LONG-DISTANCE WANDERING AND MATING BY THE DANCING WHITE LADY SPIDER (*LEUCORCHESTRIS ARENICOLA*) (ARANEAE, SPARASSIDAE) ACROSS NAMIB DUNES

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ABSTRACT.   Adult males of the Dancing White Lady Spider (*Leucorchestris arenicola*, Araneae, Sparassidae) occurring in the dunes of the Namib Desert, Namibia, frequently wander far out of their 3m radius territories on dark nights. They move across bare dune slopes in search of mating opportunities and subsequently return to their burrows. In the current study, I describe the long-distance movements and navigational ability of males and examine how their wandering behavior relates to mating and interactions with other males. In 16 observed complete excursions, male spiders walked 51 m (median, range 16–91 m) from their burrow along a path of 134 m (42–314 m). The return path was shorter than the outgoing path, had less than ⅛ as many turns, and rarely retraced the outgoing path. Typically, the return path across open terrain had a straight section (median 33 m, range 10–89 m) which was directed towards the home burrow with a maximum angle of deviation of 5°. Males crossed 0–5 territories of adult males and as many female territories, mating in about half of the encounters with females. Males avoided each other and signaled with intense sand drumming. Adult males differ in size and there are indications that they compete with each other for mates by long-distance movements, drum-signaling each other, and interfering with mating. During three years of observations of a *L. arenicola* population, 8% of the largest males did 51% of the mating. Spiders of both sexes were promiscuous, and individuals mated with each other on several occasions. The current study prompts future investigations concerning male orientation and its neurophysiological basis, their ability to locate females, as well as the inter- and intrasexual relationships of *L. arenicola*.

Keywords: Navigation, orientation, homing, signaling, mating system

Long distance navigation of animals has long fascinated scientists and the mechanisms of these remarkable capabilities are rarely understood. Spiders have been objects for investigating orientation and navigation and several kinds of mechanisms have been suggested as underlying their homing behavior (Wehner 1992). While some spiders appear to use idiothetic information, mediated by the slit-organ proprioceptors (Seyfarth et al. 1982), others may rely on visual cues, gravity, substrate characteristics, vibrations, or a mixture of several mechanisms (Crawford 1984; Suter 1984; Görner & Claas 1985; Mittelstaedt 1985; Rovner 1991; Dacke et al. 1999; Marshall 1999; Barth 2001). However, these studies were confined to short-distance movements, either on the web, or within several meters of the retreat. This is because spiders usually do not travel far and navigational precision does not appear to be important for some observed long distance movements, such as ballooning.

The Dancing White Lady Spider, *Leucorchestris arenicola* Lawrence 1962 (syn. *L. kochi* Henschel 1990a; Sparassidae), of the Namib Desert is a wandering spider that regularly walks over bare dune sand at night and returns to its burrow. Immature and female spiders confine these movements to within their foraging territory of ca. 1–3 m radius (Henschel 1994). However, adult males move considerably further, several tens of meters, and return to their original home retreat using behavior other than retracing the outgoing path (Henschel 1990a). The distances exceed the foraging territory by one to two orders of magnitude and in this paper they are referred to as long-distance movements.

Leucorchestris arenicola are so large (2–5 g) that they leave distinct tracks on dry, open, unvegetated sand dunes (Henschel 1987; Birk-

hofer 2000). In the Namib, afternoon winds usually erase previous tracks. The movements of spiders that wandered on calm nights are clearly visible at sunrise, when the shadows of spider footprints are clearly visible. During earlier studies (Henschel 1990a, b, 1994, 1997), spider tracks were compared with observed activities and this makes it possible to interpret tracks, an important component of the current study.

In the current paper, I describe the movements of male *L. arenicola* and compare the characteristics of the outgoing path with the return path in order to examine their navigational ability. Mating opportunities appear to be the motivation for the long-distance movements of *L. arenicola* (see Henschel 1990a). In this paper, I therefore also present first insights into their mating system, mating frequency and male-male competition.

