

# Spatial patterns of social spider colonies in Namibia reflect habitat features and dispersal modes

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Colonies of web building social spiders may persist at a site for several generations; therefore, their placement in the habitat is critical for survival. This study focuses on the development of spatial distribution patterns by means of different dispersal modes in a social spider species (*Stegodyphus dumicola* Pocock, 1898, Eresidae) in central Namibia. Social spiders disperse varying distances from the parent colony by ballooning or short distances by budding. Using spatial point pattern analyses we aimed to identify the dispersal pattern from source colonies and what drivers affect the resulting distribution patterns. The distribution of suitable vegetation constrained pattern development in the three study plots with mapped colonies. In a plot with isolated large trees, colonies were only aggregated over short distances and the average cluster size was small. First generation colonies were established within the same clusters by solitary ballooning females. In the two study plots with more evenly distributed shrubs, clusters were generally larger and new colonies were formed mainly by budding. In these plots, newly established colonies and older source colonies were either associated in suitable habitat patches or segregated from each other. Possible explanations include high mortality of either older colonies and replacement by newly established colonies or of dispersers in the vicinity of established colonies, or selection of “empty” sites by dispersing individuals based on cues from conspecific colonies. In conclusion, both the distribution of the vegetation and the mode of dispersal may explain the development of spatial patterns in *S. dumicola*. Our results highlight the importance of spatial pattern analyses for inferring underlying causes of distribution of sedentary organisms.

**Keywords:** Araneae, ballooning, dispersal, habitat heterogeneity, pair correlation function, point pattern analyses, spatial association.

## INTRODUCTION

Spatial distribution of sedentary organisms is strongly influenced by habitat heterogeneity and by the organism's specific habitat requirements and its means of habitat choice. Web building social spiders spend their entire lifetime in a permanent colony, and colonies survive for multiple generations at a given site (Avilés, 1997; Lubin & Bilde, 2007). Local habitat characteristics are therefore expected to influence the persistence of colonies at a site. In social spiders, new colonies are founded by individuals that disperse away from large, established colonies, and for these dispersers, the choice of a site to settle and establish a new colony is likely critical to survival. Dispersal and colony establishment occur infrequently and sporadically and thus habitat selection is difficult to investigate directly. In this study, we examined the distribution of colonies of a southern African social spider, *Stegodyphus dumicola* Pocock, 1898 (Eresidae), as a means of inferring mechanisms underlying habitat selection in this species.

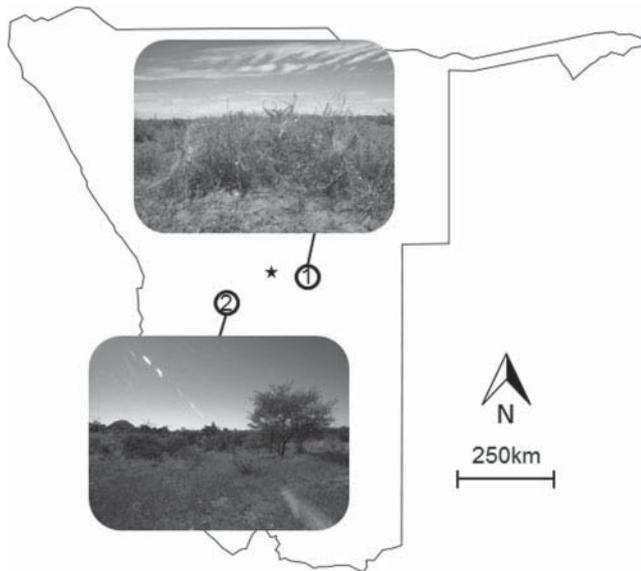
*Stegodyphus dumicola* is one of approximately 25 social spider species worldwide (Lubin & Bilde, 2007) and is distributed across parts of Southern Africa (Platnick, 2014). Colonies may consist of several hundred individuals in a single central nest (Seibt & Wickler, 1988) and spiders cooperate in web construction, prey handling and maternal care (Kraus & Kraus, 1988). Mated females may disperse from established colonies by ballooning (Schneider *et al.*, 2001) to found new

(first generation) colonies consisting of a small cone-shaped nest in which a single eggsac is produced (Bilde *et al.*, 2007). New nests can be established also by a process of budding or colony fission, whereby small groups of large juveniles use walking or bridging on silk to move short distances from the parent colony and construct new nests (Lubin *et al.*, 2009). Both budding and ballooning can result in short range dispersal, but only ballooning enables long distance dispersal (e.g. Bonte *et al.*, 2003). In this study, we aimed to shed light on the relationship between the mode of dispersal and the development of spatial distribution patterns in populations of this social spider species. We tested whether: (1) the distribution of colonies in study plots located at two sites in central Namibia deviates from a random pattern and (2) first generation colonies are associated with older colonies in suitable habitat patches.

