Geographic variation in social behaviour of white-browed sparrow-weavers, *Plocepasser mahali*

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White-browed sparrow-weavers are social birds occurring in the semi-arid parts of Africa. Large variations in the density (abundance) of these birds in different parts of the continent probably result from differences in food supply, and are correlated with differences in vegetation and rainfall. Despite these local differences in environment, the social system of the species is surprisingly uniform: group size varies by a factor of less than two, and the presence of helpers within groups has been recorded at all the study sites. This contrasts with the published data for a number of other social vertebrates. The selective force shaping sparrow-weaver sociality may be constant throughout the geographic distribution of these birds. If so, this selective factor is not related to food supply, but probably to a high mortality rate.

Koringvoëls is sosiale voëls wat in die halfwoestyngebiede van Afrika voorkom. Groot verskille in die digtheid van hierdie diere oor die vasteland korreleer met verskille in plantegroei en reënval, en is waarskynlik te wyte aan verskille in voedselbeskikbaarheid in die verskillende gebiede. Nieteenstaande hierdie verskille is die sosiale stelsel van die voëls baie stabiel: groepgrootte wissel met 'n faktor van minder as twee en helpers is 'n universele verskynsel by hierdie voëls. Hierdie waarneming kontrasteer met dié van 'n aantal ander sosiale diere. Die selektiewe krag wat verantwoordelik is vir die koringvoël se bestaande sosiale organisasie, mag deur hul hele geografiese verspreidingsgebied konstant wees. Indien wel, is dié selektiewe krag nie verwant aan voedselbeskikbaarheid nie, maar moontlik aan 'n hoë mortaliteit.

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The sparrow-weavers comprise a genus of eight species with an intermediate degree of sociality compared with related taxa like the Ploceine weavers, which breed in units of pairs (Crook 1964), and the sociable weaver which has a complex social system (Maclean 1973). The basic plocepasserine social unit often comprises a breeding pair and their offspring (Maclean 1973; Collias & Collias 1978a, 1980; Lewis 1982a). Further, they often feed in groups and co-operate in nest building. Helping, in which subadults assist breeding pairs to raise chicks, is another characteristic of this subfamily (Maclean 1973; Collias & Collias 1978a; Lewis 1982a). White-browed sparrow-weavers are found in south-western, central and north-eastern Africa in arid and semi-arid *Acacia* spp. woodland (Figure 1) and in *Colophospermum mopane* woodland of Zimbabwe and Zambia (Mackworth-Praed & Grant 1963).

Behavioural traits appear to be more labile than morphological traits. This is particularly the case in social behaviour. Among mammals, Kruuk (1972) and Macdonald (1979a, 1979b) have shown that social behaviour of hyaenas, foxes and jackals varies extensively from place to place; solitary individuals or pairs are found under some environmental conditions, while larger social units are common under others. The same phenomenon has been observed among social birds (e.g. Stacey & Bock 1978; Reyer 1980,1985).

Variation in group size of social animals can be expressed as two components: (i) intra-location variation which reflects the individual variation in social tendency and of the environmental factors affecting sociality at
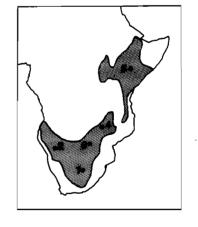

Figure 1 The geographical distribution of white-browed sparrow-weavers (shaded, after Hall & Moreau 1970), showing the various localities where these birds have been studied: 1 — Bloemhof (this study), 2 — Daan Viljoen Game Reserve (this study), 3 — Wankie Game Reserve (Vernon 1983), 4 — Luangwa Valley (Lewis 1982a), 5 — Samburu (Collias & Collias 1978).

each site, and (ii) inter-location variation which reflects differences in environmental factors causing sociality among the different sites. The latter component is often relatively easy to measure and explain. The aim of this paper is twofold: first, to describe how sociality is expressed in terms of white-browed sparrow-weaver group size and second, to determine how group size in these birds varies in different habitats and at different population densities throughout their geographic range in Africa.

