Preferred habitat of white-browed sparrow-weavers *Plocepasser mahali*

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Habitat use by white-browed sparrow-weavers *Plocepasser mahali* was studied in the Bloemhof area, South Africa. The habitat of nine sparrow-weaver groups consisted of three vegetation communities: *Acacia erioloba* community, *Nidorella resedifolia* community and *Conyza bonariensis* community. The latter community comprised disturbed, ecotonal areas along the edges of roads and maize lands and had a lower basal cover and higher terrestrial arthropod availability than the other two plant communities. The *Conyza bonariensis* community, together with areas with little vegetation cover, was well used by sparrow-weavers. Seeds eaten by sparrow-weavers also reflect the open character of feeding areas. Termites are an important sparrow-weaver food taxon and large similarities between the geographical distributions of *Trinervitermes trinervoides* and sparrow-weavers exist.

Habitatgebruik van koringvoëls *Plocepasser mahali* is te Bloemhof, Suid-Afrika ondersoek. Die habitat van nege koringvoëlgroepe het bestaan uit drie plantgemeenskappe: die *Acacia erioloba-*, *Nidorella resedifolia-* en *Conyza bonariensis*-gemeenskappe. Laasgenoemde gemeenskap kom voor op versteurde ekotoongebiede langs paaie en rondom mielielande, en het 'n laer basaalbedekking en hoër beskikbaarheid van grondlopende insekte vergeleke met die ander plantgemeenskappe. Die *Conyza bonariensis*-gemeenskap sowel as ander gebiede met lae grondbedekking is hoofsaaklik deur die koringvoëls gebruik. Sade wat deur koringvoëls gevreet word, reflekteer die oop aard van die voedingsgebiede. Termiete is 'n belangrike koringvoël-voedselbron, en groot ooreenkomste tussen die geografiese verspreiding van *Trinervitermes trinervoides* en dié van koringvoëls is opvallend.

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White-browed sparrow-weavers *Plocepasser mahali* are group-living weaverbirds found in semi-arid parts of southern and eastern Africa (Mackworth-Praed & Grant 1953, 1963). Groups typically consist of a breeding pair and up to nine non-reproductives, some of whom are offspring of the breeding pair (Lewis 1982). Sparrow-weavers often occupy contiguous territories, 0,4 ha to 12 ha in size (Ferguson 1988), Normally each territory contains a nest tree in which a large numer of roost nests and some breeding nests are built (Earlé 1983).

The plocepasserine subfamily to which both sparrow-weavers (genus *Plocepasser)* and social weavers (genera *Philetairus* and *Pseudonigrita)* belong, is typical of arid and semi-arid parts of Africa. For understanding the ecology and evolutionary biology of members of this subfamily and for understanding the floristic composition, physical character and particular constraints of the environments in which these species evolved, it is necessary to have quantitative knowledge about their habitat requirements. This paper quantifies aspects of the preferred habitat of white-browed sparrow-weavers. The following questions are addressed: (i) Are any particular plant species or genera so essential that sparrow-weavers cannot survive without them? (ii) Is any physical feature of the vegetation, e.g. foliage density or ground cover, essential for sparrow-weaver survival? (iii) Is the sparrow-weaver diet so specialized that the geographic distribution of the food limits the distribution of these birds?

Study areas and Methods

Sparrow-weavers were observed and collected during the period March 1982 to June 1984 in an area immediately south of Bloemhof Dam (27°40'S / 25°39'E) in the north-western Orange Free State, South Africa, in an area comprising Kalahari Thornveld (veld type 16a2, Acocks 1975) in which maize farming is practised in some areas. The study area was used in two ways: (i) an extensive survey of nest trees was made over an area of about 25 km^2; (ii) within this area, a smaller area of 2 km^2 was located in which intensive behavioural observations were done. In addition, sparrow-weavers were observed in Daan Viljoen Game Reserve, Windhoek (22°32'S / 16°58'E) where comparative data were obtained over a period of two weeks during July/August 1982. Ferguson (1987, 1988a) describes the study areas and behavioural observation methods in greater detail.

Food eaten

The diet of sparrow-weavers was studied by collecting 73 birds during the period May 1982 to April 1983 and analysed as described in Ferguson (1988b).

To relate these food items to particular aspects of the environment preferred by sparrow-weavers, it was necessary to determine which vegetation types or geographical areas were used most by these birds.

Habitat use

Sparrow-weaver territories are relatively small and each has at least one nest tree where individuals of a particular group roost and spend a large part of the day. The distribution of nest trees could thus be used as a crude indicator of the location of sparrow-weaver territories. The positions of 167 nest trees were plotted on a 1 : 50000 topographical map, and then related to vegetational features and agricultural practices. On a finer scale, visual observations on habitat use by focal sparrow-weavers (Altmann 1974) was determined by plotting focal animal observations at 2-min intervals on a 1 : 10000 map of the central study area and determining which areas were most intensively used.

Floristic composition of sparrow-weaver habitat

The taxonomic composition of the grass and herbaceous plants in the area was determined by performing a simplified Braun-Blanquet survey (Mueller-Dombois & Ellenberg 1974) which consisted of 50 randomly situated sample plots (called *releves* in Braun-Blanquet terminology) of dimensions 5 m × 5 m. Forty releves were situated in *Acacia erioloba* veld whereas ten were located in disturbed or ecotonal areas. Three additional releves were subjectively placed in areas where the random sampling method seemed to leave large, unsampled areas. All plants within each releve were identified and a subjective assessment of the relative importance of the biomass of each species made according to the following convention:

1 – 6% of total phytomass: Class 1
7 – 12% of total phytomass: Class 2
13 – 25% of total phytomass: Class 3
26 – 50% of total phytomass: Class 4
51 – 100% of total phytomass: Class 5

Structural characteristics of sparrow-weaver habitat

Plant cover and phytomass in three plant communities defined through Braun-Blanquet methodology were measured as follows. In order to ascertain the ground cover of each plant species, a line-intercept survey (Canfield 1941), involving 12 transects of 50 m each, was performed. In addition to the distances between plants on the transect line, the basal cover and crown cover of each plant on the line was measured. Each plant crossed by the transect line was identified. Five of the transects were situated in the *Acacia erioloba* community, three in the *Nidorella resedifolia* association and four were situated in the *Conyza bonariensis* community.

