The Biology of *Leucorchestris arenicola* (Araneae: Heteropodidae), a Burrowing Spider of the Namib Dunes

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The ecology, distribution, behaviour and life history of *Leucorchestris arenicola* Lawrence, 1962 (Araneae: Heteropodidae), a 2–5 g endemic spider of the central Namib Desert, were studied over a 20-month period. These spiders live in 33 ± 13 cm long silk-lined burrows, which are constructed in firm dune sand on dune bases and lower dune plinths. Foraging activity is inversely related to light intensity, wind speed and fog condensation. They capture prey on the surface about once a month and usually consume it in the burrow. Coleoptera form the bulk of the diet, followed by Lepidoptera and conspecific spiders. Small vertebrates are rarely eaten. Foraging activity, reproduction and development rate are seasonal, with a 4 to 5-month period of quiescence in winter. Females lay an average of 76 eggs per clutch and tend offspring for about 75 days. On average, nymphs moult every 85 days in summer and every 156 days in winter. Adulthood is reached in the 10th instar at an age of 2 years. Adult males are short-lived (1–2 months) and travel long distances (20–450 m) in pursuit of mating opportunities, while adult females are philopatric, long-lived (6–15 months) and produce up to three egg clutches in a breeding season. Territoriality and cannibalism of juveniles favour site fidelity and avoidance of neighbours at distances of about 4 m. Predation by gerbils and conspecific spiders could limit populations in a density-dependent manner. This spider appears to have a K-selected life history pattern, in which relatively constant annual food availability, variable risk of predation and climatic seasonality favour slow development, high longevity, small brood size, iteroparity and extended brood care.

INTRODUCTION

Desert sand dunes, such as are found in the Namib, are characterized by sparse vegetation, loose substrate, strong winds and a dry and thermally fluctuating surface climate (Robinson and Seely, 1980; Louw and Seely, 1982). Such desert climates do not favour aerial web-building spiders so that nocturnal wandering spiders predominate, which have specialized morphological and behavioural traits that enable them to burrow and hunt in and on sand (Main, 1957; Chew, 1961; Cloudsley-Thompson, 1983).

Spiders are an important but little studied component of the Namib dune fauna. Knowledge is limited to faunistic data and anecdotal descriptions of their biology (Lawrence, 1959, 1962, 1965a, b, 1966; Holm and Scholtz, 1980; Robinson and Seely, 1980; Wharton, 1980). Lawrence (1959) first noted the importance of large heteropodids in the Namib dunes and a discussion of distribution in different Namib dune habitats of some heteropodids was presented by Holm and Scholtz (1980).

One Namib heteropodid, the dancing white lady spider *Leucorchestris arenicola* Lawrence, 1962, is particularly well suited for ecological and physiological study owing to its large size, abundance, ease of handling and detectability in the field. The ability to track the movements of these spiders by their footprints on the smooth sand surface and to regularly inspect and recognize known individuals in their burrows without disturbing them provided a rare opportunity to investigate such aspects of their ecology as have seldom been recorded for desert spiders. These aspects include their spatial relationship to the environment, their foraging and reproductive behaviours

and, ultimately, their long-term life history strategies.

In the present paper, I present details on the biology of *L. arenicola,* including morphology, distribution, habitat use, burrow structure, foraging behaviour and predator-prey interactions, reproduction, development, population ecology, intraspecific and intraguild relationships, and mortality. Characteristics and environmental determinants of these aspects are compared with patterns exhibited by other wandering arachnids in deserts and in more mesic zones. With these data, I re-examine the hypothesis that biotic interactions may not be as important to many desert invertebrates as physical factors (Noy-Meir, 1973). Further details relating to diet, reproduction and population ecology of *L. arenicola* are being gathered for future presentation.

STUDY AREA AND METHODS

General study area

Leucorchestris arenicola were studied from October 1986 to June 1988 at 26 sites within the area 23–24° S, 14–16° E of the central Namib Desert. During a general survey, 143 *L. arenicola* were collected from burrows and 108 empty burrows were excavated at 15 sites. The habitat classification of Robinson and Seely (1980) was adopted.

Burrow and spider measurements

At all 26 sites, tracks left by active *L. arenicola* on the smooth sand surface, which were especially visible after sunrise, facilitated the discovery of burrows. Burrows located in this way were used for density estimates in some areas on
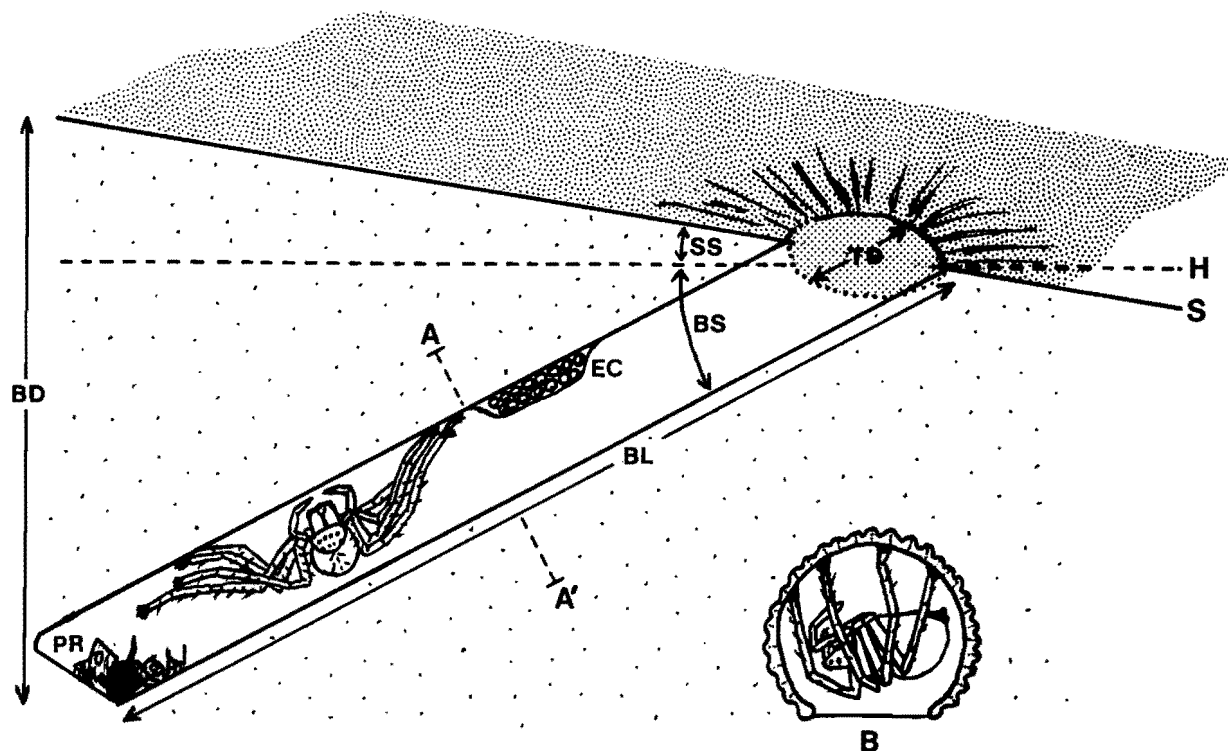
Fig. 1

Schematic representation of a transverse section through an occupied *Leucorchestris arenicola* burrow showing a female spider, her prey remains and egg cocoon in their typical position, and (B) a cross section at A-A'. S = sand surface; H = horizontal orientation; SS = surface slope; BS = burrow slope; TD = trapdoor diameter; EC = egg cocoon; BL = burrow length; BD = burrow depth; PR = prey remains.

6 m-wide line transects according to the method of Burnham, Anderson and Laake (1980).

