Does territorial behaviour in the desert-living spider *Leucorchestris arenicola* Lawrence (Araneae: Sparassidae) affect its spatial distribution?

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Summary

The endemic sparassid spider *Leucorchestris arenicola* Lawrence builds silk-lined burrows in low-lying sections of dunes in the Namib Desert. Individuals defend certain areas around the burrow against conspecifics. The hypothesis was examined whether social spacing through territorial behaviour creates regular spacing patterns. A population of *L. arenicola* was monitored for four months during the reproductive season, when all inhabited burrows inside a 3,300 m² area were recorded. Spatial patterns were analysed in terms of their degree of randomness or aggregation. The observed patterns between burrows did not fit a regular distribution, but early in the season distribution was random, followed by aggregated distribution at distances greater than 3 m, and later reverting to random again. This aggregation is explained in terms of habitat characteristics and population structure.

Introduction

The sparassid *Leucorchestris arenicola* Lawrence, 1962 is an endemic species that builds silk-lined burrows in low-lying sections of sand dunes in the Namib Desert. Spiders only leave their burrows to capture prey, mate or defend their territories. Wandering males walk for distances up to 400 m away from their burrows in search of females (Henschel, 2002). Henschel (1990) described this psammophilous spider as territorial, based on a definition formulated by Kaufman (1983): "at a given time an individual has priority of access to resources in a fixed area within its territory".

Territorial animals defend an area around a retreat for certain resources, including food, nest sites or mating possibilities (Cloudsley-Thompson, 1996). Strong intraspecific competition for space usually influences spacing (Stamps, 1990). Pielou (1960) suggested that these conditions lead to a regular spatial pattern. Regular spacing is known for a variety of territorial spiders, including Lycosidae (Fernandez-Montraveta *et al.*, 1991; Marshall, 1997; Moya-Larano *et al.*, 2002; Riechert, 1981), Agelenidae (Riechert, 1978) and some orb-weaving species (Hoffmaster, 1985).

Wise (1993) pointed out that a regular distribution is not a valid criterion to describe territoriality in a species, mainly because site choice could reflect distribution of favourable habitat conditions more than being

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a consequence of intraspecific interactions. Nevertheless, various authors cite a regular spacing pattern as a consequence of territoriality in spiders, mainly resulting from social spacing (Marshall, 1996; Moya-Larano *et al.*, 2002; Riechert, 1981). Marshall (1996) observed such a regular spacing pattern for the territorial lycosid *Geolycosa xera archboldi* McCrone, 1963. Certain areas around the burrow were defended through agonistic behaviour of larger spiders against smaller sized neighbours. A regular spacing pattern has also been reported for a second territorial lycosid species (Moya-Larano *et al.*, 1996). Riechert (1978) found a regular distribution in each of eight web-building *Agelenopsis aperta* (Gertsch, 1943) populations in North America and interpreted this to be the result of social spacing. These authors used the constancy of the mean nearest neighbour distance to indicate regularity.

Henschel (1990) reported aggregation for *L. arenicola* using grid data, rather than completely mapped data. The present study follows up on this work and evaluates whether the territorial behaviour in *L. arenicola* results in a regular spacing pattern.

Material and methods

The Gobabeb Training & Research Centre is situated in the Namib-Naukluft Park, along the ephemeral Kuiseb River. The centre is located at the intersection of three different ecosystems, the Kuiseb riverbed, the northern gravel plains and the southern Namib sand sea. The mid-section of the Namib Erg is characterised by longitudinal dunes, which are separated by approximately 2 km-wide valleys (Hüser *et al.*, 2001). These valleys include habitats with a high density of *L. arenicola* and are characterised by sparse vegetation, with plant coverage increasing close to the riverbed. The study was conducted within a 3,300 m² fenced area (Visnara) divided into 33 grid squares of 10 × 10 m each, bordering the riverbed approximately 1 km west of the Gobabeb Centre (23°33′49″S, 15°02′13″E; map datum: WGS 84).