METHODS

Taxonomy.—Lawrence described two species of *Leucorchestris* from Gobabeb. The first was *Leucorchestris arenicola* Lawrence 1962, based on an immature individual, and an adult female in 1966. While Lawrence did not describe a male *L. arenicola*, he named an adult male from Gobabeb, *Leucorchestris kochi* Lawrence 1965. Based on 34 occasions of *L. arenicola* mating with *L. kochi*, Henschel (1990a) suggested that these two are synonymous and that *L. arenicola* is the senior synonym. Despite extensive observations by Henschel (1997) near Gobabeb, no other congeners have been found in this area. The current observations of mating confirm the synonymy, and *L. arenicola* is used throughout this paper. Among 144 voucher specimens of *L. arenicola* from this project deposited in the National Museum of Namibia in Windhoek, 32 are adult females and 21 adult males.

Natural history.—*Leucorchestris arenicola* is endemic to the Great Dune Sea of the Namib Desert (Lawrence 1962, 1965, 1966; Henschel 1990a, 1997). This large, nocturnal sparassid spider, forages primarily on tenebrionid beetles or any other small animal, including conspecifics (Henschel 1990a, 1994). Probably through vibrations of the sand, moving prey are detected up to 3 m away. The preferred microhabitat is the gently sloping portions of dunes. This largest of several sympatric sparassid species appears to exclude

Figure 1.—Drumming spoor of a male spider, showing the eight indentations of the tarsae on the outside, and of the coxae in the middle. The opisthosoma has left a dent behind the coxae, and in front of them are two marks made by the pedipalps, giving the track direction (the spider was facing towards the top of the picture).

other large wandering spiders from this habitat (Henschel 1997). The population density is 9–302 *L. arenicola* ha^{-1} and neighboring burrows are located approximately 3.9 ± 2.1 m apart at a high-density site (Henschel 1990a).

Both sexes mature at two years of age, and the female continues to live for another 6 months to one year. Females are iteroparous and spend approximately 9 weeks in extended brood care. All reproductive activity is seasonal between September and April, but females and juveniles remain active throughout the year. After maturing, adult males only live for another 6–14 weeks and are absent during winter. Males have longer legs (spanning 10–14 cm) than females (6–9 cm), and they frequently stop during their long wanderings to drum the sand surface with all eight legs and the body, leaving deep impressions (Fig. 1). Wandering activity is reduced during bright nights, particularly for a week on either side of the full moon.

Study Area.—Fieldwork was conducted during late 1986 to late 1989 at Visnara (23°33.835′S; 15°02.201′E), a fenced dune area of 0.75 ha situated 1 km south of Gobabeb in the Great Dune Sea. A grid of 10 × 10 m marked with poles was placed across Visnara, enabling a spatial resolution of 1 m. Other observations were made at dune sites of

the Central Namib across the Great Dune Sea (22°–26°30′S; 14°30′–16°E).

Fieldwork.—All burrows of *L. arenicola* at Visnara were marked with numbered flags and their position in the grid noted. Size, development stage and sex were determined either by capturing and releasing spiders (Henschel 1991), or by looking into the burrow with the aid of an ophthalmic mirror to examine diagnostic features such as epigyna, pedipalps and leg spination (Henschel 1990a). Spiders were individually recognizable by their use of marked burrows, as well as by marking them with a spot of water paint (Plaka) on the dorsal side of the patella. Not all males were measured directly, but spider size is correlated with trapdoor size (carapace width vs. trapdoor diameter: $r^2 = 0.85$; Henschel 1990a), which was measured for all spiders.

Spider activity was recorded from tracks examined after sunrise. The interpretation of tracks was validated with direct observations at night, made by periodically scanning areas with known high densities of spiders using a flashlight from stationary observation points (direct following of spiders disturbs their activity). In this way, tracks left after drumming or mating were identified. All "observations" referred to in the current paper are records of tracks. Burrow entrances were checked on 21,771 occasions during the three study years, with each early-morning check representing an "observation-night" of an individual spider. The data set comprises 1201 observation-nights of 75 adult males and 3175 observation-nights of 103 adult females.

