

Repertoire and structure of duet and solo songs in cooperatively breeding white-browed sparrow weavers

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Summary

White-browed sparrow weavers (*Plocepasser mahali*) are cooperatively breeding songbirds of eastern and southern Africa that live in small groups year-round consisting of a dominant breeding pair, and subordinate, non-breeding males and females. This species possesses an elaborate vocal communication system: solo songs are exclusively produced by the dominant male, duet songs are mainly produced by the dominant pair, and chorus songs, similar in syllable structure and temporal pattern to duet songs, are produced by all group members. We analysed songs of males and females with known social status recorded from different colonies in Zimbabwe and complemented these data by studying songs of captive birds at our institute. Solo songs are produced in one performance at dawn during the breeding season. Recordings of captive males on consecutive days revealed that males sing in a single solo performance $88.4 \pm 4.1\%$ of their total solo song repertoire. This suggests that dominant males recorded in Zimbabwe have a solo song repertoire of 67.0 ± 4.0 syllables, which is similar in size to those of captive males (58.3 ± 3.7 syllables). Repertoire sizes of both free-living and captive males are not correlated with the length of the solo song performance. Duetting is both antiphonal and in unison. Dominant males and females appear to have similar sized duet repertoires (51.9 ± 2.1 syllables). Recordings from captive pairs suggest that 75–98% of the repertoire is shared with higher syllable sharing in more experienced pairs. Since all group members engage in duets and chorus singing, we estimate that each subordinate male and female shares the duet syllable repertoire with the breeding pair. For dominant males, the duet syllables are widely distinct from those of the solo songs; of their total syllable repertoire only 2.1% occur in both repertoires. Further, solo song and duet song differ in the temporal organisation.

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Introduction

In the northern temperate zone, singing of songbirds is mostly confined to males. It is known that male song functions in territory defence and mate attraction (Catchpole & Slater, 1995). In those species where females do sing, their song is often shorter and less complex than male song and usually only produced at restricted times of the year (Hoelzel, 1986; Baptista et al., 1993). However, there is evidence that female song in these species is not just a by-product of temporarily high levels of testosterone but serves functions as in males (for review, see Langmore, 1998).

Among tropical songbirds, female song is commonly found. Whereas little is known about female solo song, much attention has been paid to the phenomenon of duet singing, which refers to the acoustic interaction between both members of a pair, often occurring with precise temporal coordination Farabaugh (1982). Duets can consist of simple patterns, such as the exchange of call notes, e.g. in parrots (Wright & Dorin, 2001) or can be precisely synchronised, giving the impression that the vocalisation is produced by a single bird (Wickler & Seibt, 1980). When male and female contributions occur in a strictly alternated fashion, duets are sung 'antiphonally'; when both birds produce exactly the same pattern of syllables at the same time, duets are sung in unison (Thorpe, 1975).

Songbirds acquire the stereotyped song pattern typical of adult birds by vocal learning, a process extensively studied in males of northern temperate zone species (Konishi 1985). In several duetting songbirds, pair formation requires another learning period, in which pair members may adjust their song type repertoires to build up pair-specific duet songs (Farabaugh, 1982).

Over the last decades, many different hypotheses have been proposed to understand why some bird species combine their songs into duets while the majority of species does not. In a recent review, Hall (2004) identified the most promising hypotheses to explain the functions of duets, which are mate guarding by both sexes, joint resource defence and signalling commitment.

The complexity of duet organisation can vary tremendously from one species to another (Helversen, 1980). At the lowest level, mates exchange simple call notes as in D'Arnaud's barbet (*Trachyphonus d'arnaudii*, Wickler & Uhrig, 1969) or the Aldabra white-throated rail (*Dryolimnas cuvieri aldabranus*, Huxley & Wilkinson, 1979). At an intermediate level, one bird has a repertoire of songs, which is combined with a single sound of the mate

as in the gonolek (*Laniarius barbarus*, Grimes, 1965) or the white-browed robin chat (*Cossypha heuglini*, Wickler, 1974; Todt et al., 1982). At the highest level, both partners have large repertoires of songs and combine them to complex duets as in the African Drongo (*Dicrurus adsimilis*, Helversen & Wickler, 1971) or the plain wren (*Thryothorus modestus*, Mann et al., 2003).

In terms of song behaviour, white-browed sparrow weavers (*Plocepasser mahali*) are extraordinary because in this species two distinct types of song exist, male-female duetting and male solo song. This species is a member of the family Ploceidae (Fry & Keith, 2004) that is primarily composed of non-duetting species; only two other species belonging to the genus *Ploceus*, the African forest weaver (*Ploceus bicolor*, Wickler & Seibt, 1980; Seibt et al., 2002) and the spectacled weaver (*Ploceus ocularis*, Skead, 1953; Kunkel, 1974) are known to duet. White-browed sparrow weavers are cooperatively breeding birds of eastern and southern Africa that live in pairs or in groups of up to 11 individuals. Groups consist of a dominant breeding pair and of male and female subordinates (Collias & Collias, 1978; Lewis, 1982; Ferguson, 1988b). The species is year-round territorial and all group members engage in territory defence. The breeding season is usually restricted to the rainy season but breeding of neighbouring groups is not necessarily synchronized (Earle, 1983a). Duet songs are mainly produced by the dominant pair of the group whereas the solo song is restricted to the dominant male. Additionally, all group members engage in chorus singing. Choruses involve more than two individuals but resemble duet songs in structure. Vocalisations of this species have first been described by Ferguson (1988a). He distinguished nine different 'call' types, including the duet song (= territorial call) and the male solo song (= mating song) and recognised those as complex songs in contrast to the other call types. In a recent comparison among three closely related weaverbird species Collias & Collias (2004) extended the number of vocal signals and they distinguished 13 different types in the white-browed sparrow weaver. Wingfield & Lewis (1993) observed the male solo song and the 'highly synchronised and complex' chorus vocalisations when they studied hormonal and behavioural responses to simulated territorial intrusions. All three studies describe the male solo song as occurring seasonally in the context of breeding whereas duet and chorus songs occur throughout the year and are associated with territorial aggression. It is further thought that each group member could produce the entire duet or chorus song alone, and when

birds are singing together, different members of the group sing different sections of the song (Ferguson, 1988a; Wingfield & Lewis, 1993). However, all previous bioacoustical studies of this species are rather descriptive.

