaque box and quickly displaced several meters. He then was released again and left alone. The capture point and the release point were marked for later measurements. The displacements most often took place in the virtual darkness of moonless nights with only a dim headlight as visual aid to the experimenter so as to keep the disturbance of the spiders at a minimum. Therefore, both displacement distances and directions were random and not correlated to either burrow location or landmarks. On mornings, following the displacements, we checked whether the spiders had returned to their burrows. Complete tracking was often difficult because of morning fog diffusing the necessary sunlight but whenever possible the spider's path was followed and recorded as described by Nørgaard et al. (2003). Although there is no obvious reason to expect changes in the spiders' behaviour after repeated experiments no spider was displaced on consecutive nights.

Burrow displacement experiment

It is evident from the small ripples covering the sand surface that just above the surface the wind forms complex direction patterns, i.e. at spider height. This makes it unlikely that the spiders use any uniform wind direction as a compass. However, it also means that it is impossible to deduce from the spiders' slightly undulating paths whether the spiders could return to their burrows by means of long-distance olfactory cues. Therefore, in a second series of displacement experiments, we aimed at assessing the importance of olfactory guidance in spider homing. Instead of displacing the spiders, we moved their burrows 2 m away from their original positions while the spiders were on their journeys. This was achieved by burrowing a large bucket into the sand. A second identical bucket was then inserted into the first bucket, so that its edges were levelled with the sand surface. The inner bucket was then filled with sand. The same set-up was made 2-m apart (measured centre to centre of the buckets). In this way, the inner buckets of the two sites could readily be

interchanged. Two such experimental set-ups were placed where they did not interfere with any other spiders' territory and used in parallel. The 2-m displacement paradigm was chosen, because this distance is well within the average territory size of adult spiders. As described above, male spiders were induced to build their burrows in one of the buckets. As a control, the spiders were allowed first to embark on a journey while their burrows remained in place. This procedure ensured that the spiders accepted the location of their burrows inside the buckets. At night we checked whether or not the male spiders had left the experimental set-ups for performing one of their journeys. Whenever this was the case, the two inner buckets were exchanged thus causing a 2 m displacement of their burrows. On the mornings, following the displacements, we checked whether the spiders had returned to their burrows, and recorded any visible tracks left by the nocturnal spiders in the vicinity of the buckets.

Results

Spider displacements

During 3 months of thorough monitoring of experimental area 1 (Fig. 1), used in the spider displacement experiments, a total of 25 male spiders and their burrows were located. Out of these 25 male spiders, we succeeded in performing 12 displacement experiments yielding clear-cut results. The displacements were done with 11 spiders, i.e. only one spider was used twice and not on consecutive nights. The mean displacement distance was 27.34 ± 7.15 m (mean \pm SE), while the mean capture point distance and the mean release point distance from the burrows were 20.37 ± 3.21 and 25.72 ± 3.31 m (mean \pm SE), respectively. On ten of these occasions the displaced spiders returned to their burrows; only two spiders were lost after having been displaced in the same way. There was no significant difference between the rate of spiders not returning in the displacement group and the 3 out of 25 spiders that during the extent of the experimental period was observed to have changed location on their own for unknown reasons (Yates corrected χ^2 test: $\chi^2_1 = 0.1511$, $P = 0.6975$). The latter had resettled on new locations where they because of their markings were recognised as male spiders already caught once.

Complete tracking and recording of the spiders' paths are only possible under perfect weather conditions when wind does not erase the spiders' footprints and when morning fog does not diffuse the necessary directional light conditions. In one example, a displaced

spider while homing walked parallel to a line of trees. He first approached the tree line, then, at a distance corresponding to the distance his burrow was positioned from the same tree line, made a right-hand turn straight towards the burrow (Fig. 2b). In comparison, this path did not differ strikingly from the ones of undisturbed spiders (e.g. Fig. 2a; see also Nørgaard et al. 2003 for examples on trajectories from undisturbed spiders) besides reflecting the spatial displacements. In another example, a male spider did a series of drastic course changes initiated at, and repeatedly returning to, a position corresponding approximately to the virtual position of the burrow (Fig. 2c). However, the spider eventually continued to successfully locate his burrow.

In the first of the only two cases, in which a displaced spider had not returned to his burrow, the spider had missed the home burrow completely. In the second case, it was not possible to determine, from the tracks, whether the spider had been lost as a consequence of the displacement procedure or relocated during a second excursion performed after he had returned under the displacement paradigm. Due to this uncertainty, the spider was considered as having got lost as a consequence of the displacement.