The following measurements were made on excavated burrows (Fig. 1): slope (°; SS) of sand surface at burrow entrance, diameter of trapdoor (mm; TD), burrow circumference estimated as twice the measured width of the collapsed burrow (mm; BC), burrow slope (°; BS) for the first 30 cm of its length, burrow length (cm; BL) and vertical depth of burrow (cm; BD). Prey remains were collected from all burrows for identification by comparison with voucher specimens.

Spiders were captured from excavated burrows or in a specially designed trap (Henschel, *in press*). The age, sex and live mass (± 0,1 mg) were determined and the following measurements (± 0,1 mm) were taken: maximum width of carapace; prosoma (cephalothorax) length from the dorsal centre of the clypeus edge to the posterior end of the sternum ventrally; ventral width of opisthosoma (abdomen); dorsal length of opisthosoma; body length from clypeus to base of anal tubercle; and length of the sclerotized shaft of left femur I antero-laterally. Regression equations interrelating body dimensions were calculated and coefficients of determination obtained for their simplified formulas. For all mean values throughout this paper, ± one standard deviation is indicated.

Intensive Study Area

A fenced site of 0,75 ha (Visnara) was established on a flat stretch of interdune sand 1 km S of Gobabeb (23° 34' S, 15° 02' E) for an intensive study of reproduction, development and population ecology. The vegetation at Visnara consisted of a sparse covering of grasses, *Stipagrostis ciliata, S. gonatostachys* and *Centrapodium glaucum,* and a cucurbit, *Acanthosicyos horridus* (!Nara). On the northern side, this area was bordered by riparian vegetation: *Acacia erioloba, Euclea pseudebenus, Tamarix usneoides* and *Salvadora persica.* Meteorological conditions were monitored at the first order weather station at Gobabeb.

The herbivorous and detritivorous invertebrate fauna at Visnara comprised a diverse community of dune and riverine origin, dominated by tenebrionid, scarabid and curculionid beetles, moth larvae and adults, termites and ants. In addition to *L. arenicola,* the spider fauna consisted of a gnaphosid, *Asemesthes lineatus;* two eresids, *Seothyra* sp. and *Gandanomeno echinatus;* three salticids; one philodromid; and one dysderid. Other predators of possible significance to *L. arenicola* were geckos, *Palmatogecko rangei* and *Ptenopus* spp.; a legless lizard, *Typhlosaurus braini;* scorpions, *Opisthophthalmus flavescens* and *Parabuthus villosus;* a pompilid wasp, *Schistonyx aterrimus;* solifugids, *Metasolpuga picta, Prosolpuga schultzei, Solpugista bicolor* and *Unguiblossa cauduliger;* gerbils, *Gerbillurus paeba, G. tytonis* and *Desmodillus auricularis;* jackals, *Canis mesomelas;* mongooses, *Galerella sanguinea;* genets, *Genetta genetta;* owls,

Bubo africanus and *Tyto alba;* and various passerines, especially *Mirafra erythrochlamys, Cercomela familiaris* and *Picnonotus nigricans.*

Activity, life history and demography

During the course of intensive observations at Visnara from October 1986 to April 1987, all burrows of *L. arenicola* in a 0,5 ha area were marked with numbered flags placed 20 cm from the burrows. Spider activity was monitored by observations at night and by following tracks in the early morning, which provided detailed records of the spiders' activities on the sand surface. Burrow occupation status was ascertained by signs of activity at entrances. Data were collected for 79 nights during which 8836 observations were made of 312 burrows.

During further intensive studies from June 1987 to June 1988 at Visnara, activity data for *L. arenicola* were recorded as above for 7241 observations of 319 burrows on 122 nights in a 0,33 ha area. Nearly all individuals were captured and later recaptured after moulting (n = 309). Individuals were identified, measured, and marked using five colours of water-soluble fluorescent paint (Plaka) in various combinations. Paint was applied to the central dorsal surfaces of leg patellae, areas on the legs apparently without important sensory functions. Spiders from excavated burrows were released at the capture sites and protected in enclosures until they constructed new burrows. Trapped spiders were returned to their burrows. At approximately fortnightly intervals, optometrist's and dentist's mirrors were used to look into burrows to verify the identity and reproductive status of their occupants.

Burrows of reproducing females were examined at shorter intervals (usually < 7 days) to determine nymphal stages and their duration, litter size, development rate and duration of maternal care. After the nursery burrow was abandoned, it was excavated and all exuviae of nymphs were counted.

The minimum duration of each post-nursery instar was determined from the interval between two observed moults (n = 85). Half the interval between sightings was added to the minimum period to estimate the duration of instars. The total number of instars was calculated from successions of recorded nymphal stages of individuals that were first marked at a very young age or finally recaptured as subadults or adults.

RESULTS AND DISCUSSION

Taxonomy

The first Namib dune heteropodid described was an immature female *Leucorchestris arenicola* Lawrence, 1962, from the vicinity of Gobabeb. Later collecting yielded an adult female from the type locality (Lawrence, 1966). An adult male *L. kochi* Lawrence, 1965, described from the same locality, is probably a male *L. arenicola. Leucorchestris kochi* is the only male in the genus sharing the same distribution as *L. arenicola* and has been recorded mating with *L. arenicola* on 34 occasions. This species and another possible junior synonym, *L. sabulosa* Lawrence, 1966, will be included in a taxonomic revision of the genus (Croeser, personal communication). Voucher specimens from the present study will be kept at the State Museum, Windhoek. Throughout this paper the family name Heteropodidae is used in preference to Sparassidae (Croeser, 1986).

Table 1
Equations that can be used to estimate carapace width (mm) and mass (mg) of *Leucorchestris arenicola* using functions of body or burrow dimensions (mm).

	r^2	n
Carapace Width		
1,01 × Femur I	0,95	292
0,59 × Trapdoor diameter ^{0,93}	0,85	289
0,22 × Burrow circumference ^{0,85}	0,79	301
Mass		
Body length × Carapace width ×		
(Abdomen width + length)/3	0,98	58
0,052 × (Carapace width + Body length) ^{3}	0,96	58
0,229 × Body length ^{2,878}	0,95	58
1,495 × Carapace width ^{3,107}	0,90	58
0,393 × Trapdoor diameter ^{2,741}	0,73	312

Identification of sexes

Live adults, subadults and some pre-subadults could be sexed in the field on the basis of epigyna and pedipalps. These individuals of known sex were used to define other sex-related attributes. Of all other external characteristics examined (eye arrangement, leg spination, pedipalp structure, tibial claws, dimensions of prosoma, opisthosoma and legs), only leg spination was found to be a useful guide to sex. A median dorsal spine on the tibia was found on most (5–8) legs of adult and subadult males. This spine was rarely found on legs of adult and subadult females and then only on a maximum of 4 legs. The presence of this feature on five or more legs thus provided a guide for sexing juvenile males older than nymph stage III (carapace width > 7 mm). The sex of younger individuals could not be determined.

Morphology

Desert spiders are often larger than close congeners in less arid habitats, and as a result have low surface-to-volume ratios (Remmert, 1981; Cloudsley-Thompson, 1983). *Leucorchestris arenicola* is large, up to 5,0 g ($\bar{X}$ = 1,7 ± 0,9 g) and 32 mm ($\bar{X}$ = 20,9 ± 4,8 mm) body length; adult females are usually heavier than adult males (2,6 ± 0,9 g vs. 2,0 ± 0,5 g; t = 5,43; $d.f.$ = 120; P < 0,05). Legs of males grow allometrically during the moult to adulthood, attaining a final standing leg-span of 10–14 cm (6–9 cm for adult females).