In this study, we aimed to present a detailed quantitative analysis of the repertoire and temporal structure of solo and duet songs produced by male and female white-browed sparrow weavers. To this end, songs of individuals from different groups and with known social status were recorded in the field in Zimbabwe. These data were complemented by studying birds in captivity at Seewiesen.

Methods

Animals and study area

The white-browed sparrow weaver (*Plocepasser mahali*) belongs to the subfamily of sparrow weavers (Plocepasserinae) within the family Ploceidae (Fry & Keith, 2004). Birds were sexed according to the colouration of their beak (Earle, 1983b). In the subspecies *P. mahali terricolor* that we studied, males have a black beak and females have a horn-coloured beak. The study was conducted in the southern part of Zimbabwe on commercial farmland (20°12'S, 28°56'E). Data were collected in two consecutive years during the rainy season: from January 25 to March 19 in 2000, and from January 30 to March 1 in 2001 (photoperiod February: 12.6/11.4 L/D). During these periods, we hit the peak of the rainy seasons, which was January/February in 2000 and February in 2001.

Song recordings from birds in Zimbabwe

All vocalisations were recorded with a Sony TCD-5M portable cassette recorder (Sony Corp., Tokyo, Japan) equipped with a Sennheiser ME-88 directional microphone (Sennheiser electronic, Wedemark, Germany). Recordings were obtained within a distance of two to ten meters from the bird. All birds used for song analysis were previously captured and colour-ringed and their social status was known. Behavioural observations were conducted to identify the social status of each bird. A male was considered dominant, when it was repeatedly singing the solo song at dawn and when it was the last bird of the group entering the roosting nest at night. Additional males

within the group, which were fully mature but did not show the behaviour of the dominant male, were considered subordinate. The dominant female was identified by its breeding activity, by its frequent song output together with the dominant male and by chasing other females of the group.

Recordings of solo songs were obtained from 15 dominant males. Each male was recorded once in the morning between 5:00 and 5:45. In previous observations, we determined the approximate starting time of the solo song, which was generally coincident with or slightly before first light. Duet songs were recorded from dominant pairs of eight different groups. All duet recordings were made between 5:45 and 19:00. From most colonies, recordings of 50 to 60 duet songs could be obtained. From one group, only 34 duet songs were available.

Song recordings from birds in captivity

In March 2000, white-browed sparrow weavers were captured near our study site in Zimbabwe and imported to Germany. During the following years, the birds were kept pairwise in aviaries at the Max Planck Institute in Seewiesen (47°58'N, 11°14'E). From 2001 to 2004, pairs reproduced successfully. Offspring was separated from their parents when six to eight months old and subsequently kept singly or in pairs in aviaries with visual and acoustic contact to conspecifics.

Solo songs of six captive males were recorded at dawn during the months of April to September depending on the pairs' breeding activities (photoperiod June: 15.8/8.2 L/D). Recordings were made close to the outdoor aviaries within five meters from the roosting nest using the same equipment as in the field studies. For each male, the solo song was recorded on three different days.

For detailed analysis of duet singing, three pairs were recorded in cages (84 × 40 × 54 cm) in a soundproof room using a Sony TCD-5M portable cassette recorder (Sony Corp., Tokyo, Japan) equipped with two Sennheiser ME-67 directional microphones (Sennheiser electronic, Wedemark, Germany). Male and female of each pair were housed in separate cages with visual contact. In front of each cage a microphone was installed that was surrounded by foamed material to reduce reverberation. The two microphones were two meters apart. The female song was recorded onto the right track and the male song onto the left track of the tape. Recording levels were kept

identical for both channels. Recordings were made on different days between 10:00 and 18:00. During recording, visual contact was prevented. To stimulate singing, another pair was kept in cages in the same room but without visual contact to the pair, which was recorded. Pairs 1 and 2 were offspring raised in captivity. Pair 1 was approximately one year old; in Pair 2 the female was one and the male two years old. Pair No. 3 was wild-caught and an established pair since three years.

Song analysis

Sonographic analysis was done on a Macintosh Computer (Apple Computer Inc.) equipped with the sound analysis software Canary 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Sonographic printouts were generated with a laser printer Tektronix Phaser 840. For sound acquisition, songs were digitised with a sample rate of 22 kHz and a sample size of 16 bits. For frequency and time resolution of spectrograms, filter bandwidth was set at 342 Hz, with a frame length of 256 points and a grid resolution of 5.8 ms. For the analysis of the syllable repertoire, spectrograms of syllables used by each bird were sorted according to its structure by three independent observers. Each syllable in a bird's repertoire was assigned a type number by comparing it to a cumulative library of syllable types. For the solo song, we measured the total length of the performance ($N = 15$ males). For those males ($N = 7$) from which solo and duet songs were available we compared the temporal pattern of both types of song. The solo song performance was divided into strophes and in each strophe we determined the total number of syllables, phrase length, syllables per phrase and the repetition rate of syllables within phrases (for definitions see Results).