## MATERIALS AND METHODS

### Study regions and colony surveys

*Stegodyphus dumicola* nests are constructed of silk, prey remains and leaves and these colonies are attached to branches of shrubs or trees in savannah and grassland habitats in Namibia (Bilde *et al.*, 2007). In this study, colonies at two sites in central Namibia (Figure 1, farms Rooisand and Oupembamewa) were surveyed at the start of the study and



**Figure 1.** Map of the study sites for *Stegodyphus dumicola* population in Namibia. (1) Oupembamewa and (2) Rooisand and the location of the capital Windhoek (star). 189 × 169 mm (300 × 300 DPI).

then censused at approximately monthly intervals for a year between 2003 and 2004. At Oupembamewa two separate plots were surveyed (hereafter Oupembamewa south and north), while at Rooisand one plot was surveyed. The two sites differed in elevation and in vegetation characteristics (for region and habitat properties see Table 1; for colony distribution maps see Figure 2). At Oupembamewa, *S. dumicola* nests were found in shrubs less than 1.5 m above ground, at Rooisand nests usually occurred in trees larger than 2 m at a height of >1.5 m (Bilde *et al.*, 2007). At each visit, newly discovered colonies were marked and categorized as first generation (nests with single females or smaller than 8 cm in any dimension) or older (>8 cm) colonies and GPS coordinates (latitude and longitude, decimal degrees) were recorded.

### Point pattern analysis

We first analysed if the observed spatial patterns of colonies in the three study plots resembled patterns expected from a

homogeneous Poisson process. Spatial patterns are homogeneous when a pattern of point locations exhibits similar statistical properties throughout the entire study area. Such a pattern can be described by a homogeneous Poisson process (hereafter referred to as complete spatial randomness, CSR in Table 2) which is characterized by a constant mean density of points in an area (= constant intensity) and an independent distribution of points (Illian *et al.*, 2008). Deviations from this null model suggest that (a) environmental heterogeneity (extrinsic drivers) or (b) biotic interactions (intrinsic drivers) cause a non-random distribution of colonies (Wiegand & Moloney, 2014). We surmised that the distribution of colonies would be constrained to patches that provide the necessary structural elements on which to attach nests. The second and third spatial analysis, therefore, reflects this constraint due to site availability (extrinsic factor) by deriving an intensity function based on the observed small scale heterogeneity in colony distribution. This intensity function describes the probability of colony occurrence based on the observed local colony density and acts as proxy of variation in site availability. These analyses test if colonies, independent of their age, are associated in suitable habitat patches (Table 2, hereafter referred to as HET) or if first year colonies are spatially associated with older colonies in suitable habitat patches (Table 2, hereafter referred to as ANT).