Hagstrum (1971) found that carapace width corresponded closely with instar stages of 13 spider species. As carapace width correlated with mass, he concluded that it can be used as a field guide to size and development stages of many species. In *L. arenicola*, carapace width was 2,1–14,0 mm ($\bar{X}$ = 9,4 ± 2,1 mm; n = 386). Where it could not be measured without injuring a spider, it was estimated for nymphs and adult females from the length of the sclerotized shaft of left femur I (Table 1). A simple linear relationship could not be established for adult males because of the allometry described above (r^2 = 0,45; n = 36).

Live mass was difficult to measure accurately in the field, but could be estimated on the basis of body length, carapace
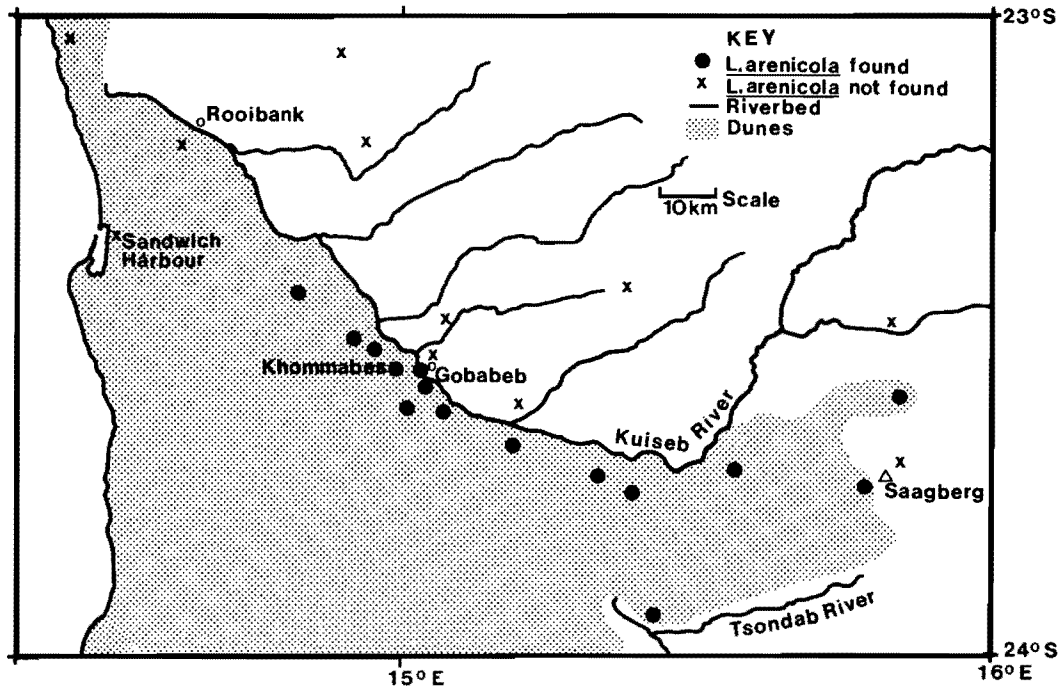
Fig. 2

Distribution of *Leucorchestris arenicola* (*n* = 452) in the central Namib Desert.

width, abdomen width and abdomen length (Table 1).

Distribution and habitat

Leucorchestris arenicola appears to be confined to the southern Namib dune sea and adjacent sandy areas (Fig. 2). It lives in the central, warm, foggy zone and the warm, inland zone where high daily fluctuations of temperature and humidity occur (Besler, 1972; Lancaster, Lancaster and Seely, 1984). It is rare or absent in the cold, foggy, coastal, crescentic dunes that extend approximately 20 km inland from the coast. This may be due to an unsuitable climate dominated by strong winds, or a scarcity of adequate habitat. Their distribution is limited in the east by the edge of the dunes and in the north by gravel plains abutting the Kuiseb River. The southern limit is unknown. *Leucorchestris sabulosa*, which may be synonymous with *L. arenicola*, is the southernmost *Leucorchestris* captured at 27° 30' S, 15° 45' E (Lawrence, 1966).

Relatively open stretches of firm, gently sloping dune sand with sparse vegetation were favoured by *L. arenicola*. Burrows were usually found within 1 to 10 m of plants (96 %). The abundance of *L. arenicola* decreased up dune slopes: 91,0 % were collected on dune bases and interdune sand accumulations surrounding vegetation mounds, 7,4 % on the lower plinth, 1,4 % on the upper plinth and only 0,2 % on the slipface. These proportions differed from the proportion of surface area covered by these habitats (Fig. 3), indicating selection (X^2 = 73,6; d.f. = 4; P < 0,05) and contradicting Holm and Scholtz's (1980) conclusion that the Heteropodidae (*n* = 16 individuals of three species) did not appear to have strong

preferences for different dune habitats. During the present survey, other heteropodid species were found in habitat adjacent to that dominated by *L. arenicola*: *Carparachne aureoflava* and *C. alba* on the upper dune plinth, slipface and dune crest; *Orchestrella browni* and *O. longipes* on the interdune gravel plains.

Burrow structure

Leucorchestris arenicola lives in straight, silk-lined burrows dug at an angle into sand (Fig. 1; Table 2). Spiders excavate burrows by removing sand from the base of a circular depression as described by Lawrence (1965a). The leg coxae, and curled pedipalps bearing stiff interlocking setae, are used to push loose sand sideways up to the entrance. Sand is dispersed from the entrance by flinging it sideways with the brush-like tarsal scopulae. The lower end of the depression is secured by lifting and interweaving loose sand with adhesive silk from the spinnerets and pressing the sand- silk mixture into the substratum. This forms a nodule of silk and sand embedded in the surrounding sand. The burrow end is secured with 25–35 adjacent nodules in an arc of about 330° (Fig. 1). A 3–10 mm wide floor remains free of silk along which sand is pushed to the entrance. The spider lengthens the burrow by 3 to 6 mm before securing another arc of silk nodules; additional arcs may be added at any time. The entrance is closed with a reinforced curtain of silk and sand. The rim is later severed to form a thin (*c.* 1 mm) circular trapdoor, flush with the sand surface (Fig. 1). A moderate wind suffices to obscure signs of the burrow.
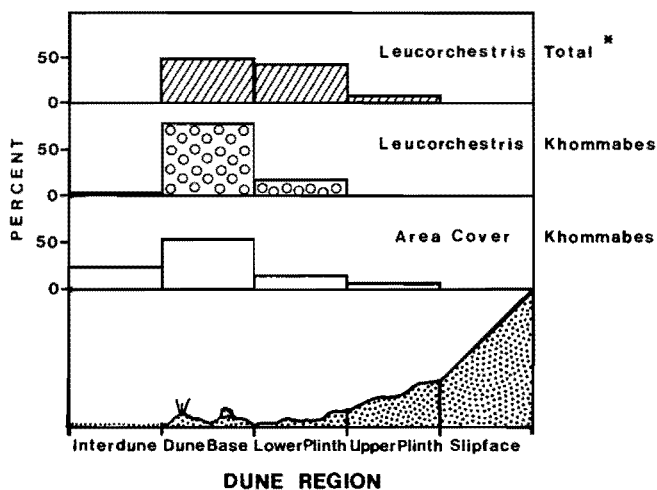
Fig. 3

Occurrence of *Leucorchestris arenicola* in various dune habitats in the central Namib Desert. The relative sizes of areas of each habitat at the 27 ha site at Khommabes are indicated.

* = sample of spiders (*n* = 94) from all regions besides Khommabes (*n* = 33) and Visnara (*n* = 309), which were analysed separately.

Spiders position themselves anywhere along the length of the burrow in an upside-down posture facing the side of the burrow (Fig. 1). The feet are in contact with the roof and appear to be sensitive to vibrations on the sand surface.