For duet songs, male and female recordings were analysed as separate tracks. Printouts of spectrograms were generated displaying the male track in the upper pane and the female track in the lower pane. From these recordings, we generated a library of syllable types for each bird and we determined the proportion of syllable types shared. Although male and female vocalisations were recorded with separate microphones into two separate channels, it was not possible to prevent that a signal recorded in one track always occurred, at lower amplitude, in the second track. To clearly distinguish between syllables sung by one individual and those sung in unison, we measured the difference in average intensity (dB) between the selected syllable on track 1 and the

same syllable appearing on track 2. The outline of a syllable was selected with cursors and intensity measurements were performed with the built-in function of the software. In harmonic syllables, we measured the intensity at the lowest frequency only. Syllables sung by a single bird on track 1 appeared on track 2 at half the intensity of track 1. Syllables with similar intensity values on both tracks were clearly sung by both birds in unison. When the difference in intensity for a selected syllable was less than two-fold between both tracks, we inspected the composition of the syllable in more detail. Intensity measurements and stereo playback at different speeds then revealed that parts of the syllable were sung in unison and other parts by a single bird. In these cases, we considered the syllable as sung by both birds. From all recordings per pair we measured the number of different syllables sung by each sex constituting the bird's duet repertoire size and the number of syllable types shared. For each duet, we determined the length, the total number of syllables, the proportion of syllables sung by each sex and the proportion of syllables sung in unison.

Statistical analysis

Statistical analyses were done with Prism 3.0 (GraphPad Inc). All data were analysed by non-parametric statistics. Performance length and repertoire size of the solo song was compared between males from Zimbabwe and those recorded in Seewiesen with the Mann-Whitney *U* test. Relationships between song length and repertoire size were analysed with Spearman rank correlation. Comparison of strophe length and number of syllables per second of solo and duet songs was done with Wilcoxon signed rank test. Fisher's exact test with Yates' correction was used to compare syllable repetitions between both types of song. All tests were two-tailed and the significance level was fixed at $\alpha = 0.05$. Data are presented as means \pm standard error.

Results

General description of vocal behaviour

Songs of white-browed sparrow weavers can be classified into solo songs, duets, and chorus songs. From field observations it was derived that solo songs were performed exclusively by the dominant male in the group. Duet

songs were mainly performed by the dominant pair, whereas all group members engaged in chorus singing and emitted calls. Solo songs were only sung at dawn. Duet songs were performed throughout the day. Duets could be initiated by either sex and were not strictly antiphonally sung but some syllables were sung in unison. The structure of chorus songs resembled that of duets except that more than two group members participated. Choruses were frequently heard during aggressive encounters with neighbouring colonies. On a diurnal basis during the breeding season, song behaviour of a group had the following pattern: At dawn, the dominant male started singing the solo song while still in the roosting nest. This song continued for up to 20 minutes with several pauses. During singing, the male usually left the roosting nest and continued to sing from different trees within the territory. After the dominant female had left her roosting nest, the pair would begin to duet. The frequency of duet singing seemed to be highest during the first hour in the morning. During the day, duet and chorus singing alternated with foraging and resting periods. In Zimbabwe, we frequently observed all group members singing chorus songs at their territory boundaries. At dusk, the dominant pair sang a series of duets while the other group members already entered the roosting nests. The dominant male was the last bird entering the roosting nest, after 5 to 10 minutes of continuous calling.

Solo songs of dominant males

The solo song consists of consecutive syllables either sung as single syllables or in phrases that are combined into strophes (Figure 1). Syllables are stereotyped motor units that consist of one to four elements. A performance of solo song is defined as the time between the first syllable sung by the male in the morning and the last syllable before it started duetting with the female. The length of such a performance differed greatly between males, ranging from 370 to 1130 s (mean = 698.0 ± 65.3 s). Strophes of the solo song are separated by pauses longer than 3 s. Mean strophe length is 19.54 ± 4.92 s with 3.77 ± 0.31 syllables sung per second. Phrases are defined as combinations of same or different syllable types where at least one type is repeated several times and which contains no pauses longer than 200 ms. Mean phrase length is 1.19 ± 0.11 s with 8.32 ± 0.69 syllables sung per second and a syllable repetition rate of 10.45 ± 0.93 Hz. On average $47 \pm 4.61\%$ of all solo song syllables occur in repetitions. Mean repertoire size for a single performance