The phytomass per unit area in the *Conyza bonariensis* community was compared with that of the two other communities, using the disc pasture meter described by Bransby & Tainton (1977). A wooden square, measuring 1 m × 1 m and weighing 6,06 kg, was dropped onto the vegetation, and the height above ground of the four diagonal centrepoints on each side of the square was then measured, this being proportional to the amount of vegetation below the wooden square. Two hundred such measurements were made in the *Conyza bonariensis* community and a further 204 in the other two communities. Calibration of the method was performed by removing the vegetation under the board and measuring the dry mass of 20 such calibration plots of 1 m^2 each. There was a high correlation between the average height above ground of the board and the phytomass/m^2 ($r = 0{,}95$; 95% confidence limits 0,88 and 0,98).

Athropod availability

Pitfall traps (Southwood 1976) were used to collect terrestrial arthropods in the *Conyza bonariensis* and the *Acacia erioloba* plant communities. Two lines of 10 traps were maintained during the period September 1982 to May 1983. Each trap (15 cm in diameter, 18 cm deep) was provided with a roof so that vertebrate predators could not remove the arthropods. Pits were placed 10 m apart and adjacent ones were joined by a plastic barrier which was approximately 18 cm high and 1 mm thick. This barrier forced terrestrial arthropods which would have passed between two pits to move along the barrier to the proximity of the pits. Trap-lines were simultaneously laid in the *Conyza bonariensis* community (ecotonal habitat) and in the *Acacia erioloba* community (thornveld). Relative arthropod abundances were calculated in terms of trap-days. The number of active traps was greatly reduced by the activities of foxes, mongooses and shrews that attempted to dig out traps, fell into them or disturbed them in some other way.

Results

Food eaten

Each stomach yielded both plant material and arthropod material, indicating that both these food sources are important to sparrow-weavers. A total of 761 seeds or fruits and 4371 arthropods were identified. A large array of plant items was consumed (Table 1). Maize, *Zea mays,* and wheat, *Triticum aestivum,* were among the most common seeds found in the stomach contents, indicating that sparrow-weavers often feed on cultivated plants. The only wild seeds that were eaten in relatively large numbers were *Urochloa* sp. (probably *Urochloa panicoides), Stipagrostis uniplumis, Limeum fenestratum* and *Celosia* sp.. These plants grow commonly in disturbed areas. Table 1 presents important plant food items taken by sparrow-weavers, a detailed report being presented in in Ferguson (1988b).

Insects from three taxa comprised most of the arthropod part of the diet: weevils (Curculionidae), ants (Formicidae) and termites (Isoptera). These and other arthropods that are eaten clearly reflect the ground-feeding habits of sparrow-weavers. Table 2 lists the arthropods identified from sparrow-weaver stomachs. Estimates of the numerical importance of different arthropod taxa in sparrow-weaver diets, as reflected by counts of arthropods, show that termites are most commonly eaten, forming more than 80% of the total arthropod food (4106 food items). The species *Trinervitermes trinervoides* was the most favoured termite (3710 food items), with *Hodotermes mossambicus* (329 food items) and *Odontotermes* sp. (67 food items) making up the rest of the termite food. The importance of *T. trinervoides* as a food source is emphasized by the fact that 71% of the sparrow-weaver stomachs contained them. Several times I saw sparrow-weavers dig small holes in the sandy soil at Bloemhof, probably into the foraging tunnels of these insects. Later, I was able to collect termites of the genus

Table 1 Important food plant taxa identified from the stomach contents of 73 sparrow-weavers. Taxa comprising 0,5% or more of the total number of identified seeds are indicated, a complete analysis being given in Ferguson (1988b). The ' % Stomachs' column indicates the percentage of sparrow-weaver stomachs containing a particular plant taxon, while 'Importance' indicates the percentage of all the identified seeds that seeds of a particular plant taxon comprised

Species name	% Stomachs	Importance
Digitaria sp.	3	0,5
Cynodon dactylon	3	0,5
Echium sp.	4	0,5
Commelina sp.	4	0,7
Ipomoa sp.	3	0,7
Vigna sp.	5	0,7
Euphorbia sp.	3	0,8
Tragus sp.	1	0,8
Gossypium sp.	9	0,9
Citrillus sp.	11	1,2
Limeum sulcatum	5	1,2
Erodium sp.	3	1,4
Solanum sp.	7	1,4
Limeum fenestratum	11	1,8
Oenothera sp.	7	2,5
Lithospermum sp.	5	3,0
Gisekia sp.	1	3,4
Portulaca oleracea	7	3,7
Celosia sp.	11	4,7
Sericorema sp.	8	5,2
Stipagrostis sp.	16	5,5
Bulbostylis collina	5	6,2
Eleusine sp.	2	6,2
Zea mays	64	7,2
Echinochloa crus-galli	5	8,3
Urochloa sp.	15	11,0
Triticum aestivum	26	14,8

Trinervitermes from these holes. Weevils formed the second most commonly eaten arthropod group (71 food items). These counts represent the minimum numbers of arthropods taken as deduced from exoskeleton parts recovered, and should be viewed with caution since some of the taxa may be seriously underrepresented. Because of fragmentation, reliable counts of commonly taken food items are not easily obtained and the data in Table 2 is therefore presented in terms of the number of stomachs containing a particular arthropod taxon. However, represented in this way, the results do not differ much from estimates of the numerical importance of the different insect taxa.