Trapdoor diameter and burrow circumference varied with body size and could be used to estimate the occupant's size (Table 1). Burrows were usually constructed in firm sand of a gentle slope (Table 2). They rarely occurred on steeper slopes associated with vegetation mounds or slipfaces. Burrow slope was 28 ± 3° from the horizontal, slightly less than the angle of repose (33°), the maximum slope at which dry sand can be swept upwards. If surface slopes were > 15°, some burrows (*n* = 7) were at angles of < 20°. Burrows with slopes of 33–40° were sometimes (*n* = 6) built in moist sand.

Leucorchestris arenicola often failed to make burrows if kept in darkness in the laboratory, but burrowed when exposed to light, suggesting that light may elicit burrowing behaviour. Similar responses have been reported for other nocturnal desert arachnids (Polis, Myers and Quinlan, 1986).

The use of burrows for protection from extreme desert climates is well known for arachnids (Polis *et al.*, 1986). In the case of *L. arenicola*, the vertical depth of the burrow end (Fig. 1), usually approximately 25 cm, provided a suitable microclimate, which differed considerably from that at the surface (Lancaster *et al.*, 1984; Seely and Mitchell, 1987). Burrow depth did not relate to surface slope (*r* = 0,06), but was primarily a function of burrow length (depth = length × 0,55; r^2 = 0,81; *n* = 210).

Of 631 burrows monitored at Visnara, 5,3 % were temporary shelters used for one day only. All others were occupied for a mean of 68 ± 53 days up to a maximum of 460 days. With one exception, re-use of an existing, vacant burrow by a second individual was not observed.

Table 2
Measurements of 560 *Leucorchestris arenicola* burrows from 15 sites in the central Namib Desert (Fig. 1).

Measurement	Unit	Mean ± S.D.	n	Range
Surface slope (SS)	°	8,7 ± 6,8	358	0–33
Burrow slope (BS)	°	28,4 ± 3,4	314	14–40
Trapdoor diameter (TD)	mm	19,6 ± 4,1	433	7–30
Burrow circumference (BC)	mm	80,6 ± 18,0	415	26–48
Burrow length (BL)	cm	33,4 ± 13,4	437	7–125
Burrow depth (BD)	cm	23,5 ± 7,0	216	4–48

Foraging behaviour and resources

Similar to large desert spiders elsewhere (Cloudsley-Thompson, 1983), Namib heteropodids are predominantly nocturnal. Diurnal activity in *L. arenicola* was observed in April 1987 during termite eruptions following rainfall of 14 mm. It was apparent from the behaviour of captured spiders which were released in the heat of the day, that diurnal conditions were stressful; moreover, their light colour against the reddish-brown sand rendered them conspicuous to predators. When released during the day, spiders commenced burrow construction immediately and sealed the entrance within 15 minutes when the burrow was about 10 cm long. Spiders sought plant cover when the sand was too hot for burrowing. Prey was usually not captured by day, but diurnally active prey species were sometimes caught at dusk.

Other limitations to activity appeared to be cold nights (ambient temperature < 15 °C), bright moonlight (≥ 3/4), strong wind (> 5 m/s) and condensing fog, which made the trapdoors clammy. Reduced activity during strong wind could be due to sand abrasion or the high noise level of moving sand particles which would mask prey and predator vibrations.

The eight eyes of *L. arenicola* are relatively small and probably are not important in locating prey. It most likely detects potential prey through the vibrations the latter makes when moving on the sand surface. Such surface vibrations are transmitted over long distances (Reichmann, personal communication) and are probably detected by sensitive mechano-receptors (tactile hairs, trichobothria and slit sensilla; Foelix, 1982; Barth, 1982) on the legs of *L. arenicola*, which would enable it to orientate accurately towards the prey, as is the case in the Central American ctenid *Cupiennius salei* (Hergenröder and Barth, 1983).

Two methods of foraging were observed in *L. arenicola*. They generally rushed out of their burrows to intercept approaching prey at distances of up to 3 m. On occasion, spiders hunted actively on the sand surface within 3 m of their burrow. At Visnara, only 47 % of the population ventured from their burrows on a given night. Of these, 75 % remained within 1 m and 92 % within 3 m of the burrow. Nearly all of those that travelled further were adult males apparently in search of mates, or, on rare occasions, any other spider that immigrated.

An attack on prey involved a short jump, re-orientation, seizing the victim with the front legs and pedipalps, and biting immediately. The fangs penetrated exoskeletons of tenebrionid and scarabid beetles ventrally, contrary to earlier

reports that they could not do so (Lawrence, 1962, 1965*b*). Captured prey was held up with chelicerae and dragged about until it ceased to move. The spider then usually dragged the prey into its burrow where it was consumed. Very small prey, such as termites, were eaten on the surface. Silk was not used during the capture and handling of prey. Carrion was not taken.

Although the fangs injected venom (observed when biting into plastic), its potency appeared to be low. For example, a Namib tenebrionid beetle which was bitten, initially became paralysed, but recovered completely three days later. A bite by *L. arenicola* merely caused local irritation in a person. Another large heteropodid, *Palystes natalius,* has very low toxicity to larger vertebrates (Newlands and Martindale, 1981), even though it occasionally captures small vertebrates (Warren, 1923).

A distinctive record of prey capture in the form of intermingled tracks of predator and prey was left on the sand near the burrow; drag marks often led away from the capture site to the spider's burrow. Although small prey items (< 0,2 g), such as termites, did not leave distinctive traces in the sand, most other prey could be identified on the basis of their tracks. Prey capture was recorded 186 times on 122 nights at Visnara during 1987 and 1988 and the estimated annual predation rate was 1670 prey captures/ha.

In summer, September to March, the average interval between prey captures for a spider was 31 nights and on average 3,2 % of the spiders caught prey on a given night, with a maximum of 14 % in December. In winter, the capture rate dropped to 1,5 % per night and most *L. arenicola* became quiescent, some even torpid, possibly in response to adverse climate as is the case in other desert spiders (Riechert and Łuczak, 1982). The ability of spiders to vary their resting metabolic rate, which is usually very low (Greenstone and Bennett, 1980), may obviate the need for emigration during periods of temporary food scarcity (Anderson, 1974).

The soft parts of prey were chewed into tight balls, whereas harder cuticle, such as elytra or legs, often remained intact. Prey remains were stored at the base of the burrow. Analysis of 377 prey items collected from 145 burrows (Table 3) showed that the diet reflected prey availability. Approximately 80 % of their prey consisted of Coleoptera, half of which were tenebrionid beetles, thus confirming previous incidental observations (Holm, 1970; Seely, 1985). The curculionid *Leptostethus waltoni* was the most frequently captured single species (14 %). Lepidopteran larvae and adults represented 8 % of the items and were also important in terms of biomass. Termites were sometimes captured and eaten on the surface, as evidenced by spider tracks leading to *Hodotermes mosambicus* exit mounds where chewed termite remains were seen, but their importance in the diet appeared to be relatively low.

Chewed remains of *L. arenicola* were found in 21 of 214 burrows and cannibalism was confirmed by direct observations. Conspecifics formed 4 % of the prey items, but could be more important in terms of biomass. Occasionally, remains of other unidentified spider species, dune scorpions (*Opisthophthalmus flavescens*) and solifugids (*Metasolpuga picta* and *Prosolpuga schultzei*) were found (*n* = 12). Some of these were bigger than their captors.

The remains of small geckos, *Palmatogecko rangei,* were found only three times and represented about 0,3 % of the

Table 3
Diet of *Leucorchestris arenicola* determined from the contents of 145 burrows from 3 sites, which contained 377 prey remains. Unidentified parts (*n* = 24) were omitted.

