Dietary overlap in plocepasserine weavers (Aves: Ploceidae)

J.W.H. Ferguson
George Evelyn Hutchinson Laboratory, University of the Witwatersrand, 1 Jan Smuts Ave, Johannesburg*

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The food taken by the closely related white-browed sparrow-weavers *Plocepasser mahali* and sociable weavers *Philetairus socius* includes both plant material and insects. An analysis placing food items into taxonomic categories indicates that the important food sources of both species are identical. Seasonal utilization of different food taxa was also similar between the two species. These similarities are interpreted in an evolutionary perspective.

Die voedsel wat deur twee naverwante voëlsoorte, nl. koringvoëls *Plocepasser mahali* en versamelvoëls *Philetairus socius* gevreet word, sluit beide plantaardige materiaal en insekte in. 'n Ontleding van die voedselitems in terme van taksonomiese kategorieë toon dat die belangrike voedseltaksa van beide voëlspesies identies is. Seisoenale gebruik van belangrike voedseltaksa van die twee voëlspesies het ook ooreengestem. Hierdie ooreenkomste word vanuit 'n evolusionêre oogpunt geïnterpreteer.

Present address: Zoology Department, University of Pretoria, Pretoria, 0002 Republic of South Africa

The sexually monomorphic weaver subfamily Plocepasserinae constitutes a distinct group of eight species in four genera (Hall & Moreau 1970). Plocepasserines are arid-adapted and occur in south-western and north-eastern Africa (Mackworth-Praed & Grant 1953, 1963). Two species occur in southern Africa, the white-browed sparrow-weaver *Plocepasser mahali* and the sociable weaver *Philetairus socius,* and are sympatric over large parts of Botswana, South West Africa/Namibia, Cape Province and Transvaal (Maclean 1973, 1985). Further, both species are locally common in *Acacia erioloba* thornveld in these areas, where they may be found nesting close to one another, or even in the same tree (Burger & Gochveld 1981). The large mass difference between the two species (*P. mahali* weighs 40 g (range 36,1 – 43,7; n = 74), compared with 27 g (range 23,8 g – 32 g; n = 116) for *P. socius* (Maclean 1973, 1985)) would suggest that these birds may exploit different food sources.

Specimens of both species collected in an area of sympatry provided an opportunity to investigate the food resources that they use. The aims of this paper are (i) to describe the food taken by each of these species and (ii) to discuss similarities in their food requirements.

Study area and Methods

Seventy-four white-browed sparrow-weavers and 39 sociable weavers were collected from May 1982 to April 1983 in an area immediately south of Bloemhof Dam (27°40'S / 25°39'E) in the north-western Orange Free State. This area is semi-arid with an annual rainfall of 420 mm concentrated in two rainfall peaks in November and March. The topography is flat and the vegetation is Kalahari Thornveld (vegetation type 16a2; Acocks 1975). *Acacia erioloba* is the most common tree in the area while *Eragrostis lehmanniana, E. tricophora, Brachiaria nigropedata* and *Tragus koeleroides* are common grasses.

Sparrow-weavers and sociable weavers were common in the area in 1982. However, after a number of sociable weaver nests had been destroyed during land clearing for maize farming, only two nests remained from which individuals could be collected. For this reason the dataset for sociable weavers was deliberately restricted compared to that for sparrow-weavers. Data were divided into four seasonal groups: December–February, March–May, June–August and September–November. Sample sizes for different seasons were of similar magnitude (Table 3). Specimens are housed in the Transvaal Museum, Pretoria and the Alexander McGregor Museum, Kimberley.

The relative importance of different plant species was assessed by counting the number of seeds of each species in the crops being analysed. Because arthropods are fragmented more than seeds, this approach could not be used for analysis of the insect diet. Rather, the mass of insect remains, dried to constant mass, was used as an indication of the importance of different taxa. The following methods were used to estimate the importance of particular food items:

(i) For estimating the importance of plant food relative to insect food, the mass of total vegetable food and of total arthropod food was measured for each crop.

