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Coloniality of birds in the Kalahari—spatial distribution of trees and nests of the Sociable Weaver (*Philetairus socius*)

Sascha Rösner*, Urs Christian Giesselmann, Jork Meyer, Monika Schwager, Thorsten Wiegand, Melanie Lück-Vogel & Roland Brandl

Summary: The spatial distribution of suitable nest sites is a limiting resource for many colonial breeding animals. Therefore, we investigated and mapped the spatial distribution of nests of Sociable Weaver (*Philetairus socius*) to evaluate whether the size and distribution of suitable nesting trees influences the variability of colony size and spatial distribution of colonies in two study sites in the Kalahari, South Africa. We used spatial statistics to describe characteristics of point patterns. Nests of communal weavers were clustered at distances up to 300 m, whereas nests were distributed regularly at distances greater than 1,000 m. We therefore suggest that functional colonies of the social weaver consist of several nests on adjacent trees. From our analyses the question arises why sociable weavers establish sub-colonies instead of adding more chambers to the natal nest.

Introduction

Coloniality is a common phenomenon of many animal species. For instance, 13% of bird species breed in colonies (Lack 1968). Brown & Brown (2001) define bird species as colonial when nests are clustered close enough to show interactions between neighbouring conspecifics. Furthermore, individuals within such a colony often feed in flocks with cooperative responses to predator approach (Brown & Brown 1996, 2001, Wittenberger & Hunt 1985).

Many studies discuss the reasons for the evolution of coloniality (e.g. Brown et al. 1992, Brown & Brown 1996, Danchin & Wagner 1997, Rolland et al. 1998, Siegel-Causey & Kharitonov 1990). Three factors seem to be of importance: 1) sufficient food supply in the nesting area, 2) limited space for nesting sites and 3) cooperative defence against predators (Siegel-Causey & Kharitonov 1990). Colony sizes vary in orders of magnitude even within single species (e.g. Ambrosini et al. 2002, Brown et al. 1990, Forero et al. 2002, Gibbs & Kinkel 1997, Griffin & Thomas 2000, Møller 1987, Safran 2004). This variation seems to be triggered by environmental heterogeneity (Lack 1968, Brown et al. 1990, Brown & Brown 1996, 2001, Danchin & Wagner 1997). Thus, temporal and spatial differences in the availability of food or nesting sites, for example, might predispose colonial birds to aggregate and influence competition among neighbouring colonies (Forbes et al. 2000, Forero et al. 2002, Furness & Birkhead 1984, Griffin & Thomas 2000).

The Sociable Weaver (*Philetairus socius*) is such a colonial breeding bird species. It is a sparrow-sized passerine, endemic to southern Africa and associated with arid savannahs (e.g. the southern Kalahari; Mendelsohn & Anderson 1997). The species forms impressive communal nests that can reach 7.5 m in diameter and weigh several hundred kilograms with up to 350 nesting chambers (Covas 2002, Maclean 1973b, Marsden 1999). Weaver nests are used over many years by successive generations of birds and are constructed on the branches of large trees like *Acacia erioloba* or *Boscia albitrunca*. Occasionally, alien trees and artificial structures like telephone poles are used (Maclean 1973b). Most authors refer to a colony as the sum of all nests on a single tree whereas Maclean (1973a) supposes that a colony might consist of several nests on nearby trees rather than of a single nest on one tree.

Our survey focussed on colony characteristics of the sociable weaver. More

Table 1: Basic characteristics of the two study sites at Askham Kerk and Inversnaid, South Africa

	Askham Kerk	Inversnaid
Study area size [km^2]	63.0	31.0
Mean vegetation cover [%]	24.0 ± 5.6	28.0 ± 6.4
Range vegetation cover [%]	8–36	0–46
Precipitation	< 200 mm year^{-1}	< 200 mm year^{-1}
Number of suitable trees [trees per km^2]	3,093 (50)	1,597 (52)
Number of occupied trees [% of all suitable trees]	222 (7.2%)	91 (5.7%)
Number of nests per km^2	3.6	2.9
Total colony number	183	58
Colony density [colony km^{-2}]	2.91	1.81
Mean colony size [chambers]	54.6 ± 44.3	62 ± 39.3
Range colony size [chambers]	1–377	2–248

Photos 1 and 2: Weaver nests in *Acacia erioloba* and on a power pole, Askham Kerk Farm, South Africa. Photos: U.C. Gießelmann.

specifically, we investigate whether 1) the variation in colony size is related to tree size and 2) the spatial distribution of occupied trees is related to the overall spatial pattern of suitable nesting trees. We propose that weaver nest trees should be clumped at smaller scales (within the dispersal radius of weavers). However, due to competition among neighbouring colonies, we expect a regular distribution at larger spatial scales. These patterns ought to be independent of the underlying pattern of suitable nesting trees.