For 131 days, between 1 October 2001 and 18 February 2002, the entire fenced area was visually searched for spider burrows, discernible from burrow-covering lids and spider tracks. This search was carried out every morning, except between 27 December and 5 January, and each survey took approximately 3 h. A total of 261 inhabited burrows were counted over this period, some being new burrows of spiders that had relocated. For each burrow, the coordinates in the grid, the diameter of the lid covering the burrow, and the status (development stage and sex) of the inhabiting spider was recorded on the date when burrow was first noted. In order to determine the status of the spiders, burrows with a lid diameter larger than 20 mm were examined fortnightly using a small handheld mirror reflecting sunlight into the burrow. The development stage and sex were determined by either counting the spines on femur I (three for a male, two for a female), or looking for the presence of the female epigyne. Spiders in burrows with lids smaller than 20 mm in diameter

	October	November	December	January
Abundance overall	44 ± 3^a	57 ± 8^b	79 ± 8^c	75 ± 3^c
Abundance of adults	15 ± 1^a	20 ± 2^b	23 ± 2^b	15 ± 1^a
Abundance of immatures	29 ± 2^a	36 ± 7^b	56 ± 6^c	60 ± 3^c
Sex ratio (F:M)	2.4 ± 0.5^b	2.5 ± 0.4^b	3.4 ± 0.5^c	1.8 ± 0.2^a
Dev. stage ratio (I:A)	1.9 ± 0.1^a	1.8 ± 0.3^a	2.5 ± 0.3^b	3.9 ± 0.4^c
Estimated territory size (m²)	12.1	12.0	10.2	11.0
L-function	random	aggregated	aggregated	random

Table 1:   Overview of population measures (mean ± SD) and spatial pattern. Letters indicate significant differences ($p<0.05$, one way ANOVA, Tukey's HSD for post hoc comparison). Abbreviations: A=adult, F=female, I=immature, M=male. L-function for distances from 3–7 m, estimated territory size for the 17th of each month.

were recorded as immatures of unknown sex. Henschel (1990) showed a strong correlation between lid diameter and prosoma width and body mass. All undetermined spiders in burrows with a lid diameter larger than 20 mm were excavated and their status determined after 18 February 2002. Using a combination of these methods, only 11 spiders could not be ascribed to immature or adult development stage, and in only six cases the sex of an adult spider could not be resolved. An initial 12-day survey period before 13 October was used to determine the number of burrows at the beginning of the study. Data collected between 13 October and 18 January were analysed in this study.

Spatial patterns were analysed using complete maps of the distribution of burrows on the 17th of each of the four observation months (October, November, December and January). Pfeiffer (1996) points out that quadrat sampling techniques aggregate information into area type data and might therefore lead to a loss of information. Ripley's K-function (Ripley, 1981) can be used to test randomness based on a homogeneous Poisson distribution, by examining the proportion of the total possible pairs of events in Euclidean space whose pair members are within a specified distance of each other (Dixon, 2002). It examines the spatial pattern at many distances and is a popular approach for completely mapped data (Dixon, 2001). To remove scale dependency and to stabilise variation the K-function

was transformed to the L-function for graphical display. Spatial analysis statistics were computed with the software Programita (Wiegand & Moloney, 2004).

Density maps show the burrow sites and estimated territories of all spiders on the 17th of each observation month. According to Marshall (1996) the shape of a territory should be circular in the absence of micro-habitat structure. Half of the mean nearest neighbour distance was used to estimate the average radius of each territory. The software CONT-DEN by J. A. Byers was used to calculate density maps and distances. Statistics were calculated using Statistica 6.0 (StatSoft Inc., Tulsa), and measures of spread are given as the standard deviation unless otherwise stated.