(ii) The proportion of crops containing a particular food taxon was expressed as a percentage of the total number of crops analysed for each bird species (FREQ; Tables 1 & 2). This measures how many birds eat a particular food taxon.

(iii) A measure of the preference particular individuals have for a specific food item was derived by calculating: (a) The mean number of seeds per plant taxon in all crops containing that particular taxon (COUNT; Table 2); (b) the mean percentage mass of arthropod remains of a particular taxon in all crops containing that taxon (MASS; Table 1).

(iv) The number of seeds of each taxon was represented as a percentage of the total number of seeds of all plant taxa in all the crops analysed (FRACT; Table 2). The mass of arthropod remains of each arthropod taxon was

Table 1 Arthropods taken by plocepasserine weavers at Bloemhof Dam

Taxon		*Plocepasser mahali*				*Philetairus socius*			
Order	Family	FREQ[1]	MASS[2]	FRACT[3]	IC[4]	FREQ	MASS	FRACT	IC
Hemiptera	Tingidae	1	2	0,03	0				
Orthoptera	Gryllidae	1	1	0,01	0				
	Acrididae	18	10	0,84	15	33	3	1,03	34
Coleoptera	Histeridae	.3	24	0,48	1				
	Buprestidae	3	11	0,23	1	5	37	0,73	4
	Carabidae	3	25	0,45	1	3	3	0,06	0
	Tenebrionidae	3	8	0,32	1	8	9	0,48	4
	Scarabaeidae	16	15	2,40	38	15	9	1,21	18
	Curculionidae	86	11	6,95	598	97	13	10,85	1052
Isoptera	Termitidae	96	12	11,87	1139	95	10	8,57	814
Hymenoptera	Formicidae	82	5	2,33	191	49	5	1,51	74
	Vespoidea	9	5	0,21	2	5	2	0,11	1
Diptera	Unidentified	1	20	0,03	0	3	6	0,09	0
Arachnida	Unidentified	4	1	0,05	0	5	3	0,11	1
Heteroptera	Pentatomidae	18	5	0,48	9	18	3	0,35	6
	Reduviidae					3	8	0,09	0
Lepidoptera	Unidentified					8	14	1,19	9
Myriapoda	Unidentified					3	1	0,02	0

[1]FREQ: percentage of individual birds containing the designated arthropod taxon in the crop.
[2]MASS: mean percentage of individual crop contents of those individuals in which the particular taxon was found, expressed as mass.
[3]FRACT: percentage of a summation of all individual crop contents, expressed as mass.
[4]IC: Importance content, an index of diet importance: FREQ × FRACT, rounded to nearest integer.

Table 2 Plant food eaten by plocepasserines at Bloemhof Dam

	Plocepasser mahali				*Philetairus socius*			
	FREQ	COUNT	FRACT	IC	FREQ	COUNT	FRACT	IC
Category 1: Taken only by *P.mahali*								
Dactylotinium aegytium	1	1	0,1	0				
Cenchrus sp.	1	1	0,1	0				
Chloris gyana	1	1	0,1	0				
Cissamopelos sp.	1	1	0,1	0				
Cleome sp.	1	1	0,1	0				
Felicia sp.	1	1	0,1	0				
Passifloraceae	1	1	0,1	0				
Phlox paniculata	1	1	0,1	0				
Plantago lanceolata	1	1	0,1	0				
Selago sp.	1	1	0,1	0				
Sida sp.	1	1	0,1	0				
Rubiaceae	1	1	0,1	0				
Brassica tournefortii	3	1	0,3	1				
Rosaceae	3	1	0,3	1				
Euclea sp.	3	1	0,3	1				
Amaranthus sp.	3	1,5	0,4	1				
Digitaria sp.	3	2	0,5	2				
Cynodon dactylon	3	2	0,5	2				
Echium sp.	4	1,3	0,5	2				
Ipomoa sp.	3	2,5	0,7	2				
Vigna sp.	5	1,3	0,7	4				
Euphorbia sp.	3	3	0,8	2				
Tragus sp.	1	6	0,8	1				
Limeum sulcatum	5	2,3	1,2	6				