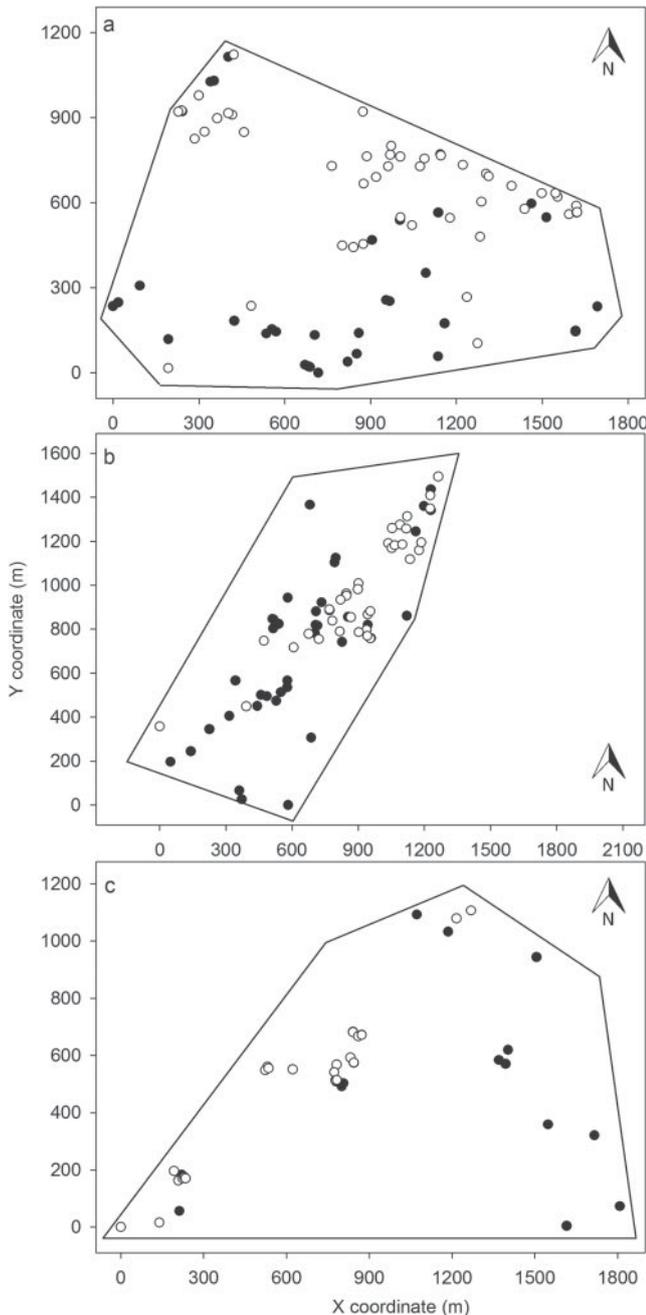
All analyses were performed based on the pair correlation function (PCF: Stoyan & Stoyan, 1994) based on an approximation of the Ohser estimator (Wiegand & Moloney, 2004) and the Hanisch edge correction (Wiegand & Moloney, 2014). The univariate pair correlation function is used to analyse the spatial relationship between colonies, independent of their age. The univariate pair-correlation function  $g(r)$  quantifies the average (intensity normalized) density of colonies at distance  $r$  away from other colonies in the pattern. The bivariate pair-correlation function  $g_{12}(r)$  measures the average (intensity normalized) density of colonies of group 2 at distance  $r$  away from the colonies of group 1. For more technical details see Wiegand and Moloney (2014) and Illian *et al.* (2008).

The bivariate pair correlation function is used to describe the spatial relationship between first generation and older potential source colonies. Under the CSR null model (Table 2), individuals are distributed randomly over the study area in simulations and the PCF is then calculated for all points in the

**Table 1.** Properties of the study plots and analysed point patterns. For a map of the study regions see Figure 1.

	Study site		
	Oupembamewa N	Oupembamewa S	Rooisand
Survey year	2004	2004	2003
Colonies	123	135	115
First generation	64	58	79
Older	59	77	36
Study area (ha)	142	36	127
Coordinates	−22.539°; 17.588°	−22.558°; 17.573°	−23.278°; 16.131°
Annual mean temp. (°C)*	18.6	18.4	19.1
Av. annual precip. (mm)*	344	359	207
Vegetation structure	dense shrubland		sparse shrubland
Shrub and tree cover	11–25%		2–10%
Remarks	intensive grazing pressure mainly small to medium shrubs (<1.5 m)		little grazing fewer shrubs, scattered trees (>2 m)

\*Mendelsohn *et al.* 2002.



**Figure 2.** Point maps for locations of *Stegodyphus dumicola* first generation (•) and older (°) colonies in the arbitrary shaped study plots (a) Oupembamewa north, (b) Oupembamewa south and (c) Rooisand. 152 × 314 mm (300 × 300 DPI).

area and for a pre-defined number of such simulations. The resulting reference functions are then compared to the PCF of the observed pattern to classify the observed spatial pattern as random if no departure from the simulation-derived confidence envelopes of the null model occurs, as aggregated if the observed PCF deviates above the upper confidence envelope and as regular if the observed PCF deviates below the lower confidence envelope. Under the HET and ANT null models (Table 2), individuals are distributed according to the estimated intensity function that reflects environmental heterogeneity. The selected antecedent condition further has locations of the observed older colonies fixed in space and only redistributes first generation colonies in all simulations

(ANT). The rationale behind this approach is that older colonies may have acted as sources for first generation colonies and therefore should have been established prior to first generation colonies. The 5th highest and lowest values of 199 Monte Carlo simulations for both models were used to generate 95% confidence envelopes (Wiegand & Moloney, 2014). The significance of deviations of the observed pair correlation functions from confidence envelopes in all null models was tested according to a Goodness-of-Fit test by Loosmore and Ford (2006).