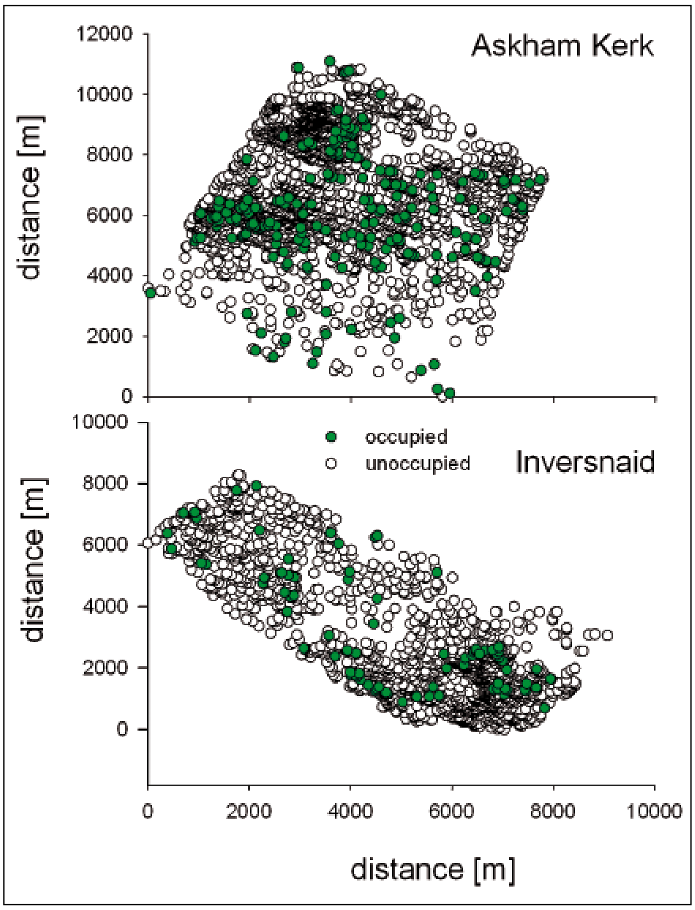

Fig. 1: Spatial distribution of occupied trees (filled circles) and unoccupied trees (empty circles) on Inversnaid and Askham Kerk, South Africa (modified after Gießelmann et al. 2008).

Material and Methods

The study was conducted in November 2004 and March 2005 on two farms, Askham Kerk (app. 27°00' S, 20°46' E) and Inversnaid (app. 26°55' S, 20°45' E) situated in close vicinity to the Kalahari Gemsbok Park in the Northern Cape Province, South Africa. The study sites were characterised by a semi-arid climate with low and unpredictable rainfall. The two farms were mainly used for sheep farming. The study areas were of different sizes (Table 1) and the vegetation on both farms consisted of open savannah with single *Acacia erioloba* trees and shrubs scattered in a grass matrix.

For our analysis we inspected all weaver colonies at the study sites. We established fixed transect lines at several hundred metres distance for inspections and counting. Colonies were recorded as active when either birds or fresh faeces were detected at sites. At all colonies we counted the number of intact nest chambers as a proxy for colony size. Furthermore, we recorded the stem diameter at breast height (DBH) and crown diameter of the trees as a measure of tree size. As controls, we collected data on randomly selected trees with no nests. We used digitised and rectified aerial photographs with a resolution of 4.0 m (Department for Land Affairs – South Africa) to identify potentially suitable trees for nesting. On the basis of pixel values, we performed a segmentation (eCognition software v3.0.6, Definiens 2006) and made a manual image object classification to extract the coordinates of the large trees in the study area. Due to the very sparse tree cover in the study region we were able to identify individual tree canopies on the aerial photographs. Field data were used to identify trees, which were occupied by our focal species as a reference to enable recognition of suitable unoccupied trees on the basis of canopy size. The classification accuracy was assessed by comparing the identification based on aerial photographs with field inventory data of a training area. We acquired an accuracy of 83%. The 17% error was caused mainly by trees that were standing close together and were therefore merged on the aerial photographs, resulting in two suitable trees being identified as one. Ripley`s K-function and pair correlation function were applied for analyses of spatial distribution patterns in relation to nest-trees and non-occupied trees (Ripley 1976, Stoyan & Stoyan 1994). All analyses were performed with the grid-based software Programita (Wiegand & Moloney 2004) using a cell size of 10 m × 10 m. For detailed information see Gießelmann et al. (2008).