Habitat use

Of the 167 surveyed nest trees, only two were not camelthorn (*Acacia erioloba*) trees. These were by far the most common trees in the area, other commonly found trees being *Rhus lancea* and *Ziziphus mucronata* (Viljoen 1979). The observed preference for camelthorn trees could therefore be the effect of their numerical dominance. However, nest trees were not found

Table 2 Comparison between trapped arthropods and those found in sparrow-weaver stomachs. The relative abundance of arthropods in the *Acacia erioloba* community (224 trap days) is compared with that of the *Conyza bonariensis* community (468 trap days) in the Bloemhof central study area during September 1982 to March 1983: Dashes indicate zero trapping success and Isoptera and Curculionidae were not subdivided into genera for this comparison. The third numeric column indicates the importance of each insect taxon as a percentage of all the insects trapped during March 1982 to March 1983 (3140 trap days). The last column indicates the importance of insect taxa as sparrow-weaver food items expressed as a percentage of 73 sparrow-weaver stomachs containing a particular insect taxon

Taxon	Abundance in communities (Insects/100 trap days)		% Of all trapped insects	% stomachs
	Acacia	*Conyza*		
Coleoptera			77	
Carabidae	19	74	6	3
Tenebrionidae	37	96	50	3
Curculionidae	6	53	11	86
Brachycerus			5	
Protostrophus			3	
Synthocos			1	
Rhytirrhinus			0,3	
Lampyridae	2	14	0,3	
Scarabaeidae	4	2	6	16
Cerambycidae	0,2	–	0,1	
Cicindelidae	0,2	–	0,1	
Elateridae	0,4	2	1	
Diverse	–	19	2	5
Orthoptera			5	19
Gryllidae	4	7	5	1
Tettigonidae	0,2	–	0,1	
Acrididae	–	–	0	18
Hemiptera			2	18
Pentatomidae	–	5	2	18
Reduviidae	0,2	1	0,5	
Tingidae	–	–	0,1	
Hymenoptera			14	
Formicidae	7	26	14	82
Vespoidea	–	–	0	9
Blattoidea			0,1	
Blattidae	–	0,5	0,1	
Isoptera	–	3	1	96
Trinervitermes			0	71
Hodotermes			1	51
Odontotermes			0	23
Lepidoptera	0,4	1	0,6	
Arachnida	–	2	0,6	4

throughout the thornveld. They were common only around the periphery of this area (Figure 1) where the thornveld adjoined open grassveld or maize lands. Despite intensive search of the interiors of the thornveld regions (A–D, Figure 1), no nest trees were found there.

These findings were corroborated by behavioural data: Sparrow-weavers in the central study area at Bloemhof spent most of their time in the ecotonal areas near thornveld/road or thornveld/maize-land boundaries (Figure 2). Areas frequented inside the *Acacia erioloba* and *Nidorella resedifolia* communities (A–D, Figure 2) were very open with few trees. Although Figure 2 represents sparrow-weaver feeding behaviour, the pattern is identical to that for all the other activities that were mapped.

Floristic composition

Because sparrow-weavers are partial to the ecotonal areas where thornveld borders onto open grassland or disturbed veld, the question arises whether this represents preference for floristic characteristics of the ecotonal areas, or whether these areas have physical or other characteristics that make them desirable.

The Braun-Blanquet survey (Appendix 1) shows that the habitat can be divided into three main floristic communities:

(1) The *Acacia erioloba* thornveld community contains large *Acacia erioloba* trees, and is characterized by the shrubs *Felicia muricata, Barleria macrostegia, Acanthosycyos naudiniana* and the grass *Eragrostis curvula.* The grass *Tragus koelerioides* is also very common. This vegetation type matches Viljoen's (1979) description of the *Acacia erioloba — Stipagrostis uniplumis* community.

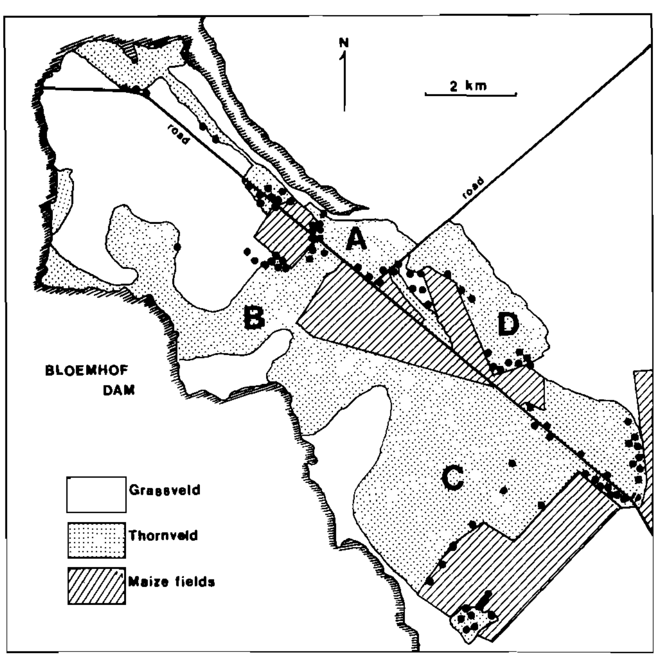

Figure 1 The locations of 96 sparrow-weaver territories (represented by nest trees, indicated by black dots) at Bloemhof show that the birds prefer the margins of thornveld areas. Thornveld/maize-land ecotones are much more intensively used compared to thornveld/grassland ecotones. The areas labelled A–D were extensively searched, but no sparrow-weaver nests were found.