Table 2 Continued

	Plocepasser mahali				*Philetairus socius*			
	FREQ	COUNT	FRACT	IC	FREQ	COUNT	FRACT	IC
Category 2: Taken often by *P. mahali* but rarely by *P. socius*								
Sericorema sp.	8	6,7	5,2	42	5	1	0,2	1
Bulbostylus collina	5	11,7	6,2	31	3	7	0,7	2
Echinochloa crus-galli	5	15,8	8,3	42	5	1	0,2	1
Stipagrostis sp.	16	3,5	5,5	88	3	2	0,4	1
Oenothera sp.	7	3,8	2,5	18	3	1	0,1	0
Lithospermum sp.	5	5,8	3,0	15	5	1,5	0,3	2
Category 3: Taken frequently by both species								
Zea mays	64	1,2	7,2	461	53	1	2,1	111
Triticum sativum	26	5,9	14,8	385	33	1	1,3	43
Urochloa sp.	15	7,6	11,0	165	35	9,7	13,6	476
Celosia sp.	11	4,5	4,7	52	42	6,1	10,4	437
Limeum fenestratum	11	1,8	1,8	20	15	2	1,2	18
Citrullus sp.	11	1,1	1,2	13	23	1,2	1,1	25
Eleusine sp.	2	23,5	6,2	12	8	5,3	1,6	13
Category 4: Taken rarely by *mahali* but often by *socius*								
Gisekia sp.	1	26,0	3,4	3	30	37,7	45,2	1356
Commelina sp.	4	1,7	0,7	3	33	8,7	11,4	376
Solanum sp.	7	2,2	1,4	10	10	2,8	1,1	11
Portulaca sp.	7	5,6	3,7	26	10	1,8	0,7	7
Category 5: Taken only by *P. socius*								
Amaranthum sp.					10	1,5	0,6	6
Sorghum almum					10	5,5	2,2	22
Glyceria sp.					3	1	0,1	0
Holcus latatus					3	7	0,7	2
Karoochloa sp.					3	1	0,1	0
Pennisetum clandestinum					3	1	0,1	0
Rumex sp.					3	3	0,3	1
Trachyandra sp.					3	2	0,2	1
Tephrosia sp.					3	1	0,1	0
Chenopodium sp.					3	3	0,3	1
Cyperus sp.					3	1	0,1	0
Category 6: Taken rarely by both *P. mahali* and *P. socius*								
***Convolvus* sp.**	1	1	0,1	0	3	1	0,1	0
Eragrostis sp.	1	2	0,3	0	5	4	0,8	4
Panicum sp.	3	1	0,3	1	5	3,5	0,7	4
Polygonum sp.	3	1	0,3	1	5	4	0,8	4
Grewia sp.	3	1,5	0,4	1	5	1	0,2	1
Gossypium sp.	9	1	0,9	8	3	1	0,1	0
Rhus sp.	4	1	0,4	2	8	1	0,3	2
Setaria sp.	1	1	0,1	0	8	2,3	0,7	6
Sorghum bicolor	4	1	0,4	2	3	1	0,1	0
Erodium sp.	3	5,5	1,4	4	3	3	0,3	1
Sample size	74 birds; 761 seeds;				39 birds; 1014 seeds			

FREQ: % of individual birds containing the designated plant taxon in the crop.
COUNT: mean no. of seeds per crop in those individuals containing the designated plant taxon.
FRACT: percentage of a summation of all individual crops, expressed as counts of seeds.
IC: Importance content, FREQ × FRACT, rounded to nearest integer.

represented as a percentage of the total mass of all remains FRACT; Table 1). This represents the importance of each food taxon in the combined diet for each of the two bird species.