Burrow displacements

In total, 15 burrow displacements were successfully carried out in experimental area 2 (Fig. 1). Within this experimental series 3 spiders found their burrows at the new locations while 12 spiders got lost. Using the same control group as before, the success (return) rates differ significantly between experimental and the control group (Yates corrected χ^2 test: $\chi^2_1 = 15.708$, $P < 0.0001$). In all of the 12 cases in which the spiders had not returned to their (displaced) burrows an area of approximately 1.0 m in diameter, densely covered with foot prints was found more or less centred around the original location of the burrow. This area of concentrated search brought one spider 0.2 m close to his burrow (at the new location), but the spider did not succeed in finding his displaced burrow. It was only in one case that a spider's search resulted in locating the displaced burrow. In the other two cases in which the spiders found their burrows at the new locations, the spiders did reach them directly on their homeward journeys.

Discussion

Whatever the means by which *L. arenicola* navigates over large distances, the spider must finally pinpoint the location of its burrow and hence must be able to

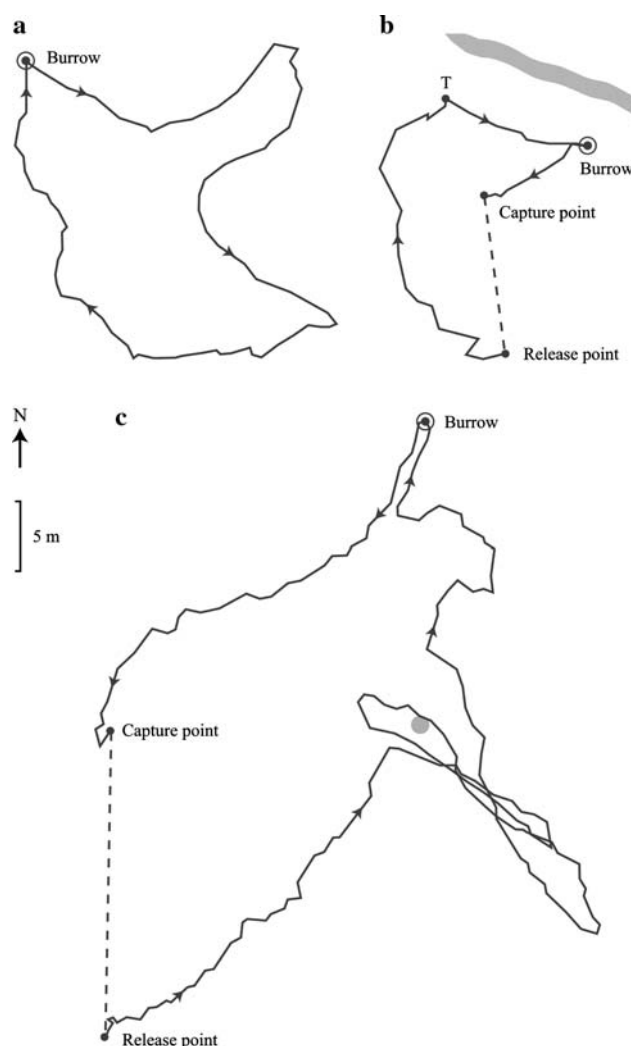


Fig. 2 **a** Path recorded from an undisturbed male *L. arenicola*. The path length was approximately 94 m. **b, c** Two paths recorded from male *L. arenicola* spiders, which were displaced during their nocturnal excursions. The dashed lines indicate the distances the spider was displaced inside an opaque box. In **b** the spider walked parallel to the tree line along the Kuiseb River from point T and back to the burrow. The broad grey line shows the approximate position of the tree line consisting of trees of various heights (5–10 m). The path length excluding the displacement was approximately 46 m. In **c** the course deviation on the spider's return path corresponds closely to the virtual position of the burrow marked by the filled grey circle. The path length excluding the displacement was approximately 178 m. The arrows on the paths **a, b,** and **c** show the direction the spiders had walked

exploit local cues of some kind or another. In order to delimit the kind of cues that could play a role in the spider's goal finding behaviour, we carried out two types of experiments. First, the male spiders were captured during their nocturnal journeys, and displaced to a nearby location. Secondly, the burrows of the spiders were displaced while the spiders were performing their journeys. As both kinds of displacements occurred over a range of only a few meters, far-off cues such as,