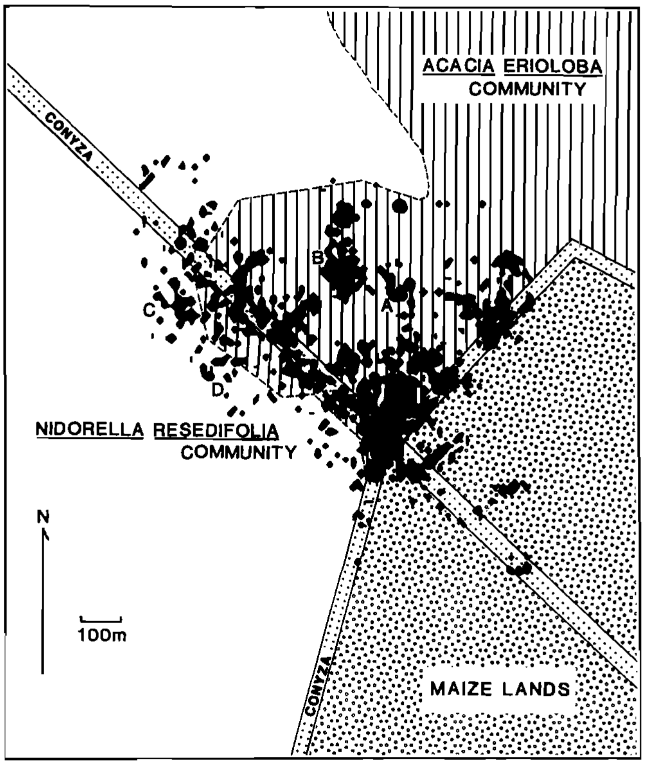

Figure 2 A map relating sparrow-weaver feeding areas (shaded black) with the plant communities at Bloemhof. The areas marked A–D have very sparse ground cover. Sparrow-weaver feeding is restricted almost exclusively to the ecotonal areas (*Conyza bonariensis* community) and other open areas.

(2) The *Nidorella resedifolia* community contains many *Acacia erioloba* shrubs, and is characterized by the shrubs *Nidorella resedifolia, Tephrosia lupinofolia, Helichrysum paronychioides* and the grass *Panicum kalaharense.* This community formed a marginal zone around the *Acacia erioloba* community. That part of the community situated on the south-western side of the road (Figure 2) contained characteristic shrubs, e.g. *Indigofera daleoides* and *Kohautia lasiocarpa,* and a more detailed botanical survey than this would probably indicate it as an independent community.

(3) The *Conyza bonariensis* community was found along the road and in the thornveld/maize-land ecotone. It contained a number of characteristic shrubs, e.g. *Conyza bonariensis, C. floribunda* and *Oenothera indecora.* It is probably not a natural plant community in the area: releves in this community adjoining thornveld showed some similarity with the thornveld, as is evident from the presence of the grass *Anthephora pubescens* and the shrub *Chrysocoma obtusata.*

It is doubtful whether the *Conyza bonariensis* community may be considered a natural association since it is not found in undisturbed, natural areas at Bloemhof. Also, this 'community' is likely to be very heterogeneous spatially and temporally. For the purpose of this study, however, its identification as a community facilitates description of the floristic and structural features of a habitat that is well used by sparrow-weavers.

Of the grasses that occurred in all the communities, some were especially common in only one community. *Cynodon dactylon* was very common in the *Conyza bonariensis* community, often forming a total cover of the area. Likewise, *Tragus koelerioides,* a grass with a similar structure to *Cynodon dactylon,* was very common only in the *Acacia erioloba* community. *Aristida stipitata* was very common in the *Nidorella resedifolia* community. The four plant species that formed the dominant component of the total biomass (excluding trees) in all the plant communities are *Eragrostis lehmanniana, Eragrostis tricophora, Aristida congesta* and *Stipagrostis uniplumis.*

When viewing sparrow-weaver habitat use as depicted in Figure 2, it is clear that the preferred habitat is the *Conyza bonariensis* community. The *Acacia erioloba* and *Nidorella resedifolia* communities were very little used, and no differential use of the latter two habitats was observed, despite the floristic differences between them. Areas frequented inside these two plant communities invariably comprised open spots with sparse vegetation.

Physical structure of vegetation

In addition, the line-intercept and disc pasture meter surveys revealed structural differences between the identified plant communities. Two creeper grass species, *Tragus koelerioides* and *Cynodon dactylon,* formed a significant part of the ground cover in all these communities. Because these species formed a dense mat of vegetation on the surface, and did not impede visibility for sparrow-weavers, two separate sets of calculations were made, one including the data for the above two species and the other excluding that data (Table 3). The results that exclude the data for the creepers are considered more applicable to the sparrow-weaver situation. The basal cover in the *Acacia erioloba* community was highest when creepers were included, but when these grasses are excluded there are no drastic differences between the basal covers of the three plant communities. However, the total cover in the *Conyza bonariensis* community was much lower than in the other communities. The means of crown width, distances between plant crowns and distances between plant bases (Table 3) also indicate that the density of vegetation in the *Conyza bonariensis* community is much lower compared to the thornveld communities. The plant biomass in the thornveld communities was 803 g/m^2 (n = 204) as compared to an equivalent figure of 593 g/m^2 (n = 200) in the *Conyza bonariensis* community; a significant difference (z = 6,4; p < 0,01) which provided additional evidence on the structural contrasts between the different plant communities.

Arthropod abundance

Inadvertently, some of the pitfall material of the *Conyza bonariensis* and *Acacia erioloba* communities were combined. As a result, the data for only 224 trap nights in the *Conyza bonariensis* community and 468 trap nights in the *Acacia erioloba* community are available as separate results (Table 2). Even though the data are limited, it is clear that the pits in the *Conyza bonariensis*

Table 3 A comparison of the structural characteristics of the three floristic communities in the central study area at Bloemhof, as reflected by a line transect survey consisting of 12 transects of 50 m each. Two sets of calculations are given: A includes the data for *Tragus koeleroides* and *Cynodon dactylon* (creeping species which do not have a large obscuring effect at sparrow-weaver height); B excludes these data

	A: including *Tragus* and *Cynodon*			B: excluding *Tragus* and *Cynodon*		
	Acacia	Periph	Ecoton	*Acacia*	Periph	Ecoton
No. transects	5	3	4	5	3	4
Basal cover (%)	19,1	9,1	7,2	5,1	8,4	4,6
Total cover (%)	88,1	63,3	57,1	72,7	60,4	35,5
Mean distance between plants on transect (cm)	24,7	23,6	18,7	28,6	26,5	40,6
Mean distance between plant bases on transect (cm)	60,9	48,2	41,1	80,0	53,4	101,9
Mean crown cross-section (cm)	21,8	15,0	10,6	20,8	16,0	14,4
Mean basal cross-section (cm)	4,7	2,2	1,3	1,4	2,2	1,8

Acacia = *Aacacia erioloba* community; Periph = *Nidorella resedifolia* community; Ecoton = *Conyza bonariensis* community.