Long distance excursions of males from known burrows were tracked, and their entire paths were drawn onto a 1 m gridded map, i.e. the resolution of movements was 1 m, and smaller deviations were ignored. Linear movements were also recorded simplified (e.g., when a spider walks in a "straight line" the path is actually slightly undulating with deviations < 1 m), but leading in the same general direction. Due to large variability in male size, it was often possible to distinguish drum-marks of different males from each other in cases where they crossed each other.

For the purpose of the current study, a subsample of 25 complete outgoing and return movements of 16 *L. arenicola* males was selected for detailed analysis from a total record of 157 excursions (the total data set includes many incompletely mapped paths). The 25 paths were digitized, and the following was calculated: total path distance, maximum linear distance from the burrow, outgoing path distance, length of the longest straight section, number of turns, and the number and location of drum-marks. The same data were obtained for the return path as for the outgoing. The target angle was the relative direction of approach towards the burrow of the longest sector on the return path, with 0° being on target (± 1 m based on map cell size); the target accuracy was the distance of the path trajectory from the burrow.

By superimposing the path onto the population map, it was possible to determine the number of territories that a wandering male crossed. Previous tests with protected, released spiders indicated that resident spiders had a territory of about 3 m radius around their burrows (Henschel 1990a). Sometimes direct interactions occurred, such as mating. Probable evidence for other more cryptic interactions were drum-marks left by a male crossing an inactive spider's territory, or two drumming males circling each other at distances of several meters. The distance of the burrows of two females situated closest to the male's burrow along his journey was measured (and if mating occurred, the mated female's distance from the male burrow was recorded).

Data analyses.—Spatial data on male movements were not normally distributed (Kolmogorov-Smirnov Test, $P > 0.05$). To describe wandering behavior, one observation per male (n = 16) was selected and 9 further observations were used to examine variation in behavior by individuals. The non-parametric Wilcoxon matched pairs test was applied to compare variables between the outgoing and return paths, as well as interactions towards males compared to females on each journey. Results are given as median, quartiles and range. Sample size (*n*) of observations of male movements was 16 unless stated otherwise. Observations of mating behavior involved the entire three year data set (*n* = 3376 observations of adults), and a chi-squared test was used to examine whether spider size affects mating frequency.

RESULTS

Movement patterns.—The 16 study males wandered up to 91 m (median 51 m) away

Table 1.—Path analyses for 16 excursions of males, showing the maximum linear distance from the burrow, details of the path, and the accuracy and angle of homing along the longest straight stretch towards the burrow.

Variable	Measure	Median	Quartiles	Range
Linear distance	(m)	51	36–74	16–91
Path distance	total (m)	134	91–231	42–314
Path distance	outgoing (m)	96	47–171	25–213
Path distance	return (m)	39	32–84	16–129
Longest straight stretch	outgoing (m)	20	16–25	6–71
Longest straight stretch	return (m)	33	19–47	10–89
Number of turns	outgoing	11	9–21	4–30
Number of turns	return	2	0–2	0–16
Distance retraced	return (m)	0	0–0	0–13
Angle at burrow	out–return (°)	65	45–98	0–180
Homing	accuracy (m)	0	0–1	0–5
Homing	angle (°)	0	0–2	0–12

from their burrows (Table 1). They often turned, and the median path distance was 134 m (range 42–314 m). The outgoing path was significantly longer than the return path by 146.2% ($P < 0.001$, Fig. 2a). However, the longest straight section was on the return path ($P < 0.05$, median = 33 m). This is because the males made fewer turns on the return path ($P < 0.001$, median = 2 turns) compared to 11 turns on the outgoing path (Table 1). Three times the outgoing path was retraced for 5–13 m. Silken draglines were occasionally produced along the paths (not quantified). Individual males that were observed repeatedly (n = 9) moved over different distances (difference from the analyzed observation: median = 73%, range = 1–84%) and did not follow similar paths, although each male returned to the same burrow. The maximum distance recorded for each male in this study was not influenced by spider size (r^2 = 0.13, P = 0.17).