e.g. stray light patterns in the sky or the distant skyline did not allow the spiders to detect the displacement either of themselves or of their burrows. If diurnal desert ants of the genera *Cataglyphis* (Wehner and Srinivasan 1981; Wehner et al. 2002) and *Melophorus* (Wehner et al. 2006) are displaced from the feeding site (the end of their outbound journey) in a similar way they select a course parallel to their pre-displacement course—if familiar landmarks are not available. Hence, these ants rely predominantly on path integration, and use skylight cues as the necessary compass component (Wehner and Srinivasan 2003). If the spiders relied exclusively on one or another kind of path integration, after displacement of either spider or burrow they should end up at a location deviating from their burrow by the displacement distance. The path example illustrated in Fig. 2c could suggest an underlying path integration mechanism as the sudden deviation in the course steered by the spider corresponds so well with the virtual position of the burrow. However, the area was rich in spiders and thus also in adult females. It is therefore difficult to determine if these detours are an effect of the detection of a receptive female or happened because the spider had run off a global path integration vector and was searching for the burrow. In any event, like the vast majority of the displaced spiders, this male also managed to return to his burrow and the spiders can do so even without doing such searching at the location predicted by the displacement (Fig. 2b). Hence, the spiders did not—at least, not exclusively—rely on path integration, but used local cues to compensate for their displacements.

Those local cues could be olfactory ones, as we have observed that *L. arenicola* males were attracted to lids taken from the burrows of adult females (unpublished observations). This behaviour was most probably caused by odours produced by receptive females (Papke et al. 2001). In order to decide whether olfactory cues could guide the spiders towards their burrows, we displaced the burrows by a few meters from their original to a new location. The spiders, however, searched persistently at the original location of their burrows and hence did not use their actual burrows as some kind of olfactory beacons. The precision with which they searched at the former locations of their burrows further indicates that they are able to return to their point of departure by missing it by no more than about 0.5 m (after they have left it during their journeys over distances of up to several hundreds meters).

Both types of experiments performed in the present account clearly show that the spiders use local cues at least in the final stage of their homeward journeys, and that these local cues are not olfactory ones. What, then,

are the cues exploited by the *L. arenicola* males? We hypothesize that the spiders, even though they are active at the darkest times of the night (Nørgaard et al. 2006a), depend on visual landmark information as provided by bushes, trees and dunes in the neighbourhood of the burrows (see Fig. 1). *L. arenicola* could accomplish this visual orientation task by employing its single-lens eyes (lens diameter 0.4–0.5 mm for the four types of eyes) and a combination of neural summation mechanisms (Warrant 1999, 2004). We are currently studying the spider's visual system in more detail (Nørgaard, Nilsson, Henschel, Garm and Wehner, in preparation). Electroretinogram measurements used to compute absolute light sensitivities have supported the hypothesis that in another nocturnal wandering spider, *Cupiennius salei* (Ctenidae), vision is certainly possible in moonlight, but most probably not in starlight, and that all four pairs of eyes are about equally sensitive at night (Barth et al. 1993). Furthermore, in the nocturnal net-casting spiders of the genus *Dinopis* (Dinopidae) intercellular recordings performed in photoreceptors of the large PL eyes reveal sensitivity thresholds that are several orders of magnitude higher than they are in *Cupiennius* (Laughlin et al. 1980).

Certainly, however, the use of local visual cues will not be sufficient to account for the spider's overall navigational strategy. Path integration mechanisms are most likely to be involved in the long-distance journeys. As the male spiders are wandering in moonless nights, at times when celestial stray light patterns are no longer available (Nørgaard et al. 2006a), the sky vault does not provide compass cues as it does in diurnal (rev. Wehner and Srinivasan 2003) and crepuscular (Dacke et al. 1999, 2003) arthropods. Furthermore, gravity cues as potentially provided by the slopes of the dunes are not necessary either (Nørgaard et al. 2003). Nevertheless, it would be premature to rule out any external compass cue as a component in an allothetic path integration strategy. The distant skyline or bright stars might be possible candidates. One way to inquire about such global path integration mechanisms is to displace the spiders within an environment that is completely devoid of local landmarks. A second is to design large-scale experiments involving positional manipulations of artificial landmarks. Video recordings of spiders finally pinpointing their goal might follow. However, the question whether global cues are used at all, and if this were the case, how they interact with the local cues addressed in the present account, remains to be tackled.

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