Results

Population structure

During 88 observation mornings an average of 63 ± 15 spiders inhabited the 3,300 m² area. The density in December and January was significantly higher than in October and November (one way ANOVA; $F_{1,87}=227.6$; $p<0.01$). The density of immatures increased with time (regression analysis, $r^2=0.493$); adults maintained a relatively constant density ($r^2=0.028$). The average number of spiders inside the 3,300 m² area increased from 44 ± 3 individuals in
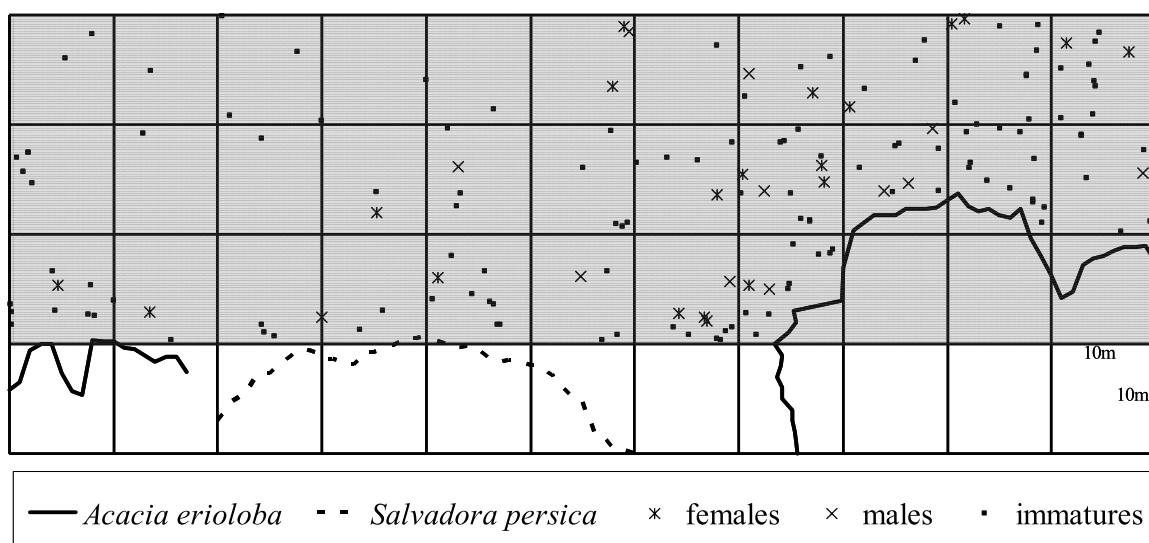

Fig. 1:   Map of the positions of all male, female and immature burrows of *Leucorchestris arenicola* marked between 13 October 2001 and 18 January 2002 inside the 3,300 m² area (shaded). Vegetation borders as recorded on 16 January.

October to 79 ± 8 individuals in December (Table 1). Over the four study months adult densities were between 0.004 and 0.008 ind.m^{-2}, while immatures had a mean density of 0.015 ind.m^{-2}, ranging from 0.007 to 0.022 ind.m^{-2}.

The observed female to male ratio was relatively constant, being 2.4:1 in October and 2.5:1 in November. The number of females increased significantly in December, resulting in 3.4 females per male, but dropped later to 1.8 females per male in January (Table 1). The majority of the population consisted of immatures. The ratio of immatures to adults increased significantly from October and November to December and again in January (Table 1). In October and November the proportion of adults was high, but decreased later with increasing numbers of immature individuals. The number of immatures peaked in late December and January, comprising 71–79% of all individuals.