Taxa			Number of species	Percent items
Insecta	Coleoptera	Tenebrionidae	30	48
		Curculionidae	4	22
		Scarabaeidae	3	8
		Other	3	1
	Lepidoptera		> 1	8
	Hymenoptera		1	3
	Orthoptera		5	2
	Other		3	1
Arachnida	Araneae	*L. arenicola*	1	4
	Araneae		> 2	
	Scorpionida		1	3
	Solifugae		3	
Reptilia	Squamata	Gekkonidae	1	0,3
Total			> 58	

spiders' diet items (Table 3). Two of these were excavated after evidence from tracks and drag marks suggested that geckos had been captured. Based on a set of tracks, Lawrence (1959, 1962, 1965*b*, 1966) noted that *L. arenicola* preyed on *P. rangei*, but did not mention observing drag marks from the attack site to the spider's burrow. This original observation has been construed as evidence that all major genera of Namib dune heteropodids frequently prey on geckos (Lamoral, 1971; McCormick and Polis, 1982; Newlands, 1987).

Although vertebrates may be minor diet items of arachnid predators that have low toxicity venom, McCormick and Polis (1982) found that their impact on certain vertebrates that are smaller than them can be substantial. The size of the Namib palmatogeckos taken by *L. arenicola* could not be established, but judging by skeleton fragments they were probably lighter than the spider.

Leucorchestris arenicola must have water to survive. In the laboratory, they died within three months if kept with food but without water. Water was imbibed directly when it was offered on wet cotton wool. Possible sources of water in the field include metabolic water and free water content of prey and condensed fog or dew water, which might be obtained by drinking from drenched trapdoors in a manner similar to that observed in the laboratory with wet cotton wool.

Reproduction and development

Reproduction was strongly seasonal in the population studied at Visnara. Adult females were present throughout the year, forming 10 to 30 % of the population. In contrast, adult males were absent in winter (May to August of 1987 and 1988). Many males moulted to adulthood in September, reached peak abundance (8–12 % of the total population) in October and declined in abundance until May (< 5 %). The frequency of mating and the number and size of egg clutches and litters all peaked in December. No mating or egg clutches were observed from May to August.

Mature *L. arenicola* males frequently (on average every 4th

Table 4
Litter size of juvenile stages of *Leucorchestris arenicola* at Visnara determined by counting live young seen within burrows, or by counting excavated exuviae.

	Live[*]			Exuviae		
	Mean ± S.D.	Range	n	Mean ± S.D.	Range	n
Eggs			24	75,8 ± 59,0[**]	25–161	4
Larvae	26,3 ± 19,6	1–74	24	41,5 ± 43,9[**]	5–161	15
Nymphs I	13,0 ± 7,2	1–23	15	45,1 ± 31,5	1–95	18
Nymphs II	8,8 ± 9,2	1–35	24	8,0 ± 9,2	2–25	6

[*] Live juveniles were difficult to count accurately until the female abandoned them at nymphal stage II.
[**] This was probably underestimated, as the exuviae of larvae were fragile and difficult to count.

Table 5
Duration (days) of various developmental stages of *Leucorchestris arenicola* determined by inspecting nursery burrows at intervals of a few days, or by recapturing marked post-nursery spiders at Visnara. The period for immatures represents the interval between observed moults; for adults it represents longevity.

Instar	Development stage	Mean	Range	n
Nursery				
1	Egg and pre-larva	15 ± 3	9–19	13
2	Larva	13 ± 3	10–16	8
3	Nymphal stage I	23 ± 10	12–38	10
4	Nymphal stage II	33 ± 9	22–45	14
	Female with nymphal stage II	14 ± 9	4–34	13
	Female with brood	75 ± 19	59–115	8
	Between broods	44 ± 21	14–77	12
Post-nursery				
4	Nymphal stage II	52		1
5	Nymphal stage III	84 ± 43	38–128	4
6	Nymphal stage IV	98 ± 4	95–101	2
7	Nymphal stage V	95 ± 66	38–278	14
8	Nymphal stage VI	114 ± 61	32–249	19
9	Nymphal stage VII	118 ± 42	37–204	31
10	Adult male	47 ± 29	17–98	22
10	Adult female	130 ± 79	31–463	47

night; $n = 233$) wandered far from their own burrows ($\overline{X} = 38 \pm 71$ m; maximum = 450 m). Silk drag-lines were often observed along their tracks. They usually returned to their burrows on direct routes, navigating at night over more than 100 m without using the drag-lines. Drag-lines were only occasionally retraced over short stretches, especially when the spiders were disturbed. It is likely that cues other than those associated with the drag-line enable *L. arenicola* to find their burrows, but the method of orientation is not known. It has been shown that other wandering spiders use landmark and kinesthetic orientation, which depend on the spiders' previous motility patterns (Seyfarth and Barth, 1972; Barth, 1982; Foelix, 1982).

On outgoing trips, males often changed direction and stopped every 0,5 m to 5 m to drum the ground with all eight legs in succession. This left an imprint of the outline of the legspan, pedipalps, leg coxae and abdomen. Drumming behaviour may inhibit attack by territorial residents and attract mates. This behaviour appears similar to leg drumming by adult male *Cupiennius salei,* a ctenid wandering spider (Rovner and Barth, 1981).

Males of *L. arenicola* mated on 14 % of their wanderings ($n = 233$) usually with different females. Mating occurred 1,6 ± 1,0 m ($n = 33$) from a female's burrow, leaving a series of long scrape marks on the surface. Females mated several times in a fortnight. In four observed cases, females laid eggs 31 to 35 days after the last mating. Four other females mated while caring for young. One female that overwintered as an adult, laid viable eggs early in the breeding season before the appearance of adult males and therefore must have stored sperm through the winter.

Each egg clutch was laid in two layers and was enclosed in a flat silk pouch, or cocoon, which was about 5 mm thick. The cocoon was spun against the burrow roof at a vertical depth of about 12 cm (Fig. 1). Average egg clutch size was 76 and incubation period 15 days (Tables 4 & 5). The mass of a single egg was approximately 4 mg. After producing a cocoon, a female's mass dropped by about 15 %, or 350–700 mg. The female guarded the eggs. When disturbed, she ate the eggs and abandoned the burrow.

The female ate the empty cocoon after emergence of the

larvae (Tables 4 & 5; terminology for juveniles according to Vachon, 1957, in Foelix, 1982). The larvae remained in the maternal burrow, or nursery, and began to feed upon moulting into nymph stage I, as evidenced by their growth. Approximately 14 days after nymph stage II was reached (Tables 4 & 5), the female abandoned the burrow and usually established a new territory. The new burrows were 0,4 to 16,0 m (6,3 ± 5,1 m; $n = 17$) away from the old ones.

While in the nursery, adult females hunted frequently and carried prey into the burrow. This food source may have been utilized by the nymphs since the total mass of litters increased about five-fold during nymphal stages I to II, but no data are available to support this notion. Some social or periodic-social spiders exchange food by trophallaxis or indirectly via the prey (Foelix, 1982; Lubin, 1982). This has not been studied in asocial species such as *L. arenicola* that have extended brood care. Attempts in the laboratory to raise two litters of orphaned *Leucorchestris* stage I nymphs, using crushed insects as food, failed.

On one occasion, an adult male from a burrow 22 m away provided stage II nymphs with prey after the female had left the nursery. He caught a large moth, dragged it 1 m into the nursery and returned to his burrow. The nymphs were feeding on the moth upon excavation. All other observations indicated that only the female provided food to her offspring.