All point pattern analyses were performed in arbitrary shaped study areas, as the survey plots were bordered by rocky/mountainous areas (Rooisand) or dry riverbeds, fences or roads (Oupembamewa). Intensity functions for heterogeneous Poisson processes were estimated based on the observed distribution of first generation and older colonies, a moving window estimator (window radius = 10 m) and a Box kernel (Wiegand & Moloney, 2014). We used a spatial resolution of 10 m for all spatial analyses, approximating the measurement accuracy of hand-held GPS receivers. This conservative approach limits us to discussions of spatial patterns larger than 10 m, but avoids identification of spurious relationships due to limited GPS precision. All analyses were performed using the software Programita (version Febrero 2014; Wiegand & Moloney, 2004; Wiegand & Moloney, 2014).

## RESULTS

The distribution of *S. dumicola* colonies in all three study regions was characterized by non-random spatial structure as confirmed by a Goodness-of-Fit test for the CSR null model (Figure 3). While colonies in the two plots at Oupembamewa deviated above the upper confidence envelope at all analysed scales up to 110 m (Figure 3(a) and (b); north  $p < 0.001$ ; south  $p < 0.001$ ), colonies at Rooisand deviated only at distances up to 40 m (Figure 3(c);  $p < 0.01$ ). The univariate null model that assumes environmental heterogeneity (HET) reflected colony aggregation in suitable habitat patches at all scales in Oupembamewa south (Figure 4(b);  $P = 0.100$ ) and at distances between 30–50 m at Oupembamewa north (Figure 4(a);  $P = 0.475$ ). At Oupembamewa north, additional aggregation that goes beyond the values expected by the underlying null model was detected for distances smaller than 30 m or larger than 50 m. At Rooisand, colonies were aggregated according to the underlying null model at distances up to 40 m (Figure 4(c);  $p = 0.205$ ), but were more regularly distributed than expected at larger distances. The cluster properties differed markedly between study areas, with Oupembamewa north being characterized by rather large but fewer clusters (6 clusters, average radius 17 m) and Oupembamewa south being characterized by many clusters of intermediate size (16 clusters, average radius 8 m). Rooisand was characterized by small but numerous clusters (19 clusters, average radius 4 m).

The spatial relationship of first generation to older colonies did not deviate significantly from the prediction of null models for distances larger than 20 m at Rooisand (Figure 5(c)) and for distances of 10–40 m and 70–110 m at Oupembamewa south (Figure 5(b)). First generation colonies were more segregated from older colonies at Oupembamewa south at distances of 40–60 m ( $p < 0.001$ ), a pattern that was evident across all distances at Oupembamewa north (Figure 5(a);  $p < 0.001$ ).

**Table 2.** Point pattern analyses, underlying null models and results.

Analysis	Null hypothesis	Null model	Result
CSR	Colonies are randomly distributed	Univariate (independent of age); Null model: complete spatial randomness	Figure 3
HET	Colonies are associated in suitable habitat patches independent of their age distributed	Univariate analysis; Null model: heterogeneous Poisson	Figure 4
ANT	1st generation colonies are associated with older colonies in suitable habitats	Bivariate analysis; Null model: heterogeneous Poisson and antecedent condition	Figure 5

## DISCUSSION

*Stegodyphus dumicola* colonies were aggregated in all study plots, but clusters differed in size. Within these suitable habitat patches, first generation and older colonies were characterized by distinctively different spatial relationships in the two study regions. Colonies in the two plots at Oupembamewa showed a strong (north) or limited (south) tendency for spatial segregation between first generation and older colonies. First generation and older colonies were more associated with each other than expected under the null model – up to distances of 20 m at Rooisand – and did not occur segregated from each other at any distance.