(v) For comparing the relative importance of food taxa within each kingdom, an importance index consisting of FREQ multiplied by FRACT for each arthropod or plant food taxon was calculated. I termed this index the Importance Content (IC) which ranged from 0,1 to 476 for plant taxa and from 0,01 to 1139 for arthropods. An IC < 10 was used to indicate taxa that were rarely eaten.

Results

Ratio of plants / arthropods in food

Both sparrow-weavers and sociable weavers eat significant amounts (> 15% of total food mass) of both arthropods and plant material throughout the year (Figure 1). In the case of sparrow-weavers, the proportion of arthropod material is about constant, varying between 0,36 of the total mass during the summer months and 0,26 during winter: however, differences between seasons are not statistically significant. The proportion of arthropods taken by sociable weavers fluctuated considerably from 0,49 during summer to 0,16 during winter, a statistically significant variation (Kruskal-Wallis $\chi^2 = 12,57$; $df = 3$; $p < 0,01$) (Figure 1). A Tukey multiple comparison of the sociable weaver data indicated significant ($p < 0,05$) differences between summer / autumn and winter / spring.

Food taxa eaten

A very large degree of overlap characterized both arthropod and plant food taken by the two bird species.

Arthropods. In terms of arthropod mass, weevils, scarabaeid beetles, termites and ants were the most important food items for both species. In addition, pentatomid bugs and crickets were frequently taken by both weavers. When combining FREQ and FRACT into IC indexes, the five most important arthropod food taxa are

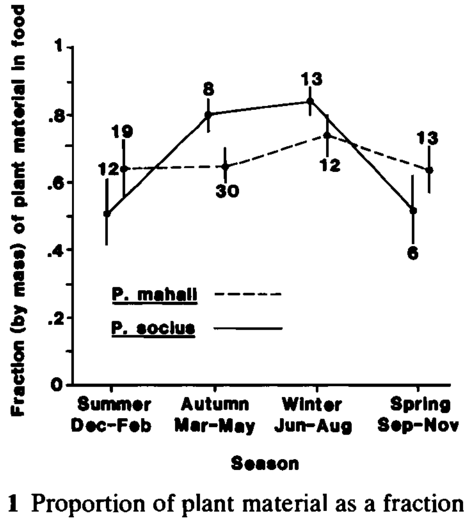

Figure 1 Proportion of plant material as a fraction of the total dried mass of food taken by white-browed sparrow-weavers *P. mahali* and sociable weavers *P. socius*. Vertical bars indicate standard error of the mean while numbers above or below bars indicate the number of crop contents examined for each season.

identical between the two weaverbird species. Wilcoxon rank sum tests of the dried mass of an arthropod taxon per crop did not reveal any differences between weaver species for any arthropod taxon.

Plant food. Cultivated crops formed an important part of the diet of both species. The plant food most commonly taken by both weavers was maize seeds (Table 2). Wheat was also commonly taken by both birds. Plant food not taken by the other species constituted 8% of the total mass of plant material taken by sparrow-weavers and 4% of that of sociable weavers. Two plant taxa, however, appeared to differ in importance between the two plocepasserine birds: the seeds of *Stipagrostis* grass species (*S. uniplumis* was common in the study area) were frequently taken by sparrow-weavers but rarely by sociable weavers. The converse applied to seeds of the shrub genus *Gisekia* (Table 2). Seeds commonly ingested by sparrow-weavers and rarely by sociable weavers constituted 31% of the total number of seed items taken by *P. mahali,* while the corresponding figure was 58% of the seed items eaten by sociable weavers. Wilcoxon rank sum tests on the number of seeds of a plant taxon in each crop did not reveal significant differences between weaver species for any plant taxon.