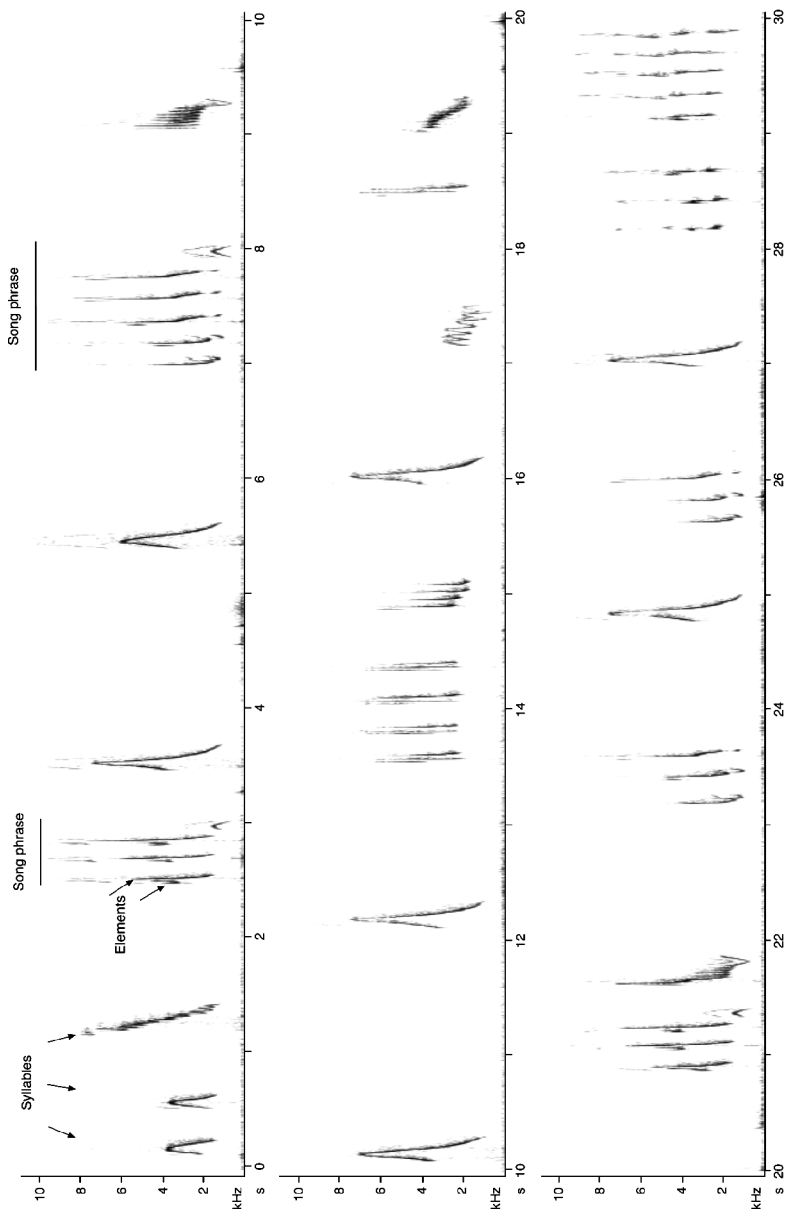


Figure 1. A sequence of 30 seconds of the solo song from a dominant male recorded in Zimbabwe. The song consists of single syllables and syllables arranged in phrases. Song phrases are combinations of same or different syllable types where at least one type is repeated several times and contains no pauses longer than 200 ms. Mean song length of males in Zimbabwe was 698.0 ± 65.3 seconds.

of solo song across 15 males recorded in Zimbabwe is 67.0 ± 4.0 syllable types. There is large variation between males, ranging from 48 to 92 syllable types. However, there is no significant correlation between length of the performance and repertoire size ($r_s = 0.30$, $p > 0.05$, $N = 15$). Males singing a longer solo song do not have larger repertoires. For all males, cumulative curves of the number of different syllable types have an asymptotic shape (Figure 2a). The bandwidth of the solo song comprises about 10 kHz, ranging from 0.5 to 10.5 kHz.

Estimates of the total syllable repertoire of the solo song could be obtained from six captive males, which were each recorded on three different days. Mean length of the solo song per single performance was 1669.4 ± 234.0 seconds. Compared to the males recorded in Zimbabwe, captive males sang significantly longer solo songs ($U = 0.0$, $p < 0.001$). However, this was not reflected in repertoire size. Mean number of different syllable types sung by captive males per single performance was 58.28 ± 3.71 , which is similar to males sampled in the field ($U = 32.0$, $p > 0.05$). Also, similar to males in the field, repertoire size was not significantly associated with song length in captive males ($r_s = -0.029$, $p > 0.05$). Comparison of the cumulative repertoire size between the three recording sessions showed a mean proportional increase from the first to the second recording session but not from the second to the third session (Figure 2b). In a single performance of the solo song, a male sings $88.4 \pm 4.1\%$ of its total solo song syllable repertoire. Based on this result, we estimated that the mean total repertoire size of the solo song of the males recorded in Zimbabwe was 75.9 ± 4.5 syllables.

Duet songs of dominant pairs

Duets are defined as overlapping bouts of sounds produced by both members of a pair (Farabaugh, 1982). A duet of a pair of sparrow weavers consists of a series of rapidly sung syllables in a continuous, precisely timed fashion and lasts usually 2 to 4 seconds (2.84 ± 0.11 s, $N = 8$, Figure 3). Syllables are produced antiphonally or in unison with 4.98 ± 0.10 syllables per second. A single bird was never observed to produce a complete duet sequence alone. Often a duet starts with a harsh buzz (type 1, Figure 3a), performed by either sex. Alternatively, duets can start with 1 to 3 introductory syllables (plain numbers; Figure 3b). During the duet, usually two and sometimes three fast frequency-modulated syllable types (indicated by numbers in squares;