Basal cover denotes the percentage of ground surface occupied by grass and shrub stems.

Total cover denotes the percentage of ground surface covered by canopies of plants.

community yielded higher arthropod numbers in almost all the taxonomic groups that were caught. This tendency is dramatic in the case of the ants (Formicidae) and weevils (Curculionidae), which are two of the most important sparrow-weaver foods (Table 2).

The birds largely ignored tenebrionid beetles, which are probably the commonest terrestrial insect taxon in the area (Table 2). Although the sparrow-weavers ate large quantities of termites, the traps failed to sample these insects effectively (Table 2).

Discussion

Why are sparrow-weavers restricted to thornveld?

Despite the preference for ecotonal or disturbed areas at Bloemhof, sparrow-weavers are commonly associated with *Acacia* spp. thorn trees. The Bloemhof area has relatively few tree species other than thorn trees. The fact that sparrow-weavers use thorn trees almost exclusively for nesting may, therefore, be an effect of the floristic composition of the area and little evidence from this study can be produced to indicate an actual preference. However, these trees are almost exclusively used for sparrow-weaver nesting in other parts of Africa (Mendelsohn 1968; Ferreira *et al.* 1972; Burger & Gochveld 1981). Both Mitchell (1966) and Lewis (1982) observed that sparrow-weavers in Zambia use thorn trees for nesting, even though there are many other tree species. Also, *Acacia* spp. trees are characteristic of the sparrow-weaver habitat in northern Kenya (Collias & Collias 1978). I propose that one of the main reasons for their association with thorn trees is related to the fact that sparrow-weavers build nests using dry grass stems which do not allow tight knotting of the nest to the branch of a tree, as is the case in the Ploceinae. Ferguson (1986) showed that erosion by wind is probably the major factor causing the loss of sparrow-weaver nests. Thorn trees have two characteristics that ensure that a nest of dry grass stems does not come loose and fall when a strong wind blows: (i) the branches are rigid and they bend and move less in the wind than do trees with more flexible branches and (ii) the thorns of these trees provide easy points of attachment on the tips of branches, without which it would be more difficult to attach a nest of dry grass stems. In addition, the thorns on the branches of these trees probably restrict movements of predators that approach occupied nests. Thorn trees are not a source of food for sparrow-weavers. No evidence could be found to indicate that the major food sources of sparrow-weavers are specifically associated with thorn trees, nor was there any suggestion that thorn trees play a role in sparrow-weaver signalling patterns.

Relation of diet to preferred habitat

The arthropods that are eaten reflect the ground-feeding habits of sparrow-weavers. All the *Trinervitermes trinervoides* taken by the birds were workers; the soldier caste of this species secretes a sticky substance that may be poisonous (Buillon 1970). In terms of ground feeding, a number of factors relating to structural characteristics of the habitat may directly influence the feeding behaviour of these birds as well as the ease with which terrestrial predators can locate feeding sparrow-weavers: (i) The lower mean crown cross-section, combined with a larger inter-plant distance in the *Conyza bonariensis* community would cause visibility at ground level to be much better here than in the other communities. (ii) The lower total cover in the *Conyza bonariensis* community causes a much larger proportion of open ground to be available to sparrow-weavers. If the birds feed mainly on open ground, the *Conyza bonariensis* areas may be advantageous. (iii) The lower phytomass per unit area causes differences in the availability of plant food to phytophagous insects. This may cause differences in the insect species compositions of the plant communities and may constitute one of the reasons why insect taxa commonly taken by sparrow-weavers are so common in the *Conyza bonariensis* community. The large inter-plant distances may also be favourable towards terrestrial insects such as termites and ants. The *Conyza bonariensis* community is therefore very suitable for ground-feeding birds; both in terms of physical structure and in terms of insect availability.

The large differences in terrestrial arthropod capture rates in traps of the two sampled habitats suggests that they reflect real differences in arthropod abundances. However, several problems surround interpretation of the results from the pitfall traps. Firstly, the thornveld (*Acacia erioloba* community) has a denser vegetation compared with the disturbed, ecotonal areas (*Conyza bonariensis* community), and this exposes a larger plant surface area on which insects can crawl. It could be argued that because the pitfall trap lines had similar lengths in both habitat types, the probability that a crawling insect will be captured in a thornveld pit is lower (Southwood 1976). However, most of the common taxa that were captured are largely terrestrial, and thus not severely affected by the plant surface area. Among the captures, weevils were the only important insect taxon that usually crawl on plants. In addition, the greater abundance of terrestrial arthropod taxa in the ecotonal area need not indicate that this area has a larger absolute arthropod abundance compared with the thornveld. Sweep net samples of insects that climb on to vegetation would have revealed a complimentary picture to indicate the absolute insect abundances in the two habitat types more accurately. However, since sparrow-weavers rarely forage on vegetation, I considered this unnecessary, and all one can firmly state is that the ecotonal areas have a greater abundance of the terrestrial arthropods eaten by sparrow-weavers.

The stomach content analyses usually did not allow the identification of arthropods down to generic level. However, the two weevil genera *Protostrophus* and *Brachycerus* formed 85% of the pit trap captured weevils and it is highly probable that the sparrow-weavers fed mainly on one or both of these genera. All the Curculionidae in Table 2 are typical of the sandy, arid parts of southern and central Africa and are common in disturbed or open areas (Gouwse 1977; Oberprieler pers. comm.). The other weevil genera caught in pitfalls, *Synthocos* and *Rhytirrhinus*, are terrestrial. Weevils of the genus *Brachycerus* have very hard exoskeletons which are likely to remain relatively undamaged in the stomachs. These were, however, not found which suggests that the relatively soft-bodied *Protostrophus* species were the most important weevils in the sparrow-weaver diet.