Seasonality in food taxa eaten

A large variation was evident in the seasonality of food taxa taken. Weavils (Curculionidae), termites and ants

Table 3 Seasonality in important plocepasserine food taxa. Numbers indicate the percentage of crops containing a designated taxon.

	P. mahali Season[a]				*P. socius* Season[a]			
Taxon	SUM	AUT	WIN	SPR	SUM	AUT	WIN	SPR
Arthropods								
Acrididae	26	10	8	30	50	38	23	17
Heteroptera	26	20	0	23	50	0	7	17
Scarabaeidae	16	20	0	23	17	25	15	0
Curculionidae	95	80	83	92	100	100	92	100
Isoptera	89	100	92	100	100	100	100	83
Hymenoptera	100	90	83	92	67	50	62	17
Plant food								
Triticum spp.	53	13	0	8	8	25	62	66
Commelina spp.	–	–	–	–	25	13	46	17
Urochloa spp.	11	17	17	8	42	0	46	17
Gisekia spp.	–	–	–	–	58	0	23	33
Celosia spp.	–	–	–	–	17	63	69	17
Zea mays	32	40	83	100	17	88	77	33
Stipagrostis spp.	0	0	58	23	–	–	–	–
Number of crops	19	30	12	13	12	8	13	6

[a]Seasons are defined as follows: Summer (SUM) Dec–Feb, Autumn (AUT) Mar–May, Winter (WIN) Jun–Aug, Spring (SPR) Sep–Nov. Dashes indicate that the sample size was too small to draw any firm conclusions.

were frequently taken throughout the year by both weavers (Table 3). Scarabaeid beetles, acridids and bugs were eaten mostly during the spring and/or summer by both species.

Maize was eaten throughout the year by both sparrow-weavers and sociable weavers. However, this food source was less often taken during summer (Table 3). Wheat *Triticum* sp. was commonly taken in spring by sociable weavers, but in summer by sparrow-weavers. The plant genera *Commelina, Urochloa* and *Gisekia* were eaten in summer and *Celosia* in winter by sociable weavers, while no such trends were evident in sparrow-weavers. *Stipagrostis* seeds were taken mostly in winter by sparrow-weavers.

Discussion

Differential digestion between seeds and insect exoskeletons, and among both arthropod and plant taxa complicates computation of the importance of different food taxa. The most quantitative way in which to compare the importance of different food taxa would be to translate these into energy values. However, differential digestion of food taxa does not make this feasible. Taxa having many weaver individuals taking them (high FREQ) and forming a large fraction of the total food taken (high FRACT) must be considered as more important food sources than those taxa having lower frequencies and / or fractions. This is why a combination of FREQ and FRACT was used in calculating IC. Differential digestion makes the use of IC in comparing taxa with others taken by the same weaver species risky. However, if we assume that digestion of food taxa is roughly similar in both weaver species, IC is valid in comparing the importance of a food taxon between the bird species.

The effect of agricultural activities on the diet of both the weavers is marked, maize and wheat being among their most important food sources (Table 2). In the absence of cultivation, the food preference of these birds may differ from that observed.

Results from this study differ in some respects from those of two other studies. Maclean (1973) reported that sociable weavers in the Kalahari Gemsbok National Park (KGNP) take some 80% by mass of their diet as arthropods, the most important of which were termites, Coleoptera, Hymenoptera, grasshoppers and Lepidoptera. Plant material rarely constituted more than 75% by mass of the sociable weaver diet measured by Maclean; the most important taxa were *Aristida* spp. and Cyperaceae. The arthropod taxa taken by KGNP sociable weavers agree closely with those taken at Bloemhof Dam. Compared with the present study, however, the plant food items of KGNP birds differed largely in quantity (ca. 20% by mass in the KGNP compared with 51–84% at Bloemhof) and in taxa. Lewis (1981) noted that the grass genera preferred by sparrow-weavers in the Luangwa Valley, Zambia, were *Urochloa, Dactyloctenium, Heteropogon, Hyparrhenia, Setaria, Echinochloa* and *Panicum,* and that grasshoppers were the insects eaten most frequently. These data on sparrow-weaver food preference differ widely from those obtained during the present study. Differences between Maclean's and Lewis's studies compared with the present one probably reflect differences in the availability of food taxa. The food preference of sparrow-weavers at Bloemhof was wide, with no main plant food taxa apart from cultivated plants. Lewis's (1981) data are not detailed enough to make a quantitative comparison with the present study, but it appears that the breadth of the Zambian sparrow-weaver plant diet is similar to that of the present study.