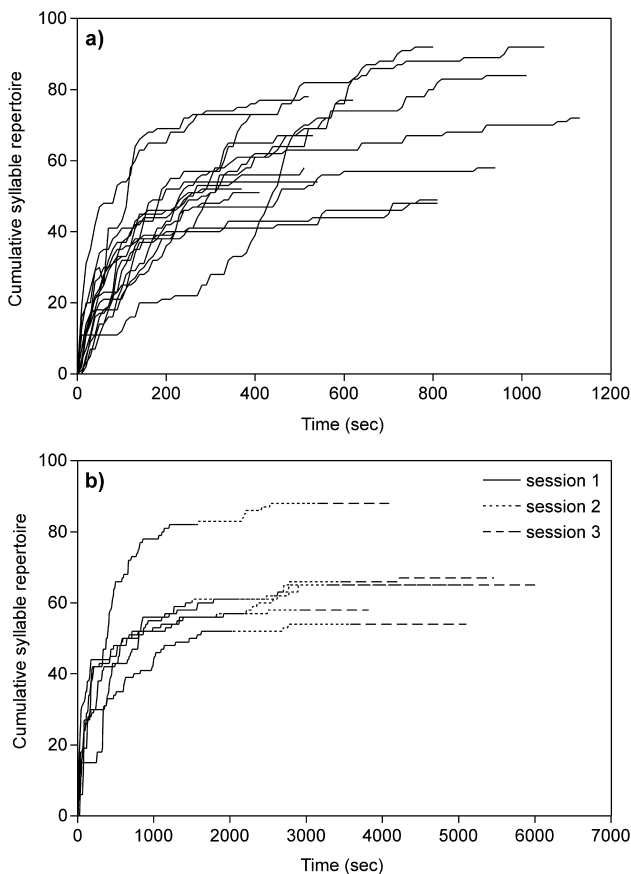


Figure 2. Cumulative curves of the syllable repertoire for a single performance of solo song of 15 males recorded in Zimbabwe (**a**). One male made large pauses in the beginning of the song, which gave a less steep increase in the first part of the curve. Mean repertoire size is 67.0 ± 4.0 syllable types. In (**b**), the cumulative syllable repertoires of solo song from six captive males recorded on three consecutive days are shown. The different line patterns indicate the different recording sessions. Repertoire sizes increased from session 1 to session 2 but not from session 2 to session 3. Analysis based on a single performance (**a**) underestimated the repertoire by about 10% and suggests a total solo song repertoire of 75.9 ± 4.5 syllables.

Figure 3a, b) are alternated with a slow frequency-modulated whistle, which is often of harmonic structure (indicated by numbers in circles; Figure 3a, b). Whistle and fast-frequency-modulated syllables differ significantly in length ($U = 0.0$, $p < 0.001$) and in bandwidth ($U = 0.0$, $p < 0.001$). Phrases do not exist within duet songs, because no syllables occur in repetitions.

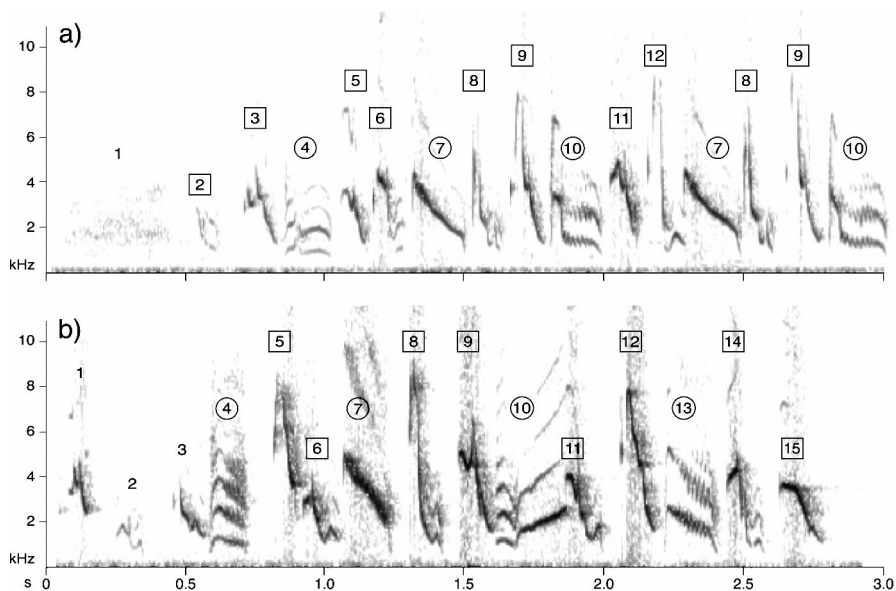


Figure 3. Spectrograms showing two duets of a dominant pair recorded in Zimbabwe. The different syllable types are numbered. Duets are initiated by either sex. Typically, duets begin with a harsh buzz (type 1 in **a**) or 1 to 3 introductory syllables (types 1 to 3 in **b**). During the duet, two frequency-modulated syllable types (numbers in squares) are alternately produced with a whistle type (numbers in circles) and this pattern is repeated several times. In **a**, syllables 7 to 10 are repeated once, in **b**, all syllables are different.

Two fast frequency-modulated syllable types could repeatedly occur in the same combination thereby building a motif. The bandwidth of duet songs comprises 0.5 to 9.5 kHz.

For duets recorded in Zimbabwe, we analysed the repertoires of pairs because it was not possible to distinguish between syllables produced by the male and those produced by the female. Mean duet length was 2.84 ± 0.11 s and on average 4.98 ± 0.10 syllables per second were sung. Mean duet repertoire size of dominant pairs was 51.9 ± 2.1 syllables (range: 45 to 61). There was no mean proportional increase in duet repertoire size between 40 and 50 duet bout recordings suggesting that 40 duets are sufficient to reveal total duet repertoire size (Figure 4).