The termites eaten by sparrow-weavers are also typical of the dryer habitats in Africa. *Hodotermes mossambicus* is not found in regions with more than 750 mm annual precipitation (Coaton 1958), but occur in arid and semi-arid east, central and south-western Africa. The occurrence of these termites in moister areas is often the result of severe overgrazing or mismanagement of the veld (Gouwse pers. comm.). They are probably adapted to the arid parts of Africa and are characteristic of open ground and hard-pan soils (Buillon 1970). Apart from the occurrence of *Hodotermes* in Swaziland and Mozambique, the geographical distributions of white-browed sparrow-weavers and *Hodotermes* are largely similar. The termite genus *Trinervitermes* consists of several species inhabiting most of the Ethiopian region. *Trinervitermes* species are characteristic of savanna areas and are generally associated with sandy soils (Buillon 1970). Sands (1965) recognized 16 species in the genus, all of which have relatively restricted distributions. Two of these species, *T. bettonianus* and *T. trinervoides*, have a joint geographical distribution largely resembling that of white-browed sparrow-weavers. *T. trinervoides* occurs in southern and south-western Africa while *T. bettonianus* occurs in central and eastern Africa (Sands 1965; Coaton & Sheasby 1973). I suspect that *T. bettonianus* is an important sparrow-weaver food source in East Africa.

The arthropod taxa eaten by sparrow-weavers show close affinities with arid and semi-arid habitats and are mostly characteristic of disturbed habitats in more mesic environments. An exact correspondence, however, between the sparrow-weaver geographical distribution and that of any of their arthropod foods does not exist, suggesting that sparrow-weavers are not dependent on any single taxon. The wide range of arthropods taken supports this point.

The vegetable food taken by sparrow-weavers also reflects the open, disturbed nature of the areas used for feeding at Bloemhof. Table 1 shows that cultivated crops are an important part of the vegetable component of the sparrow-weaver diet. Maize and wheat formed 22% of the identified vegetable food items. It is possible that the open structure of vegetation in cultivated fields presents a suitable habitat for sparrow-weaver feeding, and that the crops are taken opportunistically. The birds were often observed feeding in cultivated fields for long periods, during which much food was collected among the detritus below cultivated plants. Among the wild plants eaten, *Urochloa panicoides, Echinochloa crus-galli* and *Eleusine* spp. are all characteristic of open, disturbed areas (Henderson & Anderson 1966; Roberts & Fourie 1975) and not necessarily of sandy, arid areas. The only commonly eaten plant not characteristic of disturbed areas is the grass *Stipagrostis uniplumis* which was common in all the plant communities at Bloemhof and is characteristic of arid areas in southern Africa (Acocks 1975). Clearly, the diet of these birds reflects the open vegetation which they prefer.

The sparrow-weaver preference for areas with sparse ground cover was commented upon by Lewis (1982) and Vernon (1983) who observed these birds in *Colophospermum mopane* woodland, a vegetation type which typically has a sparse ground cover (Acocks 1975). Vernon (1983) often found the birds in clearings in the mopane woodland. Although quantitative measurements were not taken, the herbaceous and grassy vegetation at Daan Viljoen was much more open than at Bloemhof. Daan Viljoen is situated centrally within the geographical distribution of sparrow-weavers in southern Africa. At Bloemhof, which is near the moister, south-eastern boundary of the sparrow-weaver distribution, the vegetation is unlike the preferred sparrow-weaver habitat in that it is more dense than the arid, western parts of southern Africa. This causes the birds to feed in relatively small, open areas at Bloemhof which have been disturbed by man. In this respect, humans may be creating suitable sparrow-weaver habitats (Ferguson 1985).

Evolutionary interpretation

Since adaptations evolve in response to the environment (Williams 1988), we cannot discuss adaptations without considering the environmental conditions under which they arose. The concept of species' histories following a pattern of punctuated equilibria (Eldredge & Gould 1972; Gould & Eldredge 1977), as well as Paterson's (1985) recognition concept of species, hold fundamental implications for interpreting the relationship between environment and adaptations. If, following these authors, we assume that species do not change dramatically in terms of morphology, adaptations or ecology during their periods of existence, we can infer that the present adaptations of a species reflect the environment in which these arose. Also, if we assume that an animal can survive only in an environment to which it is adapted, we can infer that the present habitat of a species approximates the environment in which this species originated. These views imply that the niche of a species is defined during speciation and that it remains constant throughout the life of that species.

I suggest that sparrow-weavers evolved in an environment with open savanna area vegetated by *Acacia* spp. trees which were vital for nest building. This area must have had sparse herbacious ground cover with ubiquitous open ground. Considering the sandy habitat of many of the arthropod taxa taken, sparrow-weavers may have originated in a sandy area. All these factors suggest that white-browed sparrow-weavers evolved in an arid or semi-arid area. Only two large areas having these characteristics existed on the African continent: south-western and north-eastern Africa (Axelrod & Raven 1978).

Acacia spp. trees occur in the moister south-eastern parts of Africa (Acocks 1975) but sparrow-weavers do not: the presence of these trees is therefore not the only essential characteristic of sparrow-weaver preferred habitat. Their present preference for *Acacia* spp. trees probably stems from adaptation to an open, semi-arid habitat (containing *Acacia* spp. trees) as a total unit, including its food sources and predators, and not only because these trees offer particularly good nesting sites.

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References

ACOCKS, J.P.H. 1975. Veld Types of South Africa. *Mem. Bot. Surv. S. Afr.* 40: 1–128.

AXELROD, D.I. & RAVEN, P.H. 1978. Late Cretaceous and Tertiary vegetation History of Africa. In: Biogeography and ecology of southern Africa, (Ed. M.J.A. Werger). W. Junk, The Hague.