Even though the two bird species eat similar insect taxa, differentiation within the species of each food taxon (e.g. Curculeonidae) may take place, with identification of food items to species level precluded by fragmentation. Curculionids (a major insect food source of both bird species, Table 1) were all soft-bodied, as was evident from the massive fragmentation of exoskeletons. This suggests that the genus *Protostrophus* (the only soft-bodied weevil genus in the study area) is extensively eaten by both bird species.

Evolutionary interpretation of weaverbird dietary overlap and coexistence

Considerable dietary overlap is suggested by the fact that half of the arthropod taxa taken by both weavers species are taken by more than 10% of individuals within *P. mahali* as well as *P. socius.* In addition, six out of eight plant food taxa with IC values > 100 are taken by both species. Taking into account the size differences between these weaver species, this overlap appears unexpected: differences in gape size and beak length are assumed to be important in determining the size of food items and foraging methods employed. Numerous authors have attached great importance to the prevalence of interspecific competition in nature (e.g. Diamond 1978; Roughgarden 1983; Schoener 1984): if more than one species utilize the same resource, special explanations need to be found to explain why competitive character displacement did not take place. Connell (1983) postulated that resource overlap is favoured in environments with fluctuating resource characteristics when competition cannot operate effectively. When considering the evolutionary origins of dietary characteristics of plocepasserine weavers, dietary overlap needs to be considered separately from the sympatric distribution (geographic coexistence) of these species.

Dietary overlap. Since the existence of competition as a significant selective force is very difficult to demonstrate in any particular case (Wiens 1977; Connell 1983), more parsimonious explanations of dietary overlap may be more informative. The additional arguments relating to fluctuating environments and competition are probably unnecessary for explaining the food overlap between *P. mahali* and *P. socius* and it is more simply explained as traits which came about as adaptations to the food availability in the environments where these species evolved. If stasis characterizes the period of existence of a species (Eldredge & Gould 1972; Gould & Eldredge

1977), we could expect the food preference of modern weavers to resemble those at speciation. In this case both plocepasserine species must have evolved in arid or semi-arid habitat, as the food taxa observed for both these species observed during the present and other studies (Maclean 1973; Lewis 1981) indicate that a wide variety of arthropod and plant taxa typical of xeric habitats are utilized. The food preference which came about during the origins of the two weaverbird species have probably remained largely static during their times of existence and are still observed today. Differences in diet which arose at those times may also be independent of competition. If this were the case, arguments relating to why interspecific competition did not occur need not be invoked to explain plocepasserine dietary overlap.

Coexistence. Geographic coexistence of these birds suggests that interspecific competition between these two species was probably not intense at any time: if it did take place, one of the species would have disappeared, at least locally. In this sense Connell's (1983) and Wiens's (1977) argument about fluctuating environments and one about food resources that have not been limiting and which preclude interspecific competition, have some meaning. It could, therefore, be argued that the broad diet of both weaver species represent adaptations to an environment in which the availability of different food taxa fluctuate severely. However, such advantageous effects of a broad diet could merely be preadaptive (Gould & Lewontin 1979) and the hypothesis could only be vindicated if one could show that fluctuations in availability of food taxa are or were an important environmental constraint on these birds. Present knowledge is therefore not sufficient to show that these birds are adapted (*sensu* Williams 1966) to fluctuating food resources.

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