Methods

Sparrow-weavers were observed in two areas: immediately south of the Bloemhof Dam ($27°40'$S / $25°39'$E) in the north-western Orange Free State, South Africa, and at the Daan Viljoen Game Reserve ($22°32'$S / $16°58'$E) near Windhoek, South West Africa. Group sizes were determined by counting ringed individuals, while territories were mapped from the locations where ringed sparrow-weavers had been observed, and from the locations of agonistic interactions between neighbouring groups. Accurate group sizes were recorded at Bloemhof (34 groups) both by visual observation and nocturnal capture of the birds, while group sizes at Daan Viljoen Game Reserve (30 groups) were determined only by visual observation. Sparrow-weaver group sizes and territory sizes were studied at Daan Viljoen Game Reserve during July/ August 1982, and at Bloemhof during August/ September 1982. Both sets of observations were made immediately before the breeding season.

Nine sparrow-weaver groups resided in an area of approximately 2 km^2 at Bloemhof. Each group was visited, when possible, at least three times a week. During July 1982 to February 1984, 46 individuals in the Bloemhof study area were ringed with a numbered metal ring and two plastic colour-rings. As from December 1982 this enabled the identification of all individuals in the study area. Group size counts included the groups that had been ringed for behavioural observations.

Behavioural observations were made at Bloemhof during 548 observation hours during the period July 1982 to May 1984, while behavioural data from Daan Viljoen only contributed towards the determination of territorial boundaries during July/August 1982. Behavioural data were collected using the focal animal sampling method (Altmann 1974), when the instantaneous activity of colour-ringed sparrow-weavers was recorded every 2 min. Visual observations of predetermined individuals were made for a predetermined duration (usually 30 min). In addition, all behavioural events relating to inter- and intraspecific interactions were recorded. The social relationships within sparrow-weaver groups at Bloemhof were investigated in two ways:

(i) The number of friendly or `aggressive social interactions between two individuals reveals the nature of the social relationship between the two animals. All the observed occurrences of such interactions were used to calculate interaction rates for individuals of different age/sex classes.

(ii) The amount of time that two individuals spend together gives an indication of the strength of the social bond between them. The amount of time that each sparrow-weaver spent within 1 m of one or more fellow group-members was recorded while they were perched, because the birds were then not obscured by vegetation and could be clearly seen.

Sex was determined on the basis of bill colour, following Earlé (1983): males have black bills compared with the pinkish-brown bills of females. Because other workers (e.g. Collias & Collias 1978a, Lewis 1982a)

could not sex sparrow-weavers in this way, the method was tested by dissecting 73 sparrow-weavers shot during the course of the study. Only one individual did not conform to the above criterion. The absolute age of individuals that fledged during the study period was known. Juveniles could be identified by light-coloured marks on their culmens as well as by their distinctive calls. Individuals were therefore categorized into three age classes: juveniles (younger than six months), immatures (older than five months but not mated) and adult (mated) birds.

Results

Group composition, sex ratio and territory size

Sparrow-weavers occurred in groups ranging in size from two to nine birds (Figure 2), occupying a common territory around a single tree in which all breeding and roosting nests were built. The sizes of 34 groups at Bloemhof averaged 3,4 birds compared with a mean size of 5,0 for 30 groups at Daan Viljoen. This is a statistically significant difference (Wilcoxon rank sum large sample approximation $z = 3,39; p < 0,001$). These numbers refer to group sizes before the start of the breeding season at Bloemhof and presumably also at Daan Viljoen, where no signs of active or recent breeding were found. Groups commonly consisted of a single breeding pair associated with offspring of one or both parents. More than two breeding adults were never observed in the same group. The number of attendant non-breeders varied between none and five at Bloemhof, with up to seven being recorded at Daan Viljoen.

Table 1 shows that territories at Daan Viljoen appear to be slightly larger than those at Bloemhof. Statistical treatment of such small samples is, however, not feasible.

Social interactions within groups

No form of affiliative or mutualistic behaviour (e.g. allopreening) was observed. However, two forms of
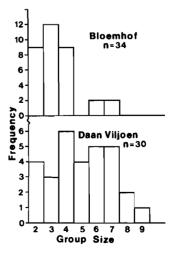

Figure 2 Histograms indicating the frequency of occurrence of different white-browed sparrow-weaver group sizes at Bloemhof and at Daan Viljoen Game Reserve.