Homing.—Males usually returned to their burrow from a different direction than the one they took on their outward journey (median deviation = 65°). In all 12 cases where there was no obstruction along the way, the longest stretch of return aimed < 5° towards the burrow, usually being 0°, i.e., going straight towards the burrow (Table 1). Males took the shortest distance back. In the remaining 4 cases, there was a !nara bush (*Acanthosicyos horridus* Cucurbitaceae) or *Acacia* tree in the way, and the returning male walked around the periphery of the obstruction. He deviated 11–31° from the shortest route, and then turned towards the burrow when the way was clear. On exceptional occasions when a male missed his burrow, his subsequent movement behavior changed (e.g., Fig. 2b). He made frequent turns and loops, and steadily moved closer to his own territory until he found the burrow. There is no record of a male not finding his burrow. Only one male constructed a new burrow several meters away from his original burrow upon returning to his territory.

Encounters.—The *L. arenicola* population at Visnara was quite densely packed, so that as soon as males moved out of their own territory (3 m radius), they crossed 2–35 territories of other known spiders at Visnara (Table 2). There were no differences in the number of adult males and adult females encountered by wandering males (quartiles: 1–2; $P > 0.05$). The closest territory of an adult female that they crossed was a median distance of 15 m (range 4–64 m) from the wandering males' home burrow, and the second female was 55 m (28–89) away. During one excursion, the wandering male did not encounter a female, even though a female burrow was 16 m from his burrow, and this male moved 74 m further than the distance to the closest female. In six (40%) of the 15 excursions where a female was encountered, this was not the closest female to the male's burrow. Five of these males did locate the closest female during other excursions. The 16 males encountered females on 22 occasions, and mated on 15 (68%) of the encounters (when examining all 25 excursions, the proportion

was 57%). Two of the males mated twice during one night's excursion.

Drumming.—Drumming (Fig. 1) was frequently performed on the outgoing journey (median 17, range 0–54 times), compared to rare instances of drumming on the return (upper quartile = 0, maximum = 15; $P < 0.001$; Table 2). For 71% of the drumming incidents, it was possible to ascertain a likely relationship to other adult *L. arenicola*, as either another male responded in kind, or the drumming occurred near the burrow of an adult spider. Drumming by wandering males occurred near another male significantly more often (95% of 239) than drumming near females (5%, $\chi^2 = 124$, $df = 2$, $P < 0.001$, Table 2). On six occasions when a wandering male walked over the territory of an inactive adult male, the wandering male drummed.

When two wandering males approached each other (n = 10), they avoided one another by several meters in eight cases and in two cases circled each other closer than 1 m (but the males apparently did not contact each other). Some of the most complex movements by males across the study area were when two males maneuvered around each other across a wide field (Fig. 2c). In the case shown on Fig. 2c and in a second case, it appeared that mating had been interrupted by the arrival of a second male.

Mating.—Data on mating were obtained in the course of 3376 observations of 178 adult spiders (75 males) at Visnara over three years. Six males performed 51% of 63 copulations recorded in the course of three years, while 24 males did the remainder. Excursions in which mating occurred were usually followed by one or more nights of inactivity. However, on six occasions (9.5%), males mated on successive nights. For 45 males, no mating was recorded in 469 observations. Mating frequency significantly increased with male size (Table 3; $\chi^2 = 8.1$, $df = 2$, n = 30, $P < 0.05$). The six males with the highest mating frequency were from the middle and largest size classes.