The reproductive cycle was estimated at about 120 days, based on observed durations of maternal care and periods between successive broods (Table 5). In one year 58 adult females produced 44 litters, or 0,76 litters/female/annum. Some females moved in from or to adjacent areas, giving rise to a slight underestimate in their reproductive rates. In one breeding season 45 % of the adult females produced no offspring, 40 % produced one litter, 10 % two and 5 % three

Table 6
Growth of *Leucorchestris arenicola* determined from recaptures at Visnara.

Stage	Carapace width		Body length		Mass		n
	Mean ± S.D. mm	Range	Mean ± S.D. mm	Range	Mean ± S.D. mg	Range	
Egg & pre-larva			2,5		4		161
Larva			2,5		4		1
Nymph I	2,8	2,1–3,5	6,8	5,9–7,6	55	27–83	2
Nymph II	4,4 ± 0,3	4,0–4,9	10,2 ± 0,9	9,2–12,5	169 ± 57	105–309	10
Nymph III	5,8 ± 0,6	5,0–6,9	13,0 ± 1,7	11,3–17,6	361 ± 172	173–846	16
Nymph IV	7,2	6,4–8,1	16,4	12,9–20,0	801	355–1247	2
Nymph V	7,6 ± 0,6	6,4–8,8	17,1 ± 2,3	13,0–22,4	824 ± 308	380–1603	14
Nymph VI	8,9 ± 1,0	6,9–11,0	20,0 ± 2,7	14,6–25,3	1371 ± 585	500–2544	27
Nymph VII	10,0 ± 1,0	7,1–13,2	22,4 ± 2,8	16,7–28,1	1904 ± 666	731–3535	62
Adult male	11,4 ± 0,9	9,6–13,3	22,4 ± 1,9	18,9–27,1	1938 ± 448	999–2749	30
Adult female	11,1 ± 1,0	7,3–14,0	24,8 ± 3,1	14,8–31,8	2570 ± 901	623–4981	71

litters. One female produced 5 litters in two breeding seasons.

Kessler (1971) noted that the size of eggs of female wolf spiders remains constant, but egg clutch size varies as a function of food supply. In *L. arenicola*, it appears that both egg clutch size and the interval between clutches may vary, while some females fail to produce any clutches in a breeding season. Differences in egg sizes were not detected.

Within a month of reaching nymphal stage II, the number of spiderlings in a litter decreased to about 9 (Table 4). No dried-up carcasses of nymphs and no evidence of early dispersal or interspecific predation were found, thus suggesting that nymphs cannibalized siblings. However, cannibalism cannot account solely for the 42-fold increase in the mass of juveniles while in the nursery. Sibling cannibalism is not uncommon among communal spiderlings of non-social species (Turnbull, 1973; Polis, 1981). Resorption or consumption of eggs by a female as well as sibling cannibalism can be considered bet-hedging by desert arachnids and would enable rapid population response to favourable conditions (Polis, 1988).

At approximately 70 days and 169 g (Table 6), remaining stage II nymphs constructed a small exit next to the trapdoor of the nursery and built individual burrows close by. They moulted to nymphal stage III about 52 days later. Each subsequent moult occurred at a mean interval of 110 ± 54 days (32–278 days; n = 85). The moulting interval did not differ significantly between nymphal stages (Table 5; t < 0,94), nor with size or magnitude of size change (carapace width; r < 0,16), but varied seasonally (see below).

Between successive nymphal stages, carapace width increased by 1,1 ± 0,7 mm, body length by 2,3 ± 1,9 mm and mass by 144 ± 44 % of initial mass (n = 55; Table 6). This was similar for both sexes. Measurements taken one day before and after ecdysis from nymph stage IV to V indicated that carapace width increased by about 20 % at the expense of a 20 % decreases in abdomen length and width. For nymphs of stages III to VII, the average rate of mass gain was 7,4 ± 10,8 mg/day (n = 53). However, some spiders (28 %) lost mass between instars, although they usually increased in carapace width. Normally this occurred if they moulted without having fed. Sometimes a large decrease in mass (> 0,5 g) was caused by the loss of a limb or of haemolymph due to injury.

Adult males were no heavier than subadults (Table 6), and they did not appear to feed in the field although they sometimes accepted food in the laboratory. The size of adults, especially females, varied considerably: by a factor of two for carapace width and body length, and by a factor of eight for mass (Table 6). Their mass could increase rapidly by as much as 50 % after eating a large prey item, or drop by 15 % when they laid eggs. Similarly, adult size of some other spiders varies by a factor of two for carapace width and by a factor of 12 for mass (Jocqué, 1981; Vollrath, 1987). Because of this, it is impossible to estimate the age or nymphal stage from size for *L. arenicola* beyond nymphal stage III.

Pronounced seasonality in activity was evident. According to the classification of Schaefer (1977, in Foelix, 1982), *L. arenicola* can be classified as a eurychronous species that overwinters in various stages of development. All *L. arenicola* instars lasted significantly longer in winter, between April and August, than in summer, September to March (156 ± 42 vs. 85 ± 41 days; t = 8,99; d.f. = 59; P < 0,05). In winter, the rate of prey capture dropped to less than half the summer rate (see above). Adult males were absent and females were reproductively inactive. Some spiders were in a torpid condition. It is not unusual for spiders to reduce activity and prolong development in winter (Almquist, 1969).

Successive recaptures indicated that *L. arenicola* of both sexes have a total of 10 instars. No evidence was found that this may vary as it does in some other spiders (Vollrath, 1987). From pre-larva and larva, *L. arenicola* went through seven nymphal stages, reaching adulthood at 24 months of age. This age was calculated by adding the nursery and the post-nursery nymph II periods (70 and 52 days respectively) to two winter and three summer instar periods (156 and 94 days each respectively) to give a total of 716 days. Adults were not observed to moult. Upon reaching adulthood, males survived for only 47 ± 29 days. In contrast, adult females survived for at least 130 ± 79 days (maximum 463). Discounting mortality by predation, the life expectancy of females was 30–40 months.

Table 7
Density of *Leucorchestris arenicola* burrows in the central Namib Desert dunes determined by various methods:
1 = counts along 6 m wide transects across suitable habitat; 2 = monitor all burrows of unmarked spiders for 6 months;
3 = monitor all burrows of marked spiders for 12 months.

Site	Census method	Census period	Sample days	Area (ha)	Number counted	Population number/ha
Khommabes Dune Base	1	May 87	1	1,00	16	32
Khommabes Dune Plinth	1	May 87	1	1,56	7	9
Far East Dune	1	Nov 86	1	1,50	23	31
Noctivaga	1	Oct 86–Jan 87	2	1,00	10	20
Visnara I	2	Oct 86–Apr 87	73	0,50	120 ± 34	239 (64–302)
Visnara II	3	Jun 87–Jun 88	122	0,33	59 ± 14	176 (75–243)

Old females sometimes (n = 4) displayed aberrant behaviour. Becoming very aggressive, they abandoned territories and moved burrows frequently. They eventually failed to construct proper burrows (burrow length < 5 cm), which became too hot in the day; these were abandoned in favour of shelter amongst plants. At night, these females moved into other territories, where they wounded or killed the residents if challenged. Eventually, they died of heat stress in shallow burrows, or were wounded or captured by predators.

In general, the phenology of *L. arenicola* appears to be similar to that of a Sonoran Desert wolf spider, *Lycosa carolinensis,* which has a period of quiescence in winter and is most active and has the largest proportions of adults in mid-summer. Females of this wolf spider produce two litters per season, development is relatively slow, and sexual maturity is achieved only in the third year of life (Shook, 1978).

Population ecology

Within a suitable habitat, densities of *L. arenicola* varied spatially and temporally. In addition to seasonal fluctuations of mature males and of reproducing females, a major factor influencing population density appeared to be predation (see below). The estimated abundances ranged from 9/ha in winter on a dune plinth at Khommabes, 5 km from Visnara, to a peak of 302/ha in summer at Visnara (Table 7); the wet biomass ranged from 15–513 g/ha.