Individuals were significantly more abundant in grid squares bordered by vegetation (Fig. 1; Mann–Whitney U-test; $Z=2.945$; $p<0.01$). Between 13 October and 18 January 7.8 ± 3.8 individuals inhabited each square with adjacent vegetation ($n=12$), whereas grid squares further away from vegetation ($n=18$) were inhabited by
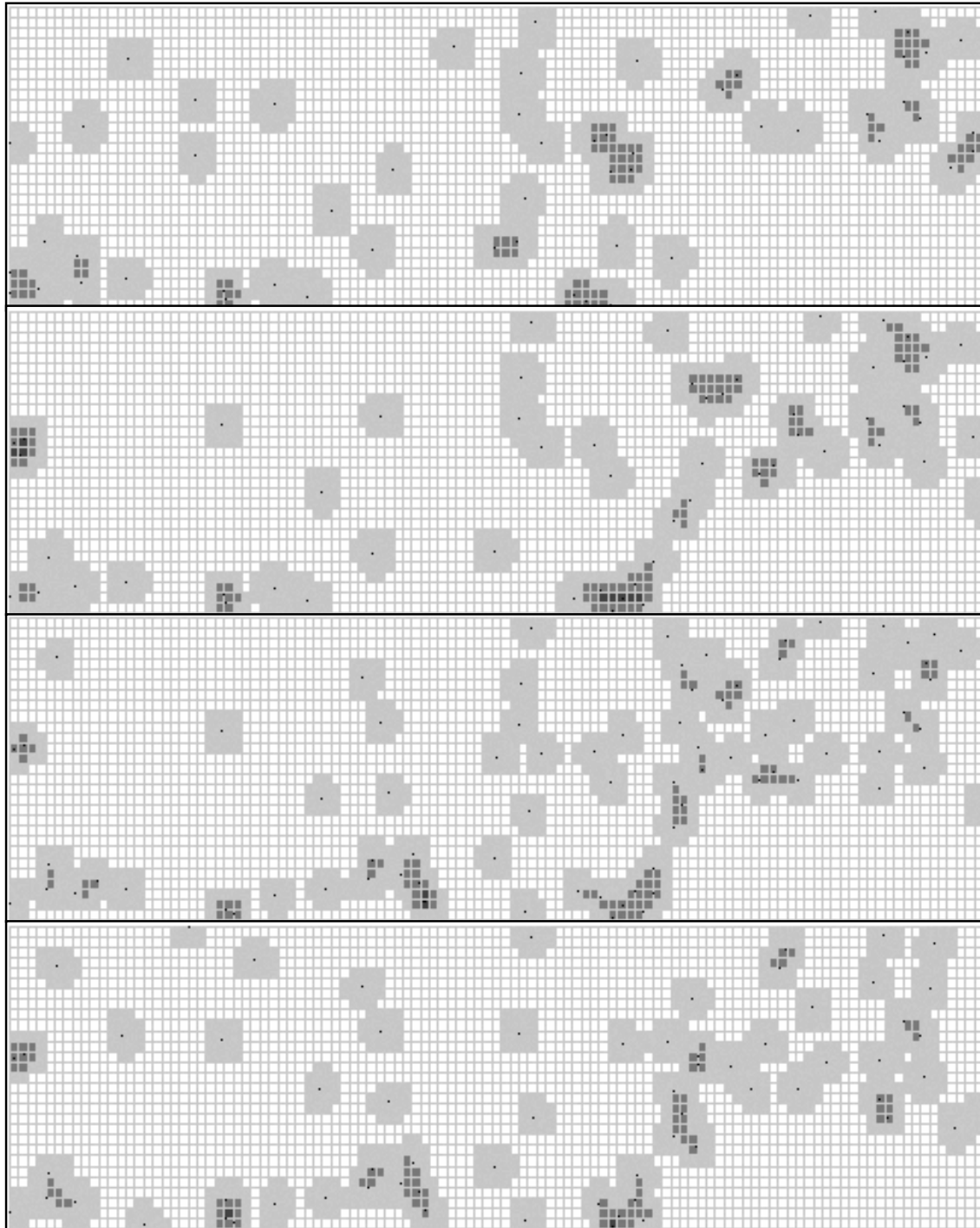

Fig. 2: Maps showing burrow sites and estimated territories of *Leucorchestris arenicola*. **a** 17 October; **b** 17 November; **c** 17 December; **d** 17 January. Shading indicates territories, assuming circular territories with the average radius being half of the mean nearest neighbour distance (one square represents 1 m²). Number of territories and territory overlap shown as: ☐=0, ▢=1, ▨=2, ▩=3.

3.4 ± 2.6 individuals. Individuals avoided areas covered by shrubs and trees, and no burrows were found in these squares (*n*=3).

The density maps show the estimated surface coverage of each spider's territory on the 17th of each month (Fig. 2a–d). The mean area of individual territories decreased from 12.1 m² on 17 October to 10.2 m² on 17 December and 11.0 m² on 17 January (Table 1). The overlap of territories decreased from 1.8 m² per territory on 17 October and 1.9 m² on 17 November to 1.1 m² on 17 December and 1.3 m² on 17 January.