Table 1 Parameters related to population densities of white-browed sparrow-weavers in different parts of Africa. Data from the present study are compared with other published data. Where two sample sizes are given, the figure in parentheses indicates sample sizes from which the respective territory sizes were calculated, the initial figure applying to the density figures

			Locality		
	Bloemhof	Daan Viljoen	Luangwa Zambia	Wankie Zimbabwe	Samburu Kenya
Birds / km²	29	41	108	839	1702
Groups / km²	8	8	26	129	276
Mean group size	3,4	5,0	4,2	4,5–6,3	4,4–4,9
Territory size (ha)	7,3	12,1	3,8	0,7–1,7	0,4
Annual rainfall (mm)	410	420	936	634	580
Sample size	34(9)	30(4)	26	44 +	17
Reference	This study	This study	Lewis (1982a)	Vernon (1983)	Collias & Collias (1978)

agonistic behaviour were observed:

(i) Chasing behaviour was observed on 11 occasions when one member of a group chased another over a short distance, usually about 10 m. This was not accompanied by any other overt acts of aggression or obvious ritualized behaviour.

(ii) One group member pecked at another on nine occasions. I suggest that this was stimulated by the colour rings, as it was invariably orientated towards the rings of another bird; the latter usually responded by pecking back at the legs and body of the aggressor.

Table 2 summarizes the observations on social interactions within groups (sample size is 548 observation hours). Intragroup agonistic behaviour is rare (0,04 interactions / h) and usually occurs between an adult and an immature sparrow-weaver, and rarely between adult

Table 2 The frequency of agonistic interactions among members of different age classes within sparrow-weaver groups during 548 focal animal observation hours, yielding a within-group interaction rate of 0,04 interactions / h

	Interaction type	
Aggressor / target	Chasing	Pecking
Adult / Adult	2*	2
Adult / Immature	7	5
Immature / Immature	2	2
Immature / Adult	0	0
Total	11	9

*This behaviour occurred shortly after pair formation.

pair members immediately after pair formation.

Time spent together

Sparrow-weavers often perched in a tree near fellow group members. When two birds spent a large proportion of time together, no functional significance could be attached to this. Rather, their proximity was probably influenced by the activities of the birds before perching and by the availability of suitable perches. However, if one assumes that proximity denotes a lack of aggression, the amount of time that two birds spent near each other could be used as an absolute minimum measure of non-aggression.

Individuals of breeding pairs consistently spent a larger proportion of time near each other than near immatures (Table 3). Also, the proportion of time that adults spent with each individual immature in a group decreased as group size increased, and immature sparrow-weavers spent about equal fractions of time near individual adults and near individual immatures.

The low incidence of agonistic behaviour between group members (Table 2), and the distribution of time spent near other group members (Table 3) indicates that there was no group hierarchy. However, the breeding pair was strongly bonded and was dominant in agonistic interactions with immatures of the same group.

Helping

Helping appeared to be a common phenomenon at Bloemhof. During the 1982/3 breeding season, three of the eight groups included helpers, and four out of seven groups during the 1983/4 breeding season.

Discussion

Population characteristics

The highest sparrow-weaver densities were found by Collias & Collias (1978a, 1978c, 1981) who studied

Table 3 Proportion of time that perched sparrow-weavers spent with individuals of different age classes as a function of group size. Statistical significance indicates results of chi-squared tests to determine whether birds of a specified age group spent more time close to their peers compared with the time spent close to the other age group. Mean % time = mean percentage of time spent near each individual of that age group with which the focal animal associated

	Group size (no. of immatures)		
Association	3 (1)	4 (2)	5 (3)
Adults			
Sample size (2-min scans)	2157	935	655
% Time with another adult	12,3	11,1	11,3
Mean % time with any individual adult in group	12,3	11,1	11,3
% Time with an immature	8,2	10,6	14,2
Mean % time with any individual immature in group	8,2	5,3	4,7
Statistical significance			
Adult time : Immature time	0,05	0,05	0,05
Immatures			
Sample size (2-min scans)	1110	679	609
% Time with another adult	15,5	24,0	15,1
Mean % time with any individual adult in group	7,8	12,0	7,6
% Time with another immature	N/A	11,5	15,1
Mean % time with any individual immature in group	N/A	11,5	7,6
Statistical significance			
Adult time : Immature time	N/A	n.s.	n.s.