An individual male (#82) was observed for 38 nights over an 11-week period. He undertook 12 excursions (3 of which are part of the mapped data set) and mated ten times with six different females, two of them twice and one three times (Fig. 3). On three excursions he apparently mated twice. Observations of him began soon after full moon, and his initial ex-

cursions were relatively short (< 20 m). However, after a fortnight, at new moon, he wandered farther (Fig. 3).

In 3175 observation-nights of 103 individual adult females, they mated on 55 occasions. Eight females (8%) performed 54.5% of the copulations, and 19 the rest, while mating was not observed for 76 females. This distribution was significantly skewed ($\chi^2 = 0.49$; n = 103; $P > 0.05$). On different nights, individual females mated with up to four different individual males. On six occasions (10.9%), females mated on successive nights. During the 6 month seasons, six females mated at least thrice, one four times and one eight times. The latter female mated with the same male on four successive nights. During a five month observation period, she again mated with this male as well as two other males, once with different males on two successive nights. On four other occasions, a female mated a previous partner. On many occasions when a male crossed a female territory, mating did not take place (43% during all 25 mapped excursions). Small females mated less frequently than large females (Table 3; $\chi^2 = 7.8$, $df = 2$, n = 27, $P < 0.05$).

During 1201 observation-nights of 75 individual adult males at Visnara during the course of three years, males wandered out of their territories on 157 (13.1%) occasions, mainly between the months of October to February (Fig. 4). Given a median natural longevity of 9 weeks after maturation (two new moons), it is calculated from the above that an adult male, on average, wanders 8.2 times during this period, or on 26.0% of the nights of low moon. Thus, a male may expect to mate 4.7 times during his life on average.

Females mated during 1.7% (n = 55) of the observations (n = 3175). It is thus calculated that during a season, an average female mates 12.1 times per 8 month breeding season, or 10.1% of the low-moon nights. Given that the sex ratio is female-biased (males: females = 0.38: 1; see also Henschel 1990a), this estimate of females mating corresponds roughly with that calculated from the frequency of males mating (26.1% × 0.38 = 9.9%).