To estimate repertoire size of individual birds and to clarify how each sex contributes to duet singing, three pairs were studied in detail in captivity. The three pairs differed in terms of mating experience, which is reflected in their duetting performance and allowed to draw conclusions about the

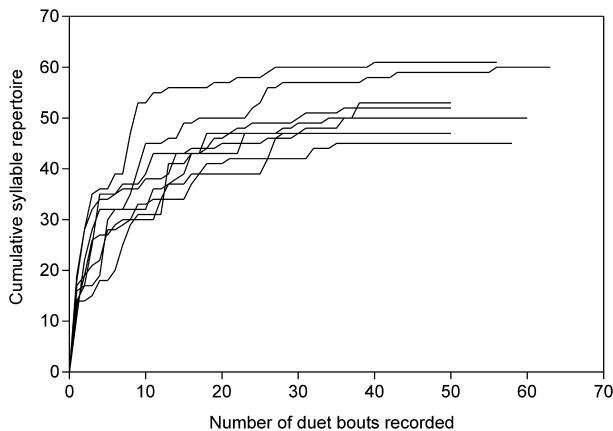


Figure 4. Cumulative curves of different syllables plotted against the number of analysed duet songs of eight dominant pairs from Zimbabwe. After 40 duet bout recordings there was no further increase in mean duet repertoire size.

development of duet singing. Pairs 1 and 2 were not paired prior to recording and, therefore, were not experienced in duet singing. Pair No. 3 was an established pair since three years.

Pair 1 vocalised simultaneously but did not produce precisely timed duets and no syllables were sung in unison. Therefore, it was not difficult to discriminate between syllables sung by the male (Figure 5a, upper panel) and those sung by the female (Figure 5a, lower panel). The number of different duet syllable types was found to be nearly identical in both sexes and surprisingly was almost twice as high as the mean number of duet syllables found in dominant pairs from Zimbabwe. Both birds shared 72 syllables types, representing 75% of the male's and 83% of the female's duet repertoire (Table 1).

Pair No. 2 vocalised in duets with syllables produced antiphonally and some syllables produced in unison. However, most of the duets were not exactly timed and were often incomplete in structure, i.e. the whistle syllable types, which usually occur several times within a duet, were missing (Figure 5b). Syllable repertoires of both sexes were of equal size and were about 15% smaller than those of Pair 1. Both birds shared 71 syllables types, representing 95% of the male's and 96% of the female's duet repertoire. Per duet, male and female contributed equal numbers of syllables and 58% of the syllables were sung in unison (Table 1).

Pair 3 behaved similar to dominant pairs observed in Zimbabwe. Duetting was frequent throughout the day, completely structured and precisely timed

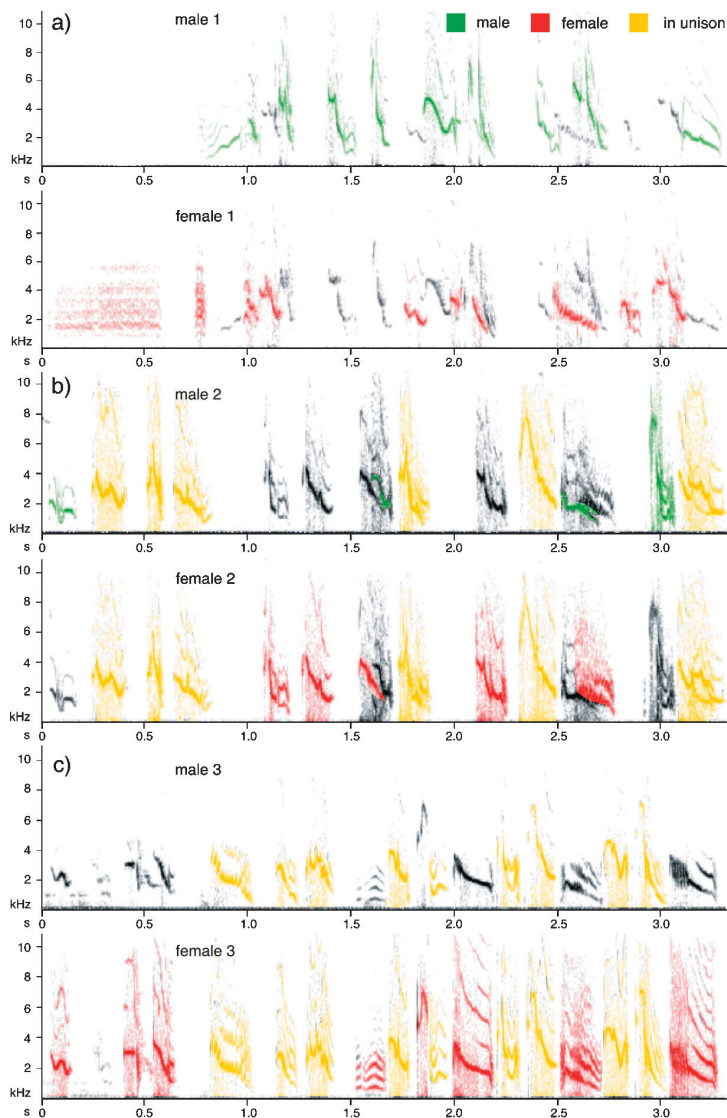


Figure 5. Duet vocalisations of the three pairs studied in captivity. Syllables produced by either sex and those sung in unison are colour-marked. Pair 1 (a) is most inexperienced. Songs were neither antiphonal nor in unison and lacked the duet structure described for pairs from Zimbabwe. Pair 2 (b) produced duets with syllables sung antiphonal and in unison but that were not always precisely timed. On two occasions, male and female were singing different syllables (time point 1.6 and 2.6). Whistle types were mostly missing. Pair 3 (c) produced duets similar to pairs recorded in Zimbabwe. Several syllables were sung in unison but the whistles were mostly produced by the female alone.

Table 1. Parameters of duet song analysed in captive pairs of white-browed sparrow weavers.