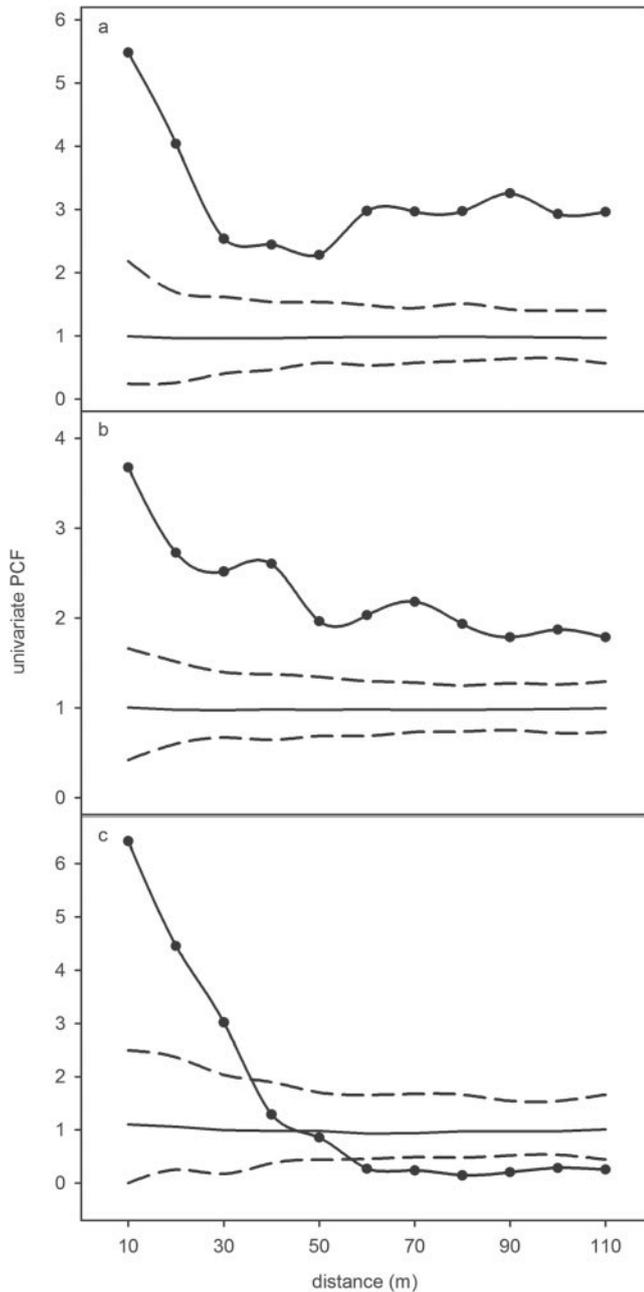
The observed aggregation of colonies in suitable habitat patches, independent of their age, resembles common patterns in the distribution of sedentary or breeding species (Moody *et al.*, 1997). It is generally assumed that habitat preferences lead to aggregated distribution patterns at certain scales, but abiotic disturbances such as climatic extremes (Birkhofer *et al.*, 2012) or biotic interactions such as territorial behaviour (Birkhofer *et al.*, 2006) are known to cause deviations from spatial randomness in burrow-constructing spider species in Namibia. *Stegodyphus dumicola* is a social spider with a very low potential for aggressive interactions with conspecifics, as both females and males, for example, are tolerated if introduced from one colony to another (Seibt & Wickler, 1988; Lubin *et al.*, 2009). It is therefore unlikely that territorial behaviour or cannibalism would cause a regular distribution of colonies and the observed aggregation most likely reflects the distribution of shrubs or trees that are suitable for colony construction. The study plots at Oupembamewa are characterized by relatively dense shrubland with limited heterogeneity of shrub distribution (Figure 1). Colonies in these plots are therefore aggregated at intermediate and large distances with individual cluster sizes between 8 and 17 m in radius. In contrast, Rooisand has a more scattered distribution of woody vegetation and a larger number of isolated or small groups of trees (Figure 1) that are often occupied by more than one colony. These vegetation characteristics most likely led to the observed aggregation of colonies at maximum distances of 40 m and to fairly small average cluster sizes of only 4 m radius. Vegetation gaps resulted in the absence of aggregation at larger distances in this study region.

While the overall patterns of aggregation of colonies likely reflect the heterogeneity in suitable habitat, the expected association between first generation and older colonies in suitable habitat patches is evident at Rooisand and only to some extent at Oupembamewa south. At Oupembamewa north, however, there was no significant association between first generation and older colonies at any scale. These differences between the two study regions may correspond to different predominant modes of dispersal in these

populations. Most first generation nests in Rooisand observed at the start of the survey (78%,  $n=95$  small nests) contained only a single adult female, indicating establishment by ballooning adults rather than budding or colony fission (Bilde *et al.*, 2007). Thus, the spatial association at short distances up to 20 m, with overall average cluster radius of 4 m, suggests that many mated female dispersers landed within the same cluster of trees or shrubs in Rooisand, while more distant dispersers were randomly distributed. This random distribution may be a consequence of ballooning spiders being affected by wind gusts during times of dispersal or mortality during long-distance dispersal.