Mortality.—It was difficult to assess the risk of long distance movements. All males suddenly disappeared for unknown reasons. In six cases, wandering males were captured by predatory gerbils, representing 3.8% mortality
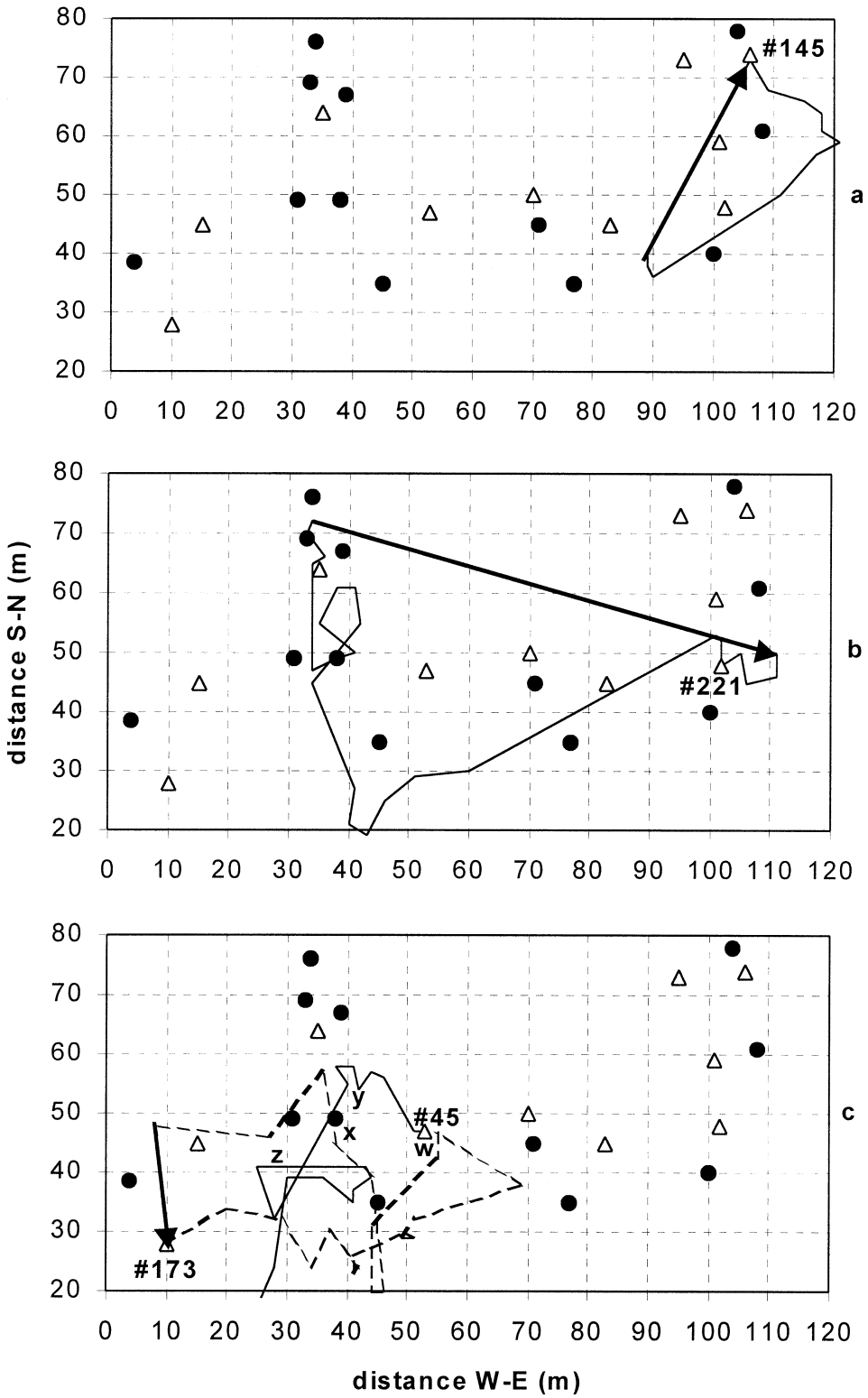
Table 2.—Number of territories crossed, encounters and drumming behavior by males during 16 excursions.

Variable	Description	Median	Quartiles	Range	n
Number of territories	all	16	7–23	2–35	16
	adult males	2	1–2	0–6	16
	adult females	1	1–2	0–5	16
Distance (m) to female	closest from burrow	10	7–15	4–35	16
	1st encounter	15	10–34	4–64	15
	2nd encounter	55	38–68	28–89	7
	diff. closest–1st	0	0–13	0–56	15
Drum-marks	outgoing	17	7–21	0–54	15
	returning	0	0–0	0–15	16
	near male	3	0–19	0–48	15
	near female	0	0–1	0–4	15

rate during excursions. Three other males died of unknown cause in their burrows. The fate of the remaining 66 other males was unknown.

DISCUSSION

A main feature of the long distance excursions by the *L. arenicola* males was their unerring return journey to their burrow. Even after long and complex outward excursions with many turns and loops, homing behavior indicated that the wanderers knew where their burrows were and returned by the shortest possible route, even when moving around obstacles. A male changed his behavior to a meandering search when he missed his burrow after a long journey.

The need to return to the home nest rather than building a new nest may be a question of the energy required to construct a new burrow (Henschel & Lubin 1992), as well as avoidance of risk of exposure to predators including conspecifics during burrow-making (Henschel 1997). Males always returned to their existing burrow, but in one case the male walked on after returning to his burrow and dug a new burrow nearby. Of 36 burrows of adult males that I excavated and more than 100 more that I examined in the Namib dunes elsewhere than at Visnara, only three had been dug during the previous night, as indicated by a burrow length of less than 15 cm, scrape-marks around entrance closed with silk curtain instead of trapdoor. This indicates that males seldom establish new burrows.