N/A = Not applicable since groups with only one immature have no immature/immature associations.

groups in the vicinity of two tourist camps in Kenya. Collias (*in litt.*) indicated that the populations around the tourist camps were higher than in the surrounding countryside. However, observations made during the present study show that birds are not attracted to human buildings or activities (Ferguson in prep.), suggesting that Kenyan sparrow-weavers have local densities much higher than their southern African counterparts. A 40% fluctuation in population density was also observed over two years at one of the sites of Collias & Collias (1978c, 1981). The relatively low population density in the Bloemhof study area indicates that the western Orange Free State is not optimal white-browed sparrow-weaver habitat. This is supported by the fact that the mean territory size at Bloemhof (7,2 ha; Table 1) was much larger than those reported elsewhere (less than 4 ha; Collias & Collias 1978a; Lewis 1981; Vernon 1983). The relatively large mean territory size at Daan Viljoen may reflect a similar situation, but could also be an artefact of the small sample size (Table 1). Bloemhof is situated

near the south-eastern edge of the white-browed sparrow-weaver geographical distribution and has relatively dense ground cover compared with the rest of the southern part of the range of these birds. Lewis (1981) showed that Zambian sparrow-weavers avoid tall, densely-matted vegetation. I believe that vegetation density is critical in determining the distribution of sparrow-weavers.

Considerable variation exists between the rainfall figures at the different study sites. Both Bloemhof and Daan Viljoen have an annual rainfall of about 415 mm (Weather Bureau 1982). Vernon's study site in Zimbabwe has an equivalent figure of 634 mm (Zimbabwe Meteorological Service 1982), while Lewis (1982a) reported an annual precipitation of 936 mm for the Luangwa Valley, Zambia. Collias & Collias (1978a) reported 580 mm of rain for the year 1975. Large differences in the vegetational characteristics of the different study sites are also apparent. The studies of Lewis (1982a) and Vernon (1983) were conducted in *Colophospermum mopane* woodland, while the present study, as well as that of Collias & Collias (1978a), was conducted in more open *Acacia* spp. savanna (Bloemhof; see Acocks 1975: vegetation type 16a2) or in mixed savanna (Daan Viljoen; see Giess 1971: Highland savannah). The common denominator in vegetational characteristics was the presence of both *Acacia* spp. trees and ample bare ground.

Table 1 shows that sparrow-weaver group sizes at various localities in Africa tend to be relatively constant, despite differences in population density over two orders of magnitude. This fact is even more remarkable in the light of the large diversity in rainfall and vegetation at the respective study sites. The published group size data of Vernon (1983) and of Collias & Collias (1978a) are not in a form suitable for statistical comparisons, leaving only the data from Bloemhof and Daan Viljoen (this study) and from Zambia (Lewis 1982a). An ANOVA suggested that significant differences exist between sparrow-weaver group sizes at Bloemhof, Daan Viljoen and Zambia (Kruskall-Wallis $\chi^2 = 11,82$; d.f. =2; $p < 0,003$). This significance was mainly the result of differences between the group sizes at Bloemhof, when compared to those of Daan Viljoen and Zambia. Group sizes at Daan Viljoen did not differ significantly from those studied by Lewis (1982a) (Wilcoxon rank sum $z = 1,21$; $p < 0,25$). The Bloemhof data represent the only apparent statistical outlier among the group size data. As explained above, this is probably due to the suboptimal vegetational characteristics of the habitat.

If suitability of habitat was measured in terms of sparrow-weaver density, there is remarkably little variation in group sizes among habitats with different suitabilities: group size varied with a factor of less than two, while population density varied with a factor of more than 50. The small territory sizes, small distances between groups and relatively high rainfall in the areas with high sparrow-weaver densities (Table 1), lead me to postulate that the large variation in sparrow-weaver densities found at the various sites stems mostly from variation in food supply or ease with which food can be