Spatial pattern

There was no significant deviation of the L-function from complete spatial randomness (CSR) on 17 October (Fig. 3a). The L-function was within the 95% confidence limits of the simulated Poisson distribution up to distances of 10 m. Similar results were obtained for the separate datasets for immatures and adults (Figs. 4a & 5a). The November data mostly deviated from randomness for distances beyond 2.0 m (Fig. 3b); the data extend above the upper limits for a Poisson distribution, suggesting a significant aggregation up to 8 m distance. As shown in Fig. 4b, the development of this pattern is a result of increased aggregation among immature spiders, as the L-function for this dataset crosses the confidence limits at smaller distances and does not return to CSR for distances up to 10 m. Adults did not have significantly more or fewer adult neighbours than expected under CSR for any distance or dates (Fig. 5a–d). The L-function for the whole population for December (Fig. 3c) was comparable to that for November (Fig. 3b), deviating significantly from CSR for all distances greater than 2 m. Immature and adult burrows (Figs. 4c & 5c) were closer to each other than expected under randomness, as the immature dataset alone does not explain the observed overall aggregation. In November the deviation of immatures from CSR was highest at burrow distances of approximately 10 m, whereas in December it was highest at 6 m, suggesting a maximum cluster radius of this size. The spiders were again randomly distributed in January, with no range of distances for the overall or for the separate immature or adult data lying outside the simulated Poisson distribution limits (Figs. 3d, 4d & 5d).

Discussion

According to Papke *et al.* (2001), agonistic behaviour serves to maintain a widely or regularly dispersed population. The observed *L. arenicola* population did not show such a regular dispersion during any of the observation dates. This is surprising given the fact that *L. arenicola* displays defensive behaviour against intruders within a radius of at least 3 m around its burrow (Henschel, 1990).

Aggregation has been shown for *L. arenicola* during two months with high immature abundance (Fig. 3b & c). In November and December significantly more immature burrows were found within distances up to

8 m than expected under CSR. Clustering or aggregation of immature spiders is known from studies by Marshall (1999) and Riechert (1978) and is usually interpreted as a consequence of low aggression levels between immatures. Leaving the maternal burrow and beginning surface activity introduces a mortality risk, which increases with the time taken to search for a burrow site. Therefore, immatures need to construct a shelter quickly in order to avoid predators and climatic extremes during the daytime. Because of the limited range of cursorial dispersal, clustering is observed during periods when the level of spiderling dispersal from the maternal burrow is high. According to Henschel (1990), the first egg clutches are produced in September, reaching a peak in December. Approximately 70 days after egg sac production, stage 2 nymphs leave the maternal burrow to construct their own burrow. Spiderlings begin dispersing in November, with an increasing dispersal rate later in
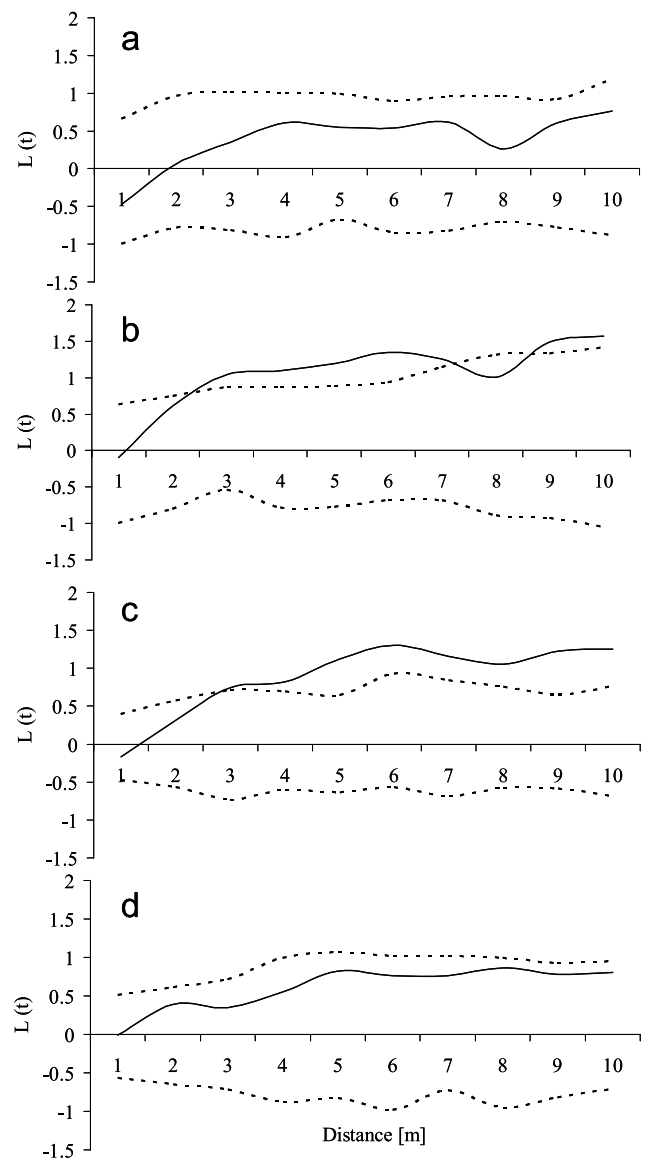