Mating System.—Excursions need to be long to encounter females. Even when walking over 130 m, males crossed territories of only 1–2 adult females. Many females did not mate when males crossed their territory, but such females did sometimes mate on other encounters. This may indicate that females do

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Figure 2.—Movements of males illustrated on a 10 × 10 m gridded map of the study area at Visnara. The locations of some burrows of *L. arenicola* adults (closed circle = female, open triangles = male) are shown. The areas devoid of burrows in the upper middle and upper left are vegetated, the remainder bare sand. Lines depict movements of four males from the burrows labelled #. Bold arrows are the longest stretches on the return journey. (a) A typical 103-m long journey of the male #145 on 26 December 1986 is shown, with several turns when going outward and a direct return journey. (b) This general pattern is also evident for #221 on 23 February 1987, but in this case there was an 80 m long return path and the male missed his burrow by 4 m, then turned and made several loops before finding his burrow. (c) On 27 February 1987 males #45 and #173 wandered simultaneously. w: #173 moved towards #45 and the two males closely circled each other at the burrow of #45 with much drumming; x: #173 mated; y: #45 drummed and circled some 5 m from x. The two males crossed each other's tracks at x, possibly interrupting mating. z: The two males walked parallel 5–10 m apart and both drummed at short intervals, with #45 following this up by making loops several meters from the female. After that #173 returns to his burrow, and #45 makes a long excursion (total 314 m, not completely shown here) before returning home.

Table 3.—Mating frequency by males and females of three size classes, as indicated by trapdoor diameter and mass.

Trapdoor Diameter (mm)	Mass (g)	Males		Females	
		Observation -nights	Mating %	Observation -nights	Mating %
<21	<1.6	376	3.7	692	0.9
21–23	1.6–2.1	436	5.0	1029	1.3
>23	>2.1	348	7.8	1363	2.4

not mate throughout their reproductive cycle. Many females, however, did not mate at all, and this was particularly true for small females, perhaps because they are less fecund. In both sexes, a few individuals mated more often than others. The most successful individuals were of large to medium size. Successful males undertook excursions every 1–4 nights and could mate twice per excursion. Both sexes mate multiple times and individuals can mate several times with each other as well as with other individuals, i.e. the current study demonstrates that both sexes are promiscuous. Relationships between the sexes are likely to influence the home range of an adult male, and this therefore warrants further study in order to understand male movements.

Although males avoided direct encounters, wandering males did approach territories of other males and signaled by drumming. *Leucorchestris* males drummed in the vicinity of other males, even if the latter were inactive (at least had not left their burrows), and seldom drummed near females. By contrast, drumming appears to be an important courting signal in another sparassid, *Heteropoda venatoria* Thorell 1878 (Rovner 1980). Drumming by *L. arenicola* towards a male may cause a rival to withdraw or keep out of the way of the signaler and can perhaps interrupt mating, as suggested by two cases. Differences in male size (1.0–2.8 g) are likely to affect such male-male competition. Besides evidence that most drumming by *L. arenicola* appears to be an intrasexual signal, the above conclusions on male-male relationships are tentative and require verification.

Navigation.—The mechanism that males use for navigation is unknown. Such precise orientation over long distances suggests either highly developed path integration (using egocentric information), or orientation in the landscape (geocentric information). The two different sets of information could be coupled, as they are in ants (Wehner & Wehner 1990; Wehner et al. 1996). There is currently no evidence for path integration by *L. arenicola*, except perhaps the knowledge of direction and distance to a burrow, demonstrated by the change in behavior when a male passed his home burrow by mistake after a long or complex journey. If path integration is involved, the complex case of Namib dune sparassids warrants further study.
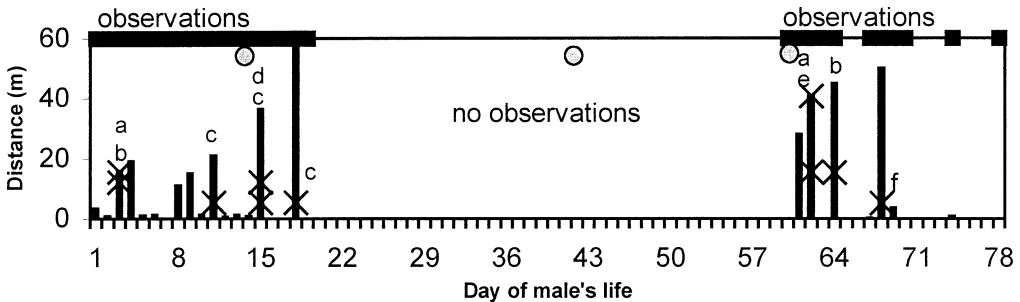

