Biodiversity is important for sustaining life on Earth yet it is threatened globally. The BIOTA Southern Africa project analysed the causes, trends, and processes of change in biodiversity in Namibia and western South Africa over nearly a full decade, from 2001 until 2010. This book, which is comprised of three volumes, offers a summary of the results from the many and diverse subprojects during this first period of long-term observation and related research, at both local and regional scales, and with a focus on sustainable land management options for the region.
Please cite this article as follows:

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

**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).


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.

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

<table>
<thead>
<tr>
<th></th>
<th>Askham Kerk</th>
<th>Inversnaid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study area size [km²]</td>
<td>63.0</td>
<td>31.0</td>
</tr>
<tr>
<td>Mean vegetation cover [%]</td>
<td>24.0 ± 5.6</td>
<td>28.0 ± 6.4</td>
</tr>
<tr>
<td>Range vegetation cover [%]</td>
<td>8–36</td>
<td>0–46</td>
</tr>
<tr>
<td>Precipitation</td>
<td>&lt; 200 mm year⁻¹</td>
<td>&lt; 200 mm year⁻¹</td>
</tr>
<tr>
<td>Number of suitable trees [trees per km²]</td>
<td>3.093 (50)</td>
<td>1.597 (52)</td>
</tr>
<tr>
<td>Number of occupied trees [% of all suitable trees]</td>
<td>222 (7.2%)</td>
<td>91 (5.7%)</td>
</tr>
<tr>
<td>Number of nests per km²</td>
<td>3.6</td>
<td>2.9</td>
</tr>
<tr>
<td>Total colony number</td>
<td>183</td>
<td>58</td>
</tr>
<tr>
<td>Colony density [colony km⁻²]</td>
<td>2.91</td>
<td>1.81</td>
</tr>
<tr>
<td>Mean colony size [chambers]</td>
<td>54.6 ± 44.3</td>
<td>62 ± 39.3</td>
</tr>
<tr>
<td>Range colony size [chambers]</td>
<td>1–377</td>
<td>2–248</td>
</tr>
</tbody>
</table>
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.

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 per-
formed 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).

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
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 <i>P. socius</i> 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.

Acknowledgements
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References
Griffin, L.R., Thomas, C.J. (2000): The spatial distribution and size of rook (<i>Corvus frugi-legus</i>) breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. – Proceedings of the Royal Society of London, Series B 267: 1463–1467.

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