Fig. 3: L-function comparing patterns of all burrow locations with complete spatial randomness (CSR). **a** 17 October; **b** 17 November; **c** 17 December; **d** 17 January. Observed L-function (solid line), expected L-function for CSR (zero line), 95% confidence limits (dashed lines) shown for distances between points up to 10 m.

the study, as shown by an increasing number of immature burrows (Table 1). The separate analysis of immature burrow locations showed that distances between immatures are smaller than expected under the assumption of CSR. This deviation from randomness is highest in the months with high abundance of both adults and immatures, suggesting the effects are not related only to the burrow choice of immatures.

Marshall (1997) could not support Wise's (1993) argument that spatial patterns might reflect the distribution of favourable habitat conditions. Marshall reported that habitat features were correlated poorly with burrow density in a desert-living lycosid. The only criterion for burrow site choice was bare sand surface, a preference also shown by the burrow-constructing sparassid *Cebrennus villosus* (Jézéquel & Junqua, 1966) in the northern Sahara (Birkhofer & Moldrzyk, 2003). We have shown in the present study that the distance from vegetation has a significant effect on burrow site choice, with decreasing densities resulting from increasing distance (Fig. 1).

In conclusion, dispersal and site choice behaviour result in the observed aggregated pattern. As no regularity was observed in *L. arenicola* it is not valid to assume that regular spatial patterns are standard features of territorial invertebrates. Environmental factors and population structure affect spatial patterns, and their influence is capable of reducing any effect of territorial behaviour on spacing.
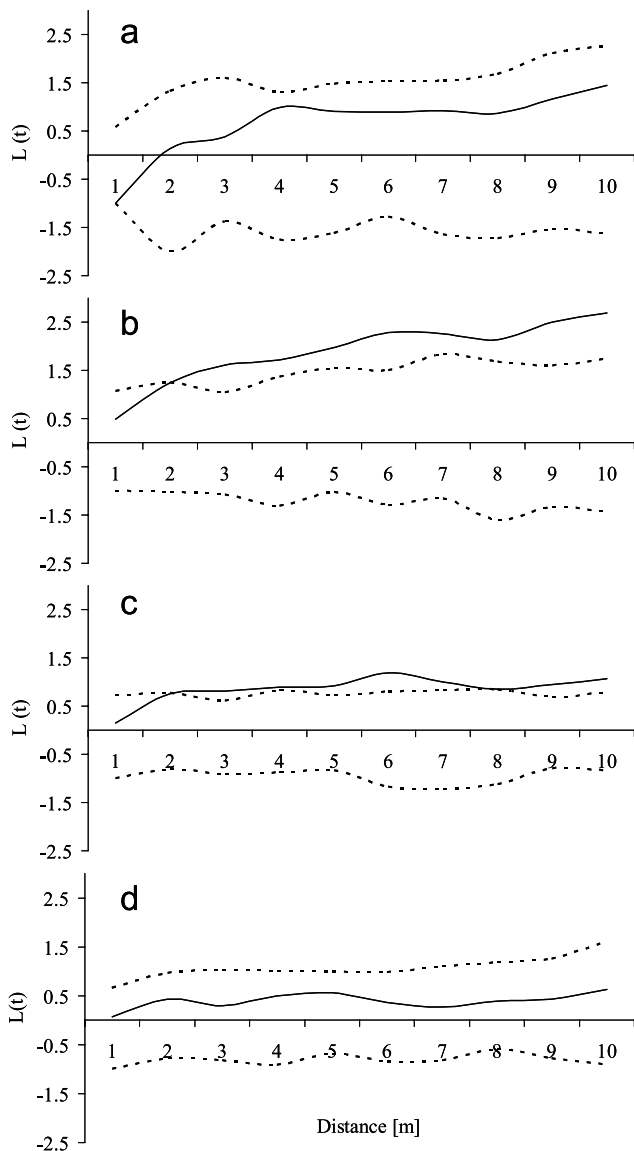
Acknowledgements