Figure 3.—Observations for 38 days during 78 days of adult life of marked male #82 from one burrow between 19 December 1986 and 6 March 1987. Days of observation are indicated at the top. Bars show the linear distance (m) that the male moved from his burrow in a night. 'X' indicates the distance of mating with six females a-f. Shaded circles represent new moon.
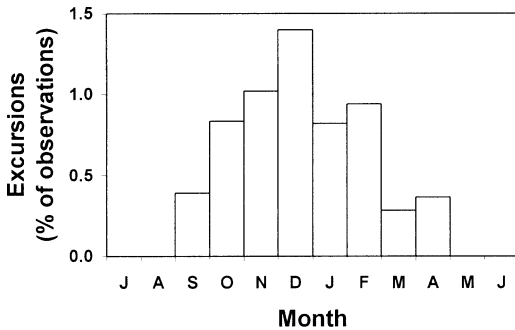
Figure 4.—Observations of male excursions in various months of the austral year, expressed as percent of observations of all spiders during each month (total $n = 21{,}771$).

For a nocturnal animal of this size, several senses could be important for orientation in the landscape. The eyes, albeit small, may be quite sensitive to light, but the spiders prefer dark to bright nights (Henschel 1990a), probably to avoid risk of predation from visually-hunting predators such as gerbils and nocturnal birds (e.g., owls). Olfaction is another possible sensory mechanism, as has been demonstrated for other sparassids (Rovner 1980; Rowell & Avilés 1995). Pompilid wasps can follow the tracks of *L. arenicola* (pers.obs.) and wheel spiders *Carparachne aureoflava* Lawrence 1966 (Henschel 1990b), suggesting that the spiders leave olfactory traces, perhaps in silken drag-lines (Schulz & Toft 1993). Drumming by *L. arenicola* males indicates that they can detect the territories of inactive males, perhaps by smell. Trichobothria enable spiders and scorpions to detect wind direction, facilitating anemotaxis (Linsenmair 1968; Barth et al. 1995). It is possible that *L. arenicola* makes use of the fairly predictable patterns of summer winds in the Namib (Tyson & Seely 1980).

Many psammophilous animals detect vibrations transmitted through sand over distances of centimeters (Brownell 2001) to meters (Narins et al. 1997). Sand is a particularly good conductor of compressional and Rayleigh waves originating from the movement of animals on or in sand (Brownell 1977). Vibrations enable small animals to detect moving insects (Brownell 1977, 2001; Narins et al. 1997; Enders et al. 1998) or wind-blown sand (Hanrahan & Kirchner 1994). Many spiders are well endowed with vibration sensors

(Barth 2001). *Leucorchestris arenicola* appear to be highly sensitive at detecting vibrations, e.g., directional interception of territorial intruders or prey over 1–3 m, apparent maneuvering of two drumming males around each other at distances of several meters. It is possible that detection of vibrations assists *L. arenicola* in navigation.

Elucidating the mechanisms of orientation and navigation of *L. arenicola* is a challenge for future studies. The sensory environment is quite different from that of other case studies. Further studies of the Dancing White Lady Spider could therefore make important contributions to the understanding of navigation on the whole, and could find applications such as broadening the scope of navigational robotics (Lambrinos et al. 1997; Wallander & Russell 2001).

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