obtained. The variance in sparrow-weaver group size may partly be an effect of population density, as one would expect that individuals in dense populations find it more difficult to disperse than in a sparse population. Similar conclusions have been reached for the acorn woodpecker (Stacey 1979) and the Australian splendid wren (Rowley 1981). Available data for the acorn woodpecker points to some similarities with sparrow-weavers. In California, these birds occur in group sizes of up to 15 birds, with a mean group size of 4,76 (Koenig 1981) whereas they are found mostly pair-wise in Arizona (mean group size 2,15: Stacey & Bock 1978). It appears that a range of intermediate group sizes are found in other areas, since they have a mean group size of 3 in intermediate habitat in New Mexico (Stacey 1979). Population densities are, however, not easily calculated from these sources. Although Lott (1984) described significant intraspecific variation in group size for a large number of animals, it appears that permanently territorial bird species do not have large amounts of variance, even if additional non-reproductives are involved.

Social relationships

Collias & Collias (1978a, 1978b) found a clear peck order within each of the five groups that they studied in Kenya. Furthermore, they found a significant correlation between the mass of a bird and its rank. Collias & Collias (1978b) found that two adjacent groups with poorly defended territories had aggressive within-group interactions at a rate of 4,2 interactions / h (sample = 55 h), whereas two other adjacent groups with well-defended territories had a similar interaction rate of 0,1 to 0,2 interactions / h (sample = 110 h). Their results contrast with those of the present study at Bloemhof, where the aggressive intra-group interaction rate was 0,04 interactions / h (Table 2), and where breeding birds were clearly dominant over the rest of the group (Table 2), but no individual rank order could be observed. This impression is also supported by the amounts of time that individuals spent near fellow group members (Table 3). The clearly-defined rank order among Kenyan sparrow-weavers compared with the non-ranked situation at Bloemhof can be understood as an effect of the high density of these birds in East Africa: high population density implies high inter-group interaction rates, which would fortuitously yield a higher intra-group interaction rate compared with low-density populations (Rasa 1979). The pronounced rank order in Kenyan sparrow-weavers is the result of a relatively high intra-group interaction rate.

Apart from differences in the rate of within-group aggressive interactions, the different studies demonstrated remarkably little variation in social relationships, with the single breeding pair being dominant over the rest of the group (Collias & Collias 1978a, Lewis 1982a). Although other studies on the breeding biology of sparrow-weavers did not indicate what proportion of groups were affected by helping

behaviour (making a comparison with my data impossible), helping appears to be a ubiquitous phenomenon, performed by a significant proportion of the population (Collias & Collias 1978a; Lewis 1982a, 1982b; Earlé 1983). This differs from the data for other social bird species (e.g. acorn woodpeckers: Stacey & Bock 1978; scrub jays: Woolfenden & Fitzpatrick 1984) which have helpers only in parts of their geographical ranges.

The relative constancy in sparrow-weaver group size and social behaviour could be explained in two ways:
(i) The selection pressure responsible for sparrow-weaver sociality has a relatively constant intensity throughout the geographical distribution of these birds, regardless of density. Such a factor may be peculiar to the ecology of this species and may be effective wherever suitable habitat is found. The apparent differences in food availability at the respective study sites (as reflected by population density as well as rainfall) suggest that this factor is not the prime selective force for sparrow-weaver sociality. Predation, on the other hand, may be important in shaping sparrow-weaver sociality. Lewis (1982a), Earle (1983) and Collias & Collias (1981) showed that sparrow-weaver mortality is high, especially in small groups. Sparrow- weaver sociality could be an adaptation to overcome a ubiquitously high mortality rate; a factor which is independent of the food supply at any particular site.
(ii) Constant group size could be the incidental effect of some other adaptation of these birds: they could be 'locked' into a phenotype exhibiting social tendencies since pleiotropic effects or other genetic processes may hinder the disappearance of this social trait. Because of a lack of knowledge about the epistatic genetic effects of different behavioural and phenotypic traits, this explanation is at this time imposssible to prove.

No conclusive evidence exists to distinguish between these two alternatives. Recent work on the causes of sparrow-weaver mortality suggests that the nesting behaviour and semi-arid habitat of these birds predispose them to high predation rates (Ferguson in prep.). This phenomenon probably contributes to sparrow-weaver sociality and would be wide-spread. No obvious adaptations of these birds have been noted that would incidently yield a constant group size.

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