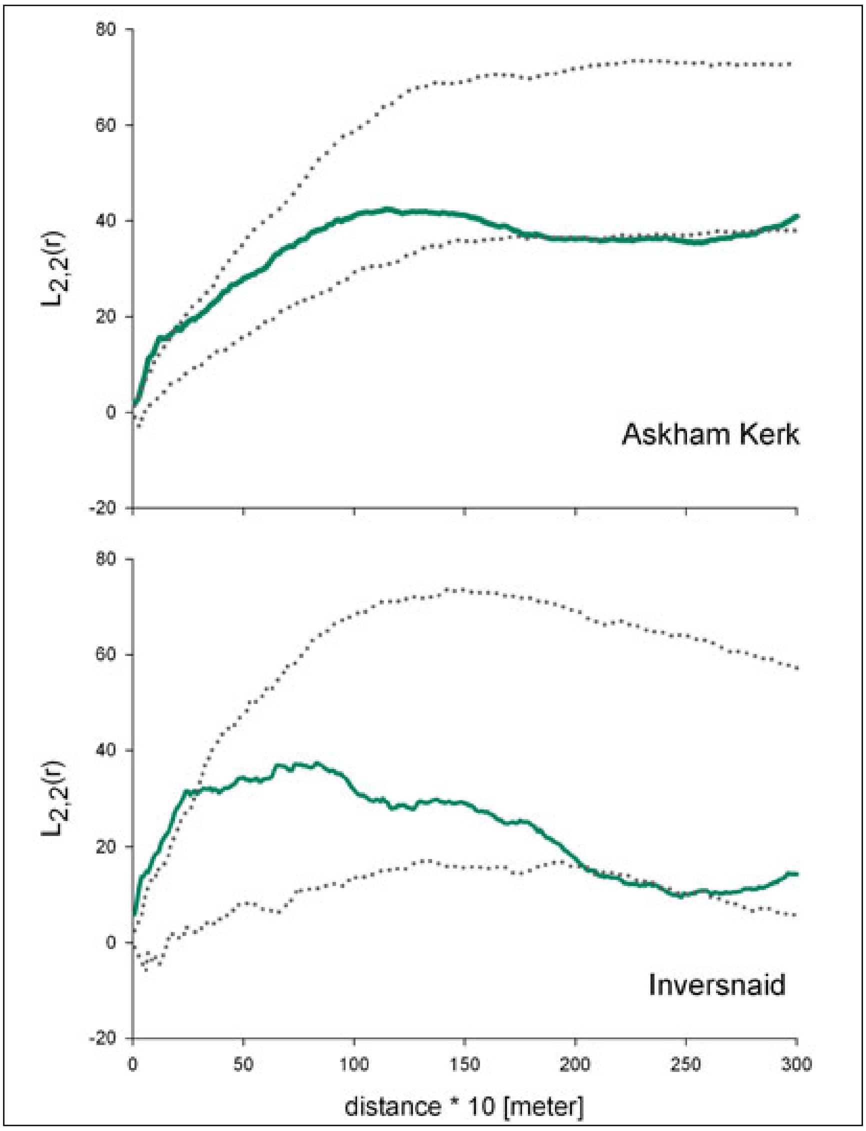

Fig. 2: Ripley's L-function for nests of the Sociable Weavers (*Philetairus socius*) on two farms (Askham Kerk and Inversnaid) in South Africa. The 99% confidence limits are shown as grey dotted lines. Maximum distances are limited to 3,000 metres to focus on the relevant sections of the functions. Graph modified after Gießelmann et al. (2008).