ALTMANN, J. 1974. The observational study of behaviour: sampling methods. *Behaviour* XLIX: 227–287.

BRANSBY, D.I. & TAINTON, N.M. 1977. The disc pasture meter: Possible applications in grazing management. *Proc. Grassld. Soc. Sth. Afr.* 12: 115–118.

BUILLON, A. 1970. Termites of the Ethiopian region. In: Biology of the termites, (eds K. Krishna & F.M. Weesner). Academic Press, New York. pp. 153–280.

BURGER, J. & GOGHVELD, M. 1981. Direction of nest placement in two species of weaver. *Ostrich* 52: 54–56.

CANFIELD, R. 1941. Application of the line intercept method in sampling range vegetation. *J. Forestry* 39: 388–394.

COATON, W.G.H. 1958. The hodotermid harvester termites of South Africa. *Science Bull. No. 375 (Entomology series No. 43),* Department of Agriculture, Pretoria, South Africa.

COATON, W.G.H. & SHEASBY, J.L. 1973. National survey of the Isoptera of southern Africa. 1. The genus *Baucaliotermes.* Sands (Termitidae: Nasutitermitinae) *Cimbebasia* (Ser. A) 3(1): 1–7.

COLLIAS, N.E. & COLLIAS, E.C. 1978. Cooperative breeding behaviour in the white-browed sparrow-weaver. *The Auk* 95: 472–484.

EARLé, R.A. 1983. Aspects of the breeding biology of the white-browed sparrow-weaver *Plocepasser mahali.* (Aves: Ploceidae). *Navors. nas. Mus., Bloemfontein* 4: 177–191.

ELDREDGE, N. & GOULD, S.J. 1972. Punctuated equilibria; an alternative to phyletic gradualism. In: Models in Paleobiology, (ed.) T.J.M. Schopf. pp. 82–115. Freeman, Cooper & Co., San Francisco.

FERGUSON, J.W.H. 1985. The influence of crop-farming on white-browed sparrow-weavers *Plocepasser mahali. Proc. Symp. Birds & Man.* Witwatersrand Bird Club, Johannesburg.

FERGUSON, J.W.H. 1986. Ecological factors affecting social behaviour of white-browed sparrow-weavers *Plocepasser mahali.* Ph.D. thesis, University of the Witwatersrand, Johannesburg.

FERGUSON, J.W.H. 1987. Vigilance behaviour in white-browed sparrow-weavers *Plocepasser mahali. Ethology* 76: 223–235.

FERGUSON, J.W.H. 1988a. Geographic variation in social behaviour of white-browed sparrow-weavers. *S. Afr. J. Zool.* 23: 1–6.

FERGUSON, J.W.H. 1988b. Dietary overlap in plocepasserine weavers (Aves: Ploceidae) *S. Afr. J. Zool.* 23(4): 266–271.

FERREIRA, J.C., OSBORNE, P.L. & WOODALL, P.F. 1972. Kirk Biological society field trip to the Chewore wilderness area. *Rhodesia Science News* 6: 289–291.

GOULD, S.J. & ELDREDGE, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Palaeobiology* 3: 115–151.

GOUWSE, H.H. 1977. 'n Vergelykende morfologiese en bio-ekologiese studie van enkele *Protostrophus*-species (Coleoptera: Curculionidae). M.Sc. dissertation, Pretoria University, Pretoria, Republic of South Africa.

HENDERSON, M. & ANDERSON, J.G. 1966. Common weeds in South Africa. *Bot. Survey of South Africa, Mem.* 37: 1–440.

LEWIS D. 1982. Cooperative breeding in a population of white-browed sparrow-weavers *Plocepasser mahali. Ibis* 124: 511–522.

MACKWORTH-PRAED, C.W. & GRANT, C.H.B. 1953. Birds of Eastern and North-eastern Africa. Longman, London.

MACKWORTH-PRAED, C.W. & GRANT, C.H.B. 1963. Birds of the Southern Third of Africa. Longman, London.

MENDELSOHN, J.M. 1968. Nest-site preferences in the white-browed sparrow-weaver in the central Transvaal. *Ostrich* 39: 263.

MITCHELL, B.L. 1966. Orientation of nests of the white-browed sparrow-weaver. *Puku* 4: 167–170.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

PATERSON, H.E.H. 1985. The recognition concept of species. In: Species and Speciation, (ed.) E.S. Vrba. Transvaal Museum, Pretoria.

ROBERTS, B.R. & FOURIE, J.H. 1975. Common grasses of the northern Cape. Northern Cape Livestock Cooperative Limited.

SANDS, W.A. 1965. A revision of the termite subfamily Nasutitermes (Isoptera, Termitidae) from the Ethiopian region. *Bull. Brit. Mus., Entomol. Suppl.* 6: 1–172.

SOUTHWOOD, T.R.E. 1976. Ecological Methods. Chapman & Hall, New York.

VERNON, C.J. 1983. Aspects of the habitat preference and social behaviour of the white-browed sparrow-weaver. *Honeyguide* 13: 11–14.

VILJOEN, A.J. 1979. Die plantekologie van die Sandveld-Natuurreservaat: Beskrywing en klassifikasie van die plantegroei. M.Sc. dissertation, University of the Orange Free State, Bloemfontein, South Africa.

WILLIAMS, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton.

Appendix 1

A diferentiated Braun-Blanquet table of the results of the survey of herbaceous plants in the intensive study area at Bloemhof. Three plant communities are discernable:

1) the *Nidorella resedifolia* community.
2) the *Acacia erioloba* thornveld community.
3) the *Conyza bonariensis* ecotonal community.

The plant species encountered clearly indicate the arid affinities of the three plant communities. F=number of releves in which a particular plant spacies was encountered. Numbers in the table represent the relative biomass index for each species in a particular releve: 5 is the highest index.