Song parameters	Pair 1 (4200 sec of song analysed)	Pair 2 (<i>N</i> = 38 duets)	Pair 3 (<i>N</i> = 27 duets)
Duet length (s)	–	3.36 ± 1.34	2.68 ± 0.97
No. of syllables per duet	–	14.95 ± 5.96	13.37 ± 4.79
No. of syllables per second	–	4.49 ± 0.61	5.00 ± 0.69
Percent of syllables sung by male per duet	–	78.84 ± 24.32	78.63 ± 18.62
Percent of syllables sung by female per duet	–	79.62 ± 14.29	83.13 ± 22.88
Percent of syllables sung in unison per duet	–	58.76 ± 27.36	62.03 ± 23.19
Female syllable repertoire size	87	74	58
Male syllable repertoire size	96	75	55
Shared repertoire size	72	71	54

(Figure 5c). Similar to the other pairs, male and female had nearly equally sized duet repertoires. However, these were about 25% smaller than in Pair 2 and 40% smaller than in Pair 1. Both birds shared 54 syllables types, representing 98% of the male's and 93% of the female's duet repertoire. Per duet song, male and female contributed equal numbers of syllables and produced 62% in unison. Compared with Pair 2, Pair 3 produced a higher number of syllables per second and duets were shorter. Summarized for all recordings, the female sang 50% of all whistles within duets alone whereas the male sang only 7% alone. In unison, the pair produced 43% of such syllables. Since the type of whistles used by the male or female alone varied between duets, there were no sex-specific sub-repertoires.

In summary, the songs from three captive pairs revealed that both members of the pair have similar sized duet syllable repertoires. Further, in the two pairs with structured duets, males and females shared 93 to 98% of their syllables. Therefore, it is likely that the repertoire sizes determined for dominant pairs in Zimbabwe can be fully assigned to each pair member.

The songs of subordinate males and females

Chorus songs were of similar structure as duet songs of dominant pairs but additional group members participated in singing (Figure 6). Therefore, syl-

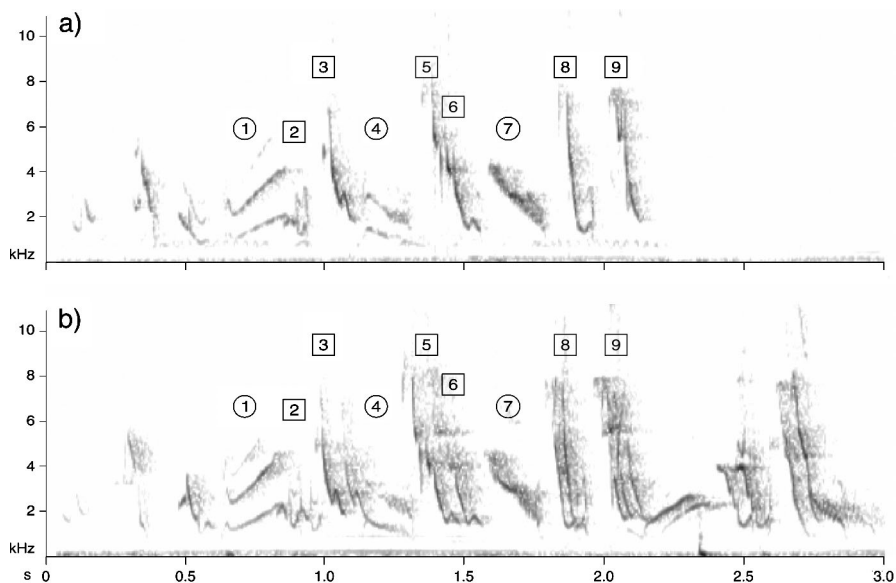


Figure 6. Spectrograms showing a duet song (a) and a chorus song (b) of the same group recorded in Zimbabwe. Choruses resemble in structure duet songs except that more than two birds are singing. Same numbers indicate same syllable types. Choruses are not as coordinated as duets. Therefore, syllables often overlap (e.g. 8, 9).

lables mostly overlapped and from recordings made in the field it was impossible to distinguish between syllables produced by different individuals. For this reason chorus songs were not subject to quantitative analysis. In captivity, birds would unfortunately not establish groups to facilitate the study of chorus songs. Besides syllables produced by subordinate group members during chorus singing that matched the syllables produced by the dominant pair (Figure 6), subordinates participated in chorus singing with syllables that differed from those currently sang by the dominant pair. These syllables were, however, part of the dominant's repertoire used in other duets. These observations suggest that subordinate males and females have similar sized duet repertoires as dominant individuals.

Comparison of solo and duet songs of dominant males

The temporal organisation of the solo song differs from duet songs in having longer strophes ($T = 28$, $p < 0.05$) and a lower number of syllables per seconds ($T = 27$, $p < 0.05$). Within duet songs, repeated syllables

were absent whereas they occurred regularly in solo songs ($p < 0.05$). The composition of the solo and duet song repertoire of males ($N = 7$) was compared by 3 independent observers. These comparisons showed that $57.2 \pm 2.3\%$ of the total repertoire consisted of syllables that are unique to the solo song and $40.7 \pm 2.4\%$ that are unique to duet songs. Only $2.1 \pm 0.6\%$ of the syllables occurred in both types of song. This means that dominant males possess two distinct syllable repertoires. In consequence, we assume that the total syllable repertoire constitutes in males the sum of duet and solo song repertoire and in females the duet song repertoire. Mean total repertoire size for those dominant males, where both types of song were available, is 128.3 ± 8.3 ($N = 7$), ranging from 104 to 158 syllables and differs from female repertoire, which is 51.9 ± 2.1 ($N = 8$), ranging from 45 to 61 syllables ($U = 0.0$, $p < 0.001$).