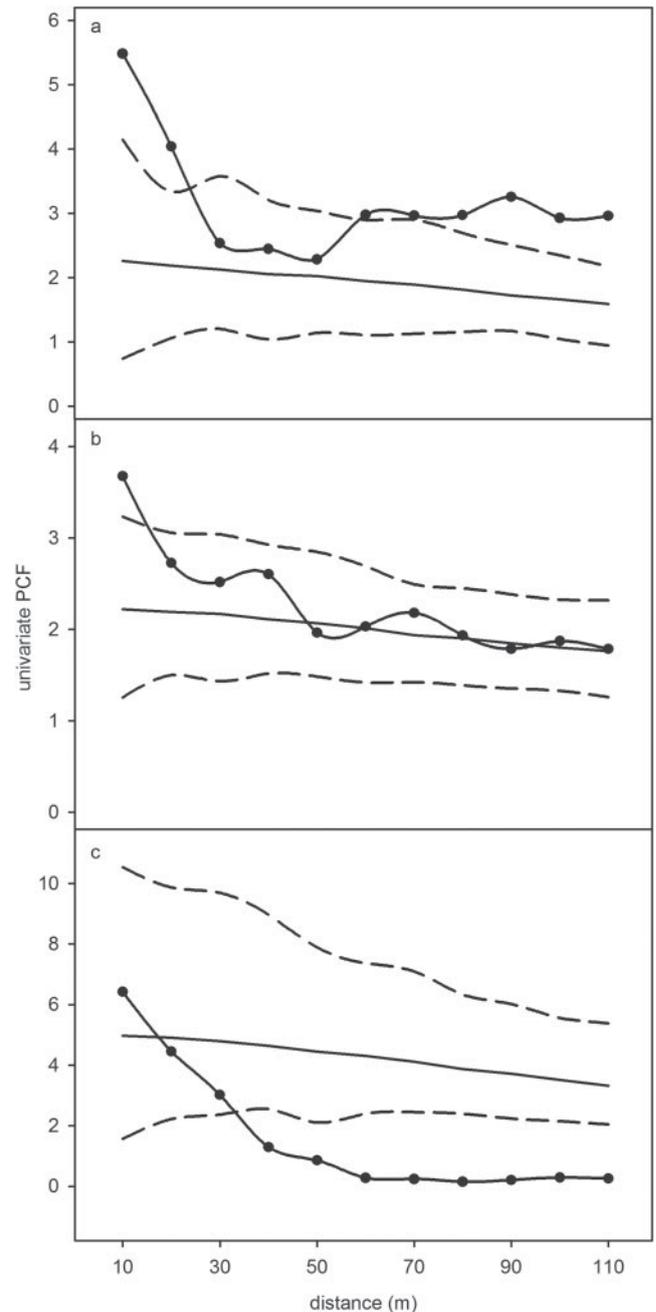
A large proportion of first generation colonies at Oupembamewa contained multiple females (79% of first generation colonies, Bilde *et al.*, 2007), indicating that they originated by budding or fission rather than by solitary, ballooning females, as was common in Rooisand. The lack of consistent spatial association between purported first generation daughter colonies and older parent colonies in Oupembamewa was an unexpected result. In these plots, first generation colonies were more segregated than expected by the underlying null model at all (north) or some (south) distance ranges. It is possible that the patterns are caused by mortality of older colonies and their replacement by first generation daughter colonies. The clustering of first generation colonies in both plots (Figure 2) could reflect such local mortality. Colonies of *S. dumicola* have a limited lifespan, estimated at around six generations (Lubin & Crouch, 2003). Colony clusters are established by means of budding or local settling of dispersing females, and in both cases the dispersers are derived from a large (old) parent colony. Consequently, a cluster of similar-age old colonies may die off, to be replaced by a new cluster of first generation colonies. An additional explanation might be that new colonies have low survivorship in the vicinity of older, parent nests, which could lead to segregation of first generation and older colonies. Finally, dispersing mated females may deliberately colonize areas that were not previously occupied. Conspecific cuing, i.e. utilizing information about established conspecific burrows or webs, has been described in web-building (Hodge & Storfer-Isser, 1997) and burrow constructing spiders (Birkhofer *et al.*, 2012).

Clustering of *S. dumicola* colonies may have important consequences for colony survival. In both Rooisand and Oupembamewa, more than 90% of first generation nests became extinct within one generation (Bilde *et al.*, 2007). In Rooisand, a single tree or large shrub often harboured as many individual colonies as a similar size area with a few smaller shrubs in Oupembamewa. Pathogens, predators and parasites of *S. dumicola* may spread more rapidly across colonies on a single large tree compared to a number of small shrubs. Furthermore, new, small colonies are at greater risk of mortality than larger ones (Bilde *et al.*, 2007). In Rooisand, we



**Figure 3.** Univariate pair correlation function for the CSR null model (Table 2) showing the spatial relationship between *Stegodyphus* colonies independent of colony age up to distances of 110 m at (a) Oupembamewa north, (b) Oupembamewa south and (c) Rooisand. Pair correlation functions (solid line with points) crossing the 95% confidence envelopes (dashed lines) indicate a deviation from spatial randomness (as estimated from simulations based on a homogeneous Poisson distribution). Crossing the upper envelope suggests aggregation, crossing the lower envelope suggests regularity at the specific distance. The solid line without points is the expected PCF. 148 × 299 mm (300 × 300 DPI).