Releve number: / Plant species.	F	344323333 701142369	33232222 80842569	1122141432101201001002100 3717631250965318894341075 2	4455545444 6821053794
Characteristic plants of the *Nidorella resedifolia* community					
Tephrosia lupinofolia	4	1 2 11			
Indigofera daleoides	4	111 1			
Kohautia lasiocarpa	3	1 1 1			
Cassia biennis	3	1 11			
Oxygonum dregenianum	2	11			
Nidorella hottentottica	2	11			
Dichoma macrocarpa	2	1 1			
Nidorella resedifolia	11	111111 11	11	1	
Tephrosia sp.	8	11 11	11 1		1
Helichrysum paronicoides	7	12 1 1	1 1 1		
Rhynchosia confusa	6	1 1111	1		
Bergia pantheriana	6	1 11	1 1 1		
Panicum kalaharense	5	11	11 3		
Requenia sphaerosperma	2	11			
Plants common to both the *Nidorella resedifolia* and the *Acacia erioloba* communities:					
Pogonarthria squarrosa	20	11 11111	1111111	22111 2	
Eragrostis pallens	16	1 112	1 1	2 1 22 131 1 2 1	
Tricholaena monachne	11	1 2 12	1111	1 1 1	
Noletia ciliaris	7	1 1	1	1 111	
Cyperus margaretaceus	6	1		1 11 1 1	
Heteropogon contortus	4	11	1	1	
Characteristic plants of the *Acacia erioloba* community					
Fellcia muricata	6			1 1 1 1 1 1	
Barleria macrostegia	4			1 1 1 1	
Acanthosycyos naudiniana	4			1 1 1 1	
Eragrostis curvula	2			1 3	
Commelina eckloniana	2			1 1	
Portulaca kermesina	2			1 1	
Plants common to both the *Acacia erioloba* and the *Conyza bonariensis* communities:					
Anthephora pubescens	16			3 1 2 113 3 113 1	22 3 11
Chrysochoma obtusata	6			1 1 11	1 1
Liliaceae	6			1 1 1 1	1 1
Mariscus rehmannianus	5			1 111	1
Solanum supinum	5			111 1	1
Schmidtia pappophoroides	5			13 3 1	1
Characteristic plants of the *Conyza bonariensis* community					
Conyza bonariensis	6				11111 1
Conyza floribunda	4				111 1
Oenothera indecora	3				1 1 1
Bidens bipinnata	3				1 11
Gnaphalium oligandrum	3				1 1 1
Delosperma cooperi	2				11
Arctotis venustra	2				11
Chenopodium album	2				11

Appendix 1 Continued

Releve number: / Plant species.	F	344323333 701142369	33232222 80842569	11221414321012010010021000 37176312509653188943410752	4455545444 6821053794
Plants that are common to all the plant communities:					
Eragrostis lehmanniana	49	23 111123	41111111	2313331 23331 33321234322	1131223111
Eragrostis tricophora	44	1 2 1 1	111 121	13211212112222322112112311	211 11221
Aristida congesta	43	112111121	11111 11	12111121 2211 112111 3131	11 1 11
Stipagrostis uniplumis	39	1341 1	113 1235	1211131 22321111231221 34	1 111
Walafrida densiflora	33	11 3 11	11213 12	21 13121 1 11 2 11	2111 1212
Hermannia tomentosa	31	11 11 111	11113111	11 1111 1 1111 11	11 1
Eragrostis superba	29	212111 21	21213	21222 21 1 14	22 112 1
Aristida stipitata	27	223153132	13112 31	22211 11 1	11 1
Trichoneura grandiglumis	23	232 11132	11211131	1 2 1 11 1	1
Cynodon dactylon	30	2112 114	11 121	2 14 1 2 323	4555551354
Tragus koeleroides	20	3 1		3 3 3 32433333 413 1	1 11
Brachiaria nigropedata	16	1 1	1 3	1 3 12 133	1 1122
Citrillus sp.	18	11 1 1	11 111 1	1 1	1111 11
Hibiscus microcarpus	15	111 111	1 1	1 11 1 1 1	1
Selago welwitschii	15	111 1 1	1 1 1	1 1 1 1 1 2	1
Shrub sp. (no. 127)	11	1 1 1 1	1 1	11	1 1 1
Plinthus sericeus	18	1 1	111	11111 1 1 1 1	1111
Sericorema remotiflora	12	1 1		1 111 1 1 11	11
Anthospermum rigidum	11		1 1	1 11 11 1	1 1 1
Acacia erioloba	11	1	1	1 11 1 11 1	1 1
Cleome rubella	7	1	1	1 1 1 1	1
Commmelina sp.	7		1	1 1 1 1	1 1
Pollichia campestris	7	1		1 1	1 1 11
Elephantorrhiza sp.	5		1	1 1	1 1
Themeda triandra	4	1		1 1 1	
Lithospermum cinereum	3	1			1 1
Indigofera filipes	3	1	1	1	
Casssia sp.	3			1 1	1
Asparagus sp.	3			1 1	1
Lightfootia denticulata	3	1	11		
Ipomoa ommaneyi	2			1 1	
Trachyandra laxa	2			3	1
Hertia pallens	2		1		1
Aristida mollissima	2		4	1	
Limeum fenestratum	2		1 1		
Indigofera sp.	1	1			
Cyperus sphaerospermus	1	1			
Salsola kali	1				1
Convulvulus sagittatus	1				1
Asclepias sp.	1				1
Stipagrostis sp.	1			1	
Hibiscus pussilus	1			1	
Setaria flabbelata	1	1			
Rhyncholytrum repens	1	1			
Sida ovata	1	1			
Solanum panduraeforme	1		1		
Acrotome inflata	1			1	
Rhynchosia venulosa	1		1		
Brachiaria sp.	1			2	
Osteospermum muricatum	1				1
Kylinga alba	1			1	
Senecio inaequidens	1			1	
Dichoma schinzii	1			1	
Elionurus muticus	1			5	
Amaranthus thunbergii	1				1
Helichrysum cerastioides	1			1	
Hermannia quartiniana	1			1	
Chenopodium carinatum	1				1
Lotononis calycina	1	1			
Tribulus sp.	1				1