Results and discussion

We found similar characteristics for both study sites concerning the density of nesting trees and the spatial distribution of colonies (Table 1). The density of suitable trees per square kilometre was 50 on Askham Kerk and 52 on Inversnaid. Only 222 (7.2%) and 91 (5.7%) of the suitable nesting trees were occupied by social weavers, respectively (Table 1, Fig. 1). Even though nesting trees showed considerable variation in stem and crown diameter (range stem diameter: 0.16–1.03 m, crown diameter: 4.0–9.0 m) the size of nesting trees did not differ significantly between Askham Kerk and Inversnaid (Tukey HSD for unequal N; both $p = 0.08$). At both study sites weaver birds preferred large trees for nesting and the colony size, in terms of chamber numbers, increased with tree size. However, besides tree size, which only explained a small part of the variation in colony size, other factors such as rainfall or predation seem to affect colony size too. For instance, the weaver`s breeding success is strongly affected by rainfall and predation by, for example, the Cape Cobra *Naja nivea* and Pygmy Falcon *Polierax semitorquatus* (see Covas 2002, Maclean 1973c, d, Marsden 1999).

Our analyses revealed the following spatial distribution patterns of weaver nests. Sociable Weavers aggregated their nests stronger than expected by chance, with Ripley`s K showing a significant clustering of trees with nests up to of 200 m (Askham) and 280 m (Inversnaid; Fig. 2, Gießelmann et al. 2008). Furthermore, the results of Gießelmann et al. (2008) indicate that nesting trees are significantly more clustered than trees without nests. This suggests that *P. socius* might enlarge their colonies by adding new nests to adjacent and suitable tree instead of building new chambers on existing nests. This might be due to space limitations on the trees of the source colonies. The aggregation of nest trees on a small spatial scale points to a lack of intraspecific competition between nearby nests. Thus, we conclude that groups of weaver nests clustered on small spatial scales are single colonies.

Contrary to the findings on small spatial scales (colony level), we found a

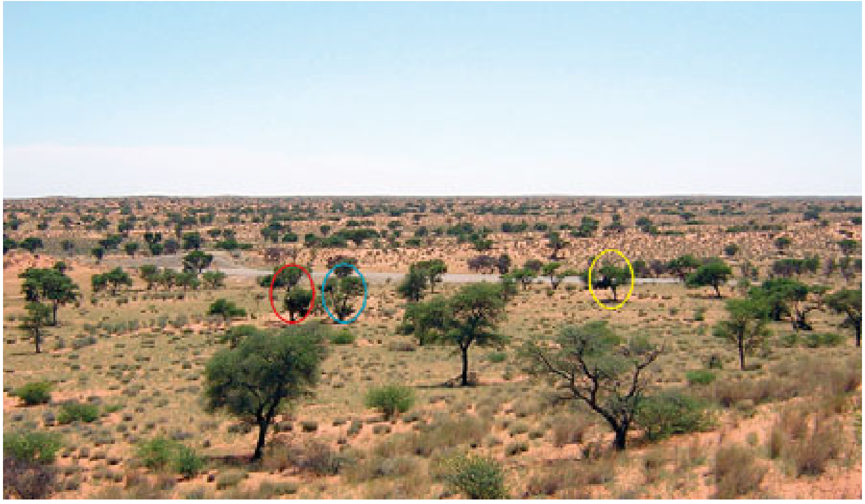

Photo 3: Savannah images (landscape) from the same area as illustrated in Photo 4. Photo: U.C. Gießelmann.

Photo 4: Savannah images from the same area as illustrated in Photo 3. Satellite image: Google Earth.

significant trend towards evenly distributed nesting trees at scales larger than 1,000 m (see Fig. 2). This trend towards regularity was consistently stronger for trees with nests than for trees without nests (Gießelmann et al. 2008). This suggests intercolonial territoriality and therefore competition between nests or groups of nests (Maclean 1973a). The scale at which this regular distribution occurred, corresponds approximately with the foraging range of this species (Maclean 1973e). However, our approach does not allow the inference of processes unambiguously from the observed pattern. For example, there might be other factors influencing the arrangement of nests in space and time, such as the size of foraging ranges, food availability (sufficient grass and bush cover) or other habitat requirements.

To conclude, while trees with weaver nests were evenly distributed at larger spatial scales, single colonies of *P. socius* seem to consist of several nests on clustered trees at smaller spatial scales. We therefore predict that individuals from such clustered nests are more closely related than individuals from more distant colonies.

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Photo 5: Weaver nests in *Acacia erioloba*, Askham Kerk Farm, South Africa.
Photo: U.C. Gießelmann.