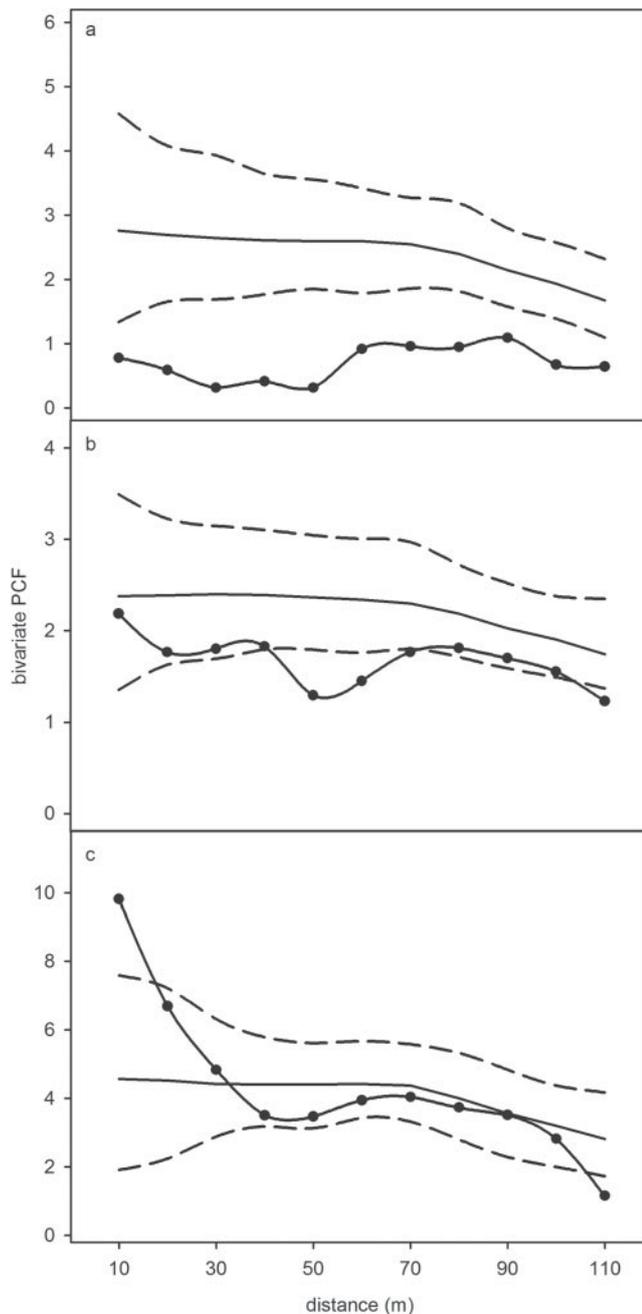
noted many nests invaded by spiders of the family Palpimanidae: a family whose species show morphological and behavioural adaptations to feed on other spiders (Pekár et al., 2011). Social spiders also have several other predators and kleptoparasites which further may affect colony survival (Henschel, 1998; Lubin & Bilde, 2007). A more scattered distribution of colonies across individual shrubs or larger



**Figure 4.** Univariate pair correlation function for the HET null model (Table 2) showing the spatial relationship between *Stegodyphus* colonies independent of colony age up to distances of 110 m at (a) Oupembamewa north, (b) Oupembamewa south and (c) Rooisand. Pair correlation functions (solid line with points) crossing the 95% confidence envelopes (dashed lines) indicate a deviation from the underlying null model (as estimated from simulations based on a heterogeneous Poisson distribution). Crossing the upper envelope suggests association of colonies that goes beyond the simulated patterns, crossing the lower envelope suggests segregation of colonies beyond the simulated patterns. The solid line without points is the expected PCF. 145 × 299 mm (300 × 300 DPI).

clusters may reduce the risk of local extinction due to attacks by pathogens or natural enemies.

In conclusion, both the distribution of the vegetation as well as the distribution of conspecifics may have affected the development of the observed spatial patterns in *S. dumicola*.