Between June 1987 and June 1988, 58 adult females and 22 adult males were resident in 0,33 ha at Visnara. Another 12 males wandered through the area. During that year, 44 litters were produced with approximately 9 stage II nymphs entering the population from each litter (Table 4). The potential recruitment rate was thus 1188/ha/annum, or 6,8/female/annum. Assuming that emigration balanced immigration for all instars and that recruitment and development rates were similar in previous generations, the probability of post-nursery nymphs surviving to adulthood was calculated as 0,134 (egg to adult: 0,016).

Visnara had a peak of 81 burrows (0,025/m²) on 8 January 1988. These were occupied by 24 adult females (4 of which had a total of 55 nymphs), 1 adult male, 14 subadult females, 6 subadult males and 33 immature spiders, with a total mass of 111 g. The population was distributed unevenly: 52 % of the burrows occurred in 24 % of the area (0,05/m²) with a maxi-

mum of 0,11 burrows/m² in one patch of 0,01 ha.

Females and nymphs of other species of wandering spiders have relatively small home ranges (Turnbull, 1973). In *L. arenicola,* an area described by a 1–3 m radius around a burrow was usually defended against intrusion by smaller conspecifics. The presence and size of the defended area was confirmed by releasing spiders in small enclosures close to known burrows and monitoring the response of the resident. According to Kaufmann's (1983) definition, *L. arenicola* is territorial: at a given time an individual has priority of access to resources in a fixed area within its home range. Territory boundaries were not clearly delimited by natural boundaries or marks and occupation was advertised physically.

Energy-based territoriality is widespread in desert spider families (Cloudsley-Thompson, 1983). Territorial agelenids (*Agelenopsis aperta*) adjust the cost of physical defence according to resource quality at a site (Riechert, 1979). Although the contest situation favours the territory owner, its intensity may serve as a cue of site quality to the intruder. More energy is required to gain or maintain territories in regions where spider densities are high than where they are low. Territory sites should thus be selected optimally (Riechert, 1979). In this respect, the uneven distribution of *L. arenicola* burrows in an area warrants further investigation.

The average nearest-neighbour distances of 997 different pairs of *L. arenicola* burrows measured in one year was 3,90 ± 2,10 m. Close neighbours (< 2 m apart) remained in their relative positions for shorter periods than more distant pairs. Distant neighbours (91 %) with burrows > 2 m apart remained in position for 20 ± 28 days, 14 % of them for > 1 month. In contrast, closer neighbours remained in position for only 9 ± 16 days (t = 3,01; *d.f.* = 159; P < 0,05), with only 6 % lasting > 1 month, which is indicative of instability among close pairs.

Juvenile and adult sex ratio was uneven. Owing to their short natural life expectancy upon reaching adulthood (7 weeks), the number of adult males in an area was usually low. During the breeding season at Visnara, there were usually only one or two adult males to 19–32 adult females, except in early October 1987, when there was a peak of 8 adult males to 19 adult females (1 : 2,4). In the course of a year, the proportion of resident males to females was 1 : 2,6 for adults (n = 80) and 1 : 1,6 for nymphs V to VII (n = 105). These ratios differed

significantly from parity ($X^2 > 6,5$; $d.f. = 1$; $P < 0,01$), but not from each other ($X^2 = 2,8$; $d.f. = 1$; $P > 0,05$).

Cannibalism

Cannibalism was observed among marked individuals at Visnara on 14 occasions. Additional remains of conspecifics were found in 21 of 214 excavated burrows (see above). Although conspecifics formed a minor proportion (4 %) of the total diet of post-nursery spiders, cannibalism was an important mortality factor, contributing 19,4 % of the known causes of death.

All post-nursery cannibals, but one, were subadult or adult females larger than their victims (difference in carapace width = 1,5 ± 1,2 mm; $n = 14$). Victims were captured at distances of 5,4 ± 4,2 m from their own burrows by cannibals that were 1,4 ± 1,9 m from their burrows. In 13 cases, smaller spiders survived the attack of larger ones by retreating into their burrows 0,2 ± 0,4 m away. When interactions with close nearest-neighbours (mean distance = 2,3 ± 2,3 m) were repeated, smaller individuals were prevented from foraging and relocated their burrows ($n = 13$).

Hallander (1970) described similar behaviour in two species of wolf spider, both in the field and in the laboratory. Conspecific lycosids made up 20 % of their diet. In particular, adult females caught nymphs and adult males, and spiderling siblings ate each other. These lycosids, like L. arenicola, countered cannibalism by having very distinctive courtship signals and by juveniles that remain concealed beyond the reach of adults.

In a review of the occurrence of intraspecific predation among animals, Polis (1981) found that generally the more cannibalistic individuals were large, female and hungry. Starvation increased the likelihood of choosing conspecifics as prey and the vulnerability of juveniles. Cannibalism increased as other resources decreased, forming a type of reserve for times of stress (Hallander, 1970; Polis, 1988). Furthermore, the rate of cannibalism was density- dependent and increased when nearest neighbours were close (Polis, 1981). This makes cannibalism a potentially sensitive regulator of population densities.

Other causes of mortality

Cannibalism was one of eight identified causes of death of L. arenicola that were observed in 72 incidents at Visnara (Fig. 4). Four old females died after exposure to adverse climate or injury. Non-feeding adult males became inactive and died after several periods of intense activity in pursuit of mating opportunities. Some spiders, unable to free their legs, died during ecdysis. This was recorded four times in the field and often in the laboratory. Once, a coleopteran larva killed and partially consumed a L. arenicola during ecdysis in the field.

The most important predators of L. arenicola were gerbils, Gerbillurus paeba, G. tytonis and Desmodillus auricularis, accounting for 64 % of known deaths. The density of gerbils at Visnara was determined in February 1988 by Dednam (1988) over a 1 ha area containing about 207 L. arenicola burrows. Using a mark-recapture technique for 8 trapping nights, the gerbil density was calculated as 66/ha, with 47 ± 7,3 G. paeba, 13 ± 5,1 G. tytonis and 6 ± 1,3 D. au-
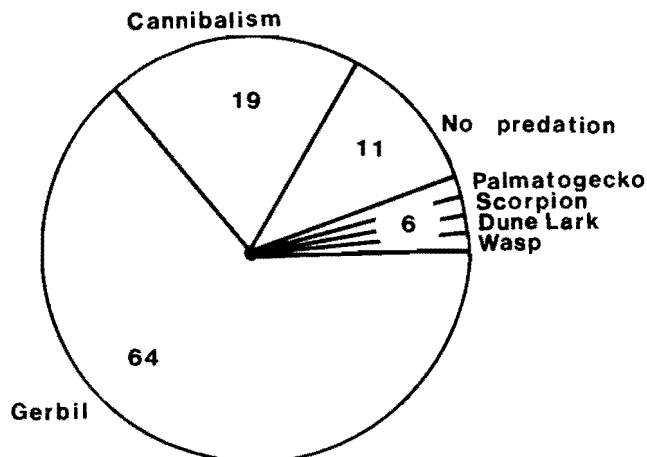

Fig. 4

Cause of death of Leucorchestris arenicola in 72 incidents at Visnara. Percentages are indicated.

ricularis. This density of gerbils was high compared with a maximum of 18,2 gerbils/ha found elsewhere in the dunes (Boyer, 1988). Namib dune gerbils are omnivores with 53–59 % of their diet, determined from stomach contents, consisting of invertebrate matter, including spiders (Boyer, 1988).