Fig. 4: L-function comparing patterns of immature burrow locations with complete spatial randomness (CSR). **a** 17 October; **b** 17 November; **c** 17 December; **d** 17 January. Observed L-function (solid line), expected L-function for CSR (zero line), 95% confidence limits (dashed lines) shown for distances between points up to 10 m.
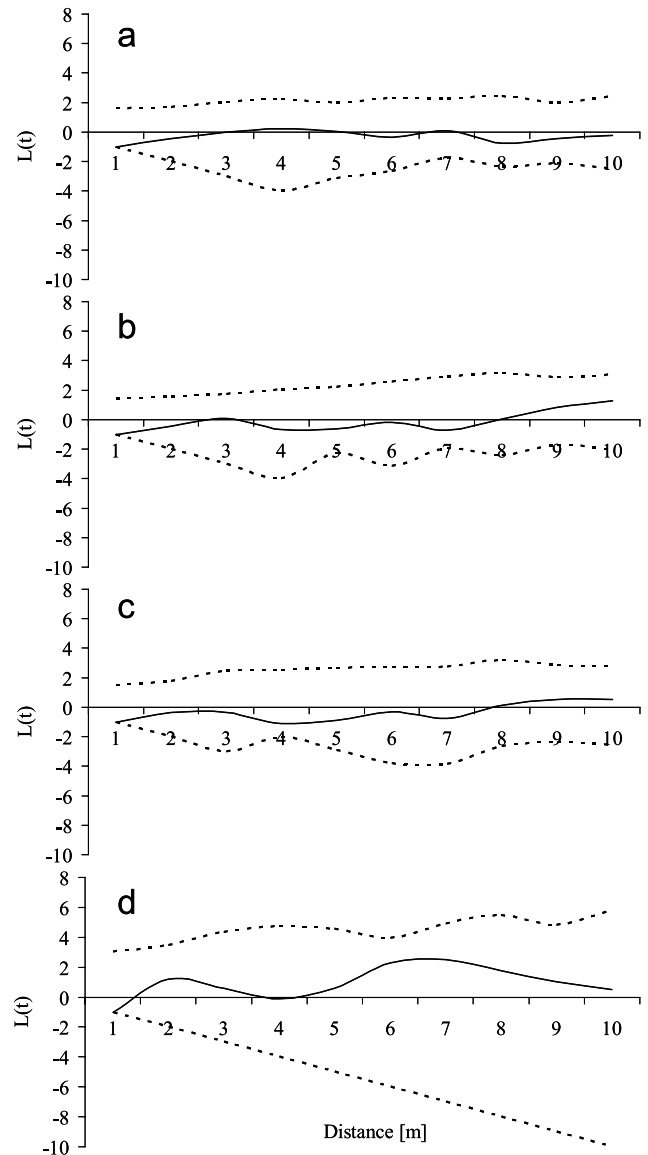
Fig. 5: L-function comparing patterns of adult burrow locations with complete spatial randomness (CSR). **a** 17 October; **b** 17 November; **c** 17 December; **d** 17 January. Observed L-function (solid line), expected L-function for CSR (zero line), 95% confidence limits (dashed lines) shown for distances between points up to 10 m.

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