**Figure 5.** Bivariate pair correlation function for the ANT null model with antecedent condition (Table 2) showing the spatial relationship between first generation (re-distributed) and older (fixed) *Stegodyphus* colonies up to distances of 110 m at (a) Oupembamewa north, (b) Oupembamewa south and (c) Rooisand. Pair correlation functions (solid line with points) crossing the 95% confidence envelopes (dashed lines) indicate a deviation from the underlying null model (as estimated from simulations based on a heterogeneous Poisson distribution). Crossing the upper envelope suggests association of first generation to older colonies that goes beyond the simulated patterns, crossing the lower envelope suggests segregation of first generation from older colonies beyond the simulated patterns. The solid line without points is the expected PCF. 145 x 299 mm (300 x 300 DPI).

Our results further highlight the importance of understanding the natural history of study objects and demonstrate the need to account for habitat heterogeneity in spatial point pattern analyses.

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## REFERENCES

- AVILÉS, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. In Crespi, B & Choe, J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge, MA, Cambridge University Press. pp. 476–498.
- BILDE, T., COATES, K.S., BIRKHOFFER, K., BIRD, T., MAKLAKOV, A.A., LUBIN, Y. & AVILES, L. 2007. Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology* **20**: 2412–2426.
- BIRKHOFFER, K., HENSCHER, J.R. & SCHEU, S. 2006. Spatial-pattern analysis in a territorial spider: evidence for multi-scale effects. *Ecography* **29**: 641–648.
- BIRKHOFFER, K., HENSCHER, J.H. & LUBIN, Y. 2012. Effects of extreme climatic events on small-scale spatial patterns: A 20-year study of the distribution of a desert spider. *Oecologia* **170**: 651–657.
- BONTE, D., VANDENBROECKE, N., LENS, L. & MALFAIT, J.-P. 2003. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society B* **270**: 1601–1607.
- HENSCHER, J.R. 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *Journal of Arachnology* **26**: 61–69.
- HODGE, M.A. & STORFER-ISSER, A. 1997. Conspecific and heterospecific attraction: a mechanism of web-site selection leading to aggregation formation by web-building spiders. *Ethology* **103**: 815–826.
- ILLIAN, J., PENTTINEN, A., STOYAN, H. & STOYAN, D. 2008. *Statistical Analysis and Modelling of Spatial Point Patterns*. Chichester, John Wiley & Sons.
- KRAUS, O. & KRAUS, M. 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origins of social living. *Verhandlungen des naturwissenschaftlichen Vereins Hamburg* **30**: 151–254.
- LOOSMORE, N.B. & FORD, E.D. 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* **87**: 1925–1931.
- LUBIN, Y. & BILDE, T. 2007. The evolution of sociality in spiders. *Advances in the Study of Behavior* **37**: 83–145.
- LUBIN, Y. & CROUCH, T. 2003. Trial by fire: Social spider colony demographics in periodically burned grassland. *African Zoology* **38**: 145–151.
- LUBIN, Y., BIRKHOFFER, K., BERGER-TAL, R. & BILDE, T. 2009. Limited male dispersal in a social spider with extreme inbreeding. *Biological Journal of the Linnean Society* **97**: 227–234.
- MOODY, A.L., THOMPSON, W.A., DE BRUIJN, B., HOUSTON, A.I. & GOSS-CUSTARD, J.D. 1997. The analysis of the spacing of animals, with an example based on oystercatchers during the tidal cycle. *Journal of Animal Ecology* **66**: 615–628.
- PEKÁR, S., ŠOBOTNÍK, J. & LUBIN, Y. 2011. Armoured spiderman: morphological and behavioural adaptations of a specialised araneophagous predator (Araneae: Palpimanidae). *Naturwissenschaften* **98**: 593–603.
- PLATNICK, N.I. 2014. The world spider catalog, version 15. American Museum of Natural History. Online: <http://research.amnh.org/entomology/spiders/catalog/index.html>
- SCHNEIDER, J.M., ROOS, J., LUBIN, Y. & HENSCHER, J.R. 2001. Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): They do balloon after all! *Journal of Arachnology* **29**: 114–116.

SEIBT, U. & WICKLER, W. 1988. Bionomics and social structure of "Family Spiders" of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneidae, Eresidae). *Verhandlungen des naturwissenschaftlichen Vereins Hamburg* **30**:255–303.

STOYAN, D. & STOYAN, H. 1994. *Fractals, Random Shapes and Point Fields*. Chichester, John Wiley & Sons.

WIEGAND T. & MOLONEY, K.A. 2004. Rings, circles and null-models for point pattern analysis in ecology. *Oikos* **104**: 209–229.

WIEGAND T. & MOLONEY, K.A. 2014. *A Handbook of Spatial Point Pattern Analysis in Ecology*. Boca Raton, FL, Chapman and Hall/CRC press.