Between June 1987 and June 1988 at Visnara, 253 attacks by gerbils on spiders on the surface or in their burrow entrances were recorded. In one extreme night, 51 % of the burrows were disturbed and 18 % of the post-nursery population was killed. Attacks were concentrated during January and June when the spider population abruptly decreased by 27 % and 51 % respectively. Many attacks destroyed the burrow entrances but did not harm the spiders. Spiders were often attacked again when they were repairing the damage. Those attempting to build new burrows were sometimes captured by gerbils or by conspecifics.

Infrequently, pompilid wasps opened L. arenicola trapdoors and entered burrows. Usually they were evicted by the spider. Once, a wasp did not emerge from a burrow in 15 minutes and the unharmed wasp was excavated together with a live immobilized spider (wasp body length 13,6 mm; spider nymph stage III, body length 11,9 mm, mass 240 mg). This behaviour resembles the pattern of hunting, paralysis and oviposition by Anoplius spp. pompilid wasps on Geolycosa wolf spiders (Gwynne, 1979) and several other wasp-spider pairs (Grout and Brothers, 1982). It is not known whether Namib pompilids specialize in hunting only one family of spiders, but it is likely that the finding and excavation of heteropodid burrows requires particular skills. Gess and Gess (1980) suggest that one South African pompilid species is a specialist hunter of Heteropodidae, although other species capture several other spider families as well (Gess and Gess, 1974).

In the present study, two L. arenicola were caught on the surface at dawn by a dune lark, Mirafra erythrochlamys. The scorpion Opisthophthalmus flavescens was recorded once as predator and twice as prey, an example of cross-predation (McCormick and Polis, 1982). Similarly, a large Palmatogecko rangei once caught an L. arenicola on the surface and three

small geckos were consumed by spiders.

Cross-predation has previously been recorded for several arachnids, when they prey on juveniles of a species, but themselves fall prey to larger individuals of the same species (McCormick and Polis, 1982). Besides the acquisition of food, the benefits of cross-predation include reductions in future risks of predation for the predator or its offspring.

Leucorchestris arenicola display several anti-predator behaviour patterns. Spiders at the bottom of their burrows appear to be safe from most predators. Risk-sensitive foraging, as seen by Polis (1988) for the scorpion *Paruroctonus mesaensis,* may enable *L. arenicola* to avoid the time and region where their predators forage. The suggestion that *L. arenicola* has the capability to flee by cartwheeling (Newlands, 1987) in the manner of *Carparachne aureoflava* (Henschel, 1990) was not confirmed. In a series of trials, no *L. arenicola* of any size showed an ability to wheel on a slope.

Many spiders of sandy deserts, like *L. arenicola,* are very pale and lack distinct markings, which may render them less visible to predators at night (Cloudsley-Thompson, 1983). When approached by potential predators on the surface, *L. arenicola* scuttled for their burrows, sheltered in a nearby plant, or froze motionless if shelter was remote, as in the case of wandering males. When confronted closely, they showed overt aggression, jumping forwards, then standing threateningly with body up, some legs raised and spines erect. Approach and threat posture alternated to give the appearance of a dance (Lawrence, 1962). Upon contact with the foe, the spider vigorously embraced it with the legs and chelicerae and then tried to flee.

Aggression can account for dominance of temporal zones by one arachnid species over others in an area (Polis and McCormick, 1986*a*). Polis and McCormick (1986*b*) found no evidence of exploitation competition among sympatric desert arachnids of a guild, but suggested that intraguild predation directly influenced their behaviour, distribution and abundance. Similar circumstances may apply to *L. arenicola* in the Namib Desert.

GENERAL DISCUSSION

The biomass of Namib spiders appears to be at least an order of magnitude lower than that of wandering spiders in other temperate regions (Chew, 1961; Turnbull, 1973). In the present study, most of the surveyed areas were selected for their high densities of *L. arenicola.* On visits to other sparsely vegetated firm dune slopes in the central Namib that were not surveyed systematically, searches on calm mornings usually revealed the presence of *L. arenicola* burrows. The general impression was gained that within suitable habitat, *L. arenicola* densities were approximately 5–10/ha and that this species appears to be the dominant spider in terms of biomass (8–17 g/ha) although small gnaphosids, *Asemesthes* spp. (< 0,1 g), and an eresid, *Seothyra* sp. (< 0,3 g) appear to be locally more abundant (Henschel, unpublished data). Accepting Seely and Louw's (1980) estimate of 55 g/ha biomass of all invertebrate carnivores on a dune plinth during a dry year, *L. arenicola* would constitute 15–30 % of the carnivore biomass.

The *L. arenicola* population at Visnara underwent five and three-fold density fluctuations in two successive years. Based on measurements of minimum territory size, the theoretical maximum population density is 1000 spiders/ha, a density that was actually achieved only in small patches of 0,01 ha. Variable predation pressure, which reached catastrophic proportions in some patches, produced uneven density patterns of spiders in suitable habitat with abundant prey.

It has been proposed that populations of many other desert organisms are not affected by biotic interactions, but that climate plays a fundamental role in producing autecological effects (Noy-Meir, 1973). For example, although Namib tenebrionids have many predators, these do not appear to limit their populations, but densities probably depend on environmental conditions (Seely, 1985). In contrast, *L. arenicola* and many other desert arachnids appear to be affected to a large degree by biotic interactions, especially intra- and inter-specific predation (Polis and McCormick, 1986*b*).

Several common tenebrionid beetles, prey species of *L. arenicola,* foraged on detritus and reproduced throughout the year (Seely, 1983, 1989). Soil temperatures at a depth of 20–30 cm, where *L. arenicola* reside, fluctuate little on a daily basis, but vary seasonally, dropping from approximately 30 °C in summer to approximately 20 °C in winter (Lancaster *et al.,* 1984). Cooler soil temperatures during winter may decrease the metabolic rate of *L. arenicola,* suppressing activity and eliciting torpor in some cases. Climate, rather than prey availability, could thus explain seasonal patterns in the foraging behaviour, reproduction and development rate of this chthonic nocturnal spider.

Wandering spiders that live in burrows are generally longer-lived in deserts (Cloudsley-Thompson, 1983) than similar spiders in more mesic regions (Foelix, 1982). In a few known cases, the longevity of large aranaeomorph spiders was found to be more than two years in deserts, whereas elsewhere such spiders usually have annual life-cycles. This may be related to food availability, which appears to be less predictable on a daily basis in a desert than it is in wetter temperate and tropical regions.

Unpredictable environmental extremes may affect food availability and offspring survival of many desert invertebrates (Louw and Seely, 1982). Under such circumstances, a pattern of bet-hedging (Murphy, 1968) is often adopted, indicated by the long life of females, iteroparity and small broods as seen in many Namib tenebrionids (Seely, 1983). *Leucorchestris arenicola* is iteroparous and produces relatively small egg clutches compared with semelparous spiders, for example many orb-weavers (Foelix, 1982). Although reproductive effort of *L. arenicola* females in the form of brood care is high (62 % of reproductive cycle) in contrast to some other Namib invertebrates (Seely, 1983), the reproduction of *L. arenicola* is consistent with a pattern of bet-hedging. This may enable a rapid population response in the form of increased survival of offspring if conditions should suddenly improve, such as after rare events of rainfall (Seely and Louw, 1980).

It is concluded that the phenology of *L. arenicola* closely fits a K-selected life history strategy (Pianka, 1970). On an annual basis, this spider has a fairly predictable supply of food, but its foraging activity and spatial organization are influenced by the risk of predation, whereas its metabolism and development

rate appear to be subject to climatic seasonality. Under these conditions, *L. arenicola* grows and develops slowly, has a high

longevity, produces relatively small clutches of eggs, is iteroparous and has an extended period of brood care.

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