Discussion

Pattern of solo song

In the present study, we have described the song behaviour of male and female white-browed sparrow weavers. The solo song is exclusively performed by the dominant male once a day at dawn and can last up to 20 minutes and in captivity even longer. Importantly, syllable types used in solo singing were found to be different from those used for duetting, which contrasts with the descriptions of Collias & Collias (2004). In difference to the present study, these authors did not perform detailed quantitative measurements and did not relate vocalisations to individual birds. Next to this difference in repertoire composition, duets and solo song differ in the temporal organization: compared to duets, strophes of solo songs are longer, fewer syllables are sung per second, and about half of the syllables in solo songs occur in repetitions. Although similar phrases could occur repeatedly, song types defined as fixed patterns of phrases could not be identified. Among duetting species, male solo song occurs frequently, e.g. in the southern bou-bou shrike (*Laniarius ferrugineus*, Harcus, 1977), in the white-browed robin chat (Todt et al., 1982), in the spotted morning warbler (Todt & Fiebelkorn, 1980) or in *Thryothorus* wrens (Farabaugh, 1983; Levin, 1988). However, in all of the species studied so far, solo singing is referred to as when males or females sing parts of their duet contributions alone. The pattern found in white-browed sparrow weavers, where males have two different repertoires, which

they sing with different motor programs at distinct times on a diurnal basis can therefore be regarded as unique. Preliminary observations of anteater chats (*Myrmecocichla aethiops*), a group living and duetting turdid species of eastern Africa, suggests that this species has a similar pattern of song behaviour, with males singing solo songs only at dawn (Helvesen, 1980).

Repertoire size and length of solo songs

Single recordings of solo song from males in Zimbabwe revealed repertoires ranging from 48 to 92 different syllable types, representing almost 100% difference between males. Such differences are also known from other species with large repertoires, e.g. the starling (Eens et al., 1992), the sedge warbler (Catchpole, 2000) or the northern mockingbird (Derrickson, 1988). The variation found by Eens et al. (1992) was attributable to the fact that yearling males had significantly smaller repertoires than older males. An age related increase in repertoire size could account for the variation found in white-browed sparrow weavers. Currently, no data are available whether these birds can acquire new syllable types as adults. Single performances of captive males covered 84 to 96% of their total solo song repertoire. The measure of syllable repertoire size obtained from males in Zimbabwe is therefore a good estimate of total repertoire size and enables to make comparisons among males. The finding that captive males sang significantly longer solo songs than males in the wild is certainly related to conditions associated with captivity, e.g. reduced foraging time due to high food abundance, fewer interactions with neighbouring groups and natural day light of up to three hours longer compared to Zimbabwe.

Among white-browed sparrow weavers the length of the song performance was highly variable. Because larger repertoires were not related to singing longer songs, such variation might represent different singing strategies. In nightingales, three forms of temporal performance roles have been identified, namely birds being inserters, overlappers or autonomous singers, which are thought to convey different types of information between territorial neighbours (Hultsch & Todt, 1982). Neighbouring groups of white-browed sparrow weavers in Zimbabwe were about 50 meters apart providing the opportunity for vocal interaction among solo singing males. Counter singing of males during solo vocalisations has been observed for example in the tropical anteater chat (Helvesen, 1980).

Pattern of duet song

The duet songs of white-browed sparrow weavers are complex vocalisations, consisting of parts produced either antiphonal or in unison and comprise a large number of different syllable types. In individual duets, syllables are arranged in motifs that are combined with whistles in various ways to form longer sequences. Some of these sequences were repeatedly produced in its complete structure, indicating that duets are not random sequences of syllables and may be seen as song types. Nonetheless, due to the high number of possible syllable combinations, we measured the syllable repertoire instead of a song type repertoire.

Duet repertoires of dominant pairs in Zimbabwe ranged from 45 to 61 different syllables. Studies on two captive pairs showed that each partner possesses most (93-98%) of the duet syllable repertoire suggesting that both pair members had similar repertoire sizes and contributed equally to individual duets. In terms of the level of complexity defined by Helversen (1980), the white-browed sparrow weaver clearly performs at the highest level together with species such as the African drongo (Helversen & Wickler, 1971) or the plain wren (Mann et al., 2003). In the drongo, single duets can comprise as many as 40 syllables and each individual contributes up to 20 syllables. These birds sing strictly antiphonal and have sex-specific repertoires. Further, the occurrence of a particular syllable within the Drongos' duet depends on the preceding syllable of the partner and on that of the bird's own song. Although white-browed sparrow weavers have no sex-specific repertoires the use of some syllable types, e.g. whistles, appears to be sex-typical. A whistle mostly sung by the female alone precedes a particular combination of fast frequency-modulated syllables constituting a motif (personal observation).

Concerning the size of the female repertoire, the white-browed sparrow weaver is the species with by far the largest syllable repertoire reported. Repertoires of females of duetting *Thryothorus*-wrens, for example, comprise maximally 15 different syllable types (Gahr et al., 1998). Similar to the female, the size of the male duet repertoire is among the largest reported repertoires (Gahr et al., 1998). Since subordinate males and females participate in chorus singing, a 'duet' with several or all group members, and since these songs appear to be similar to the duet of the dominant pair, it is likely that all group members share the same repertoire size.

Beside the large repertoires of both the male and the female, the white-browed sparrow weaver is special regarding the temporal pattern of duets.

Most species possess a distinct temporal pattern, which is either antiphonous and often based on sex-specific repertoires, e.g. in buff-breasted wrens, bay wrens or several shrikes of the genus *Laniarius*, or synchronous e.g. in the African forest weaver. In contrast, captive white-browed sparrow weavers produce on average 60% of the syllables within duets in complete synchrony whereas the remaining syllables are uttered antiphonally. Although both pair members were capable of producing all syllables, a single bird never produced a complete duet alone. Since the amount of antiphonal and unisono singing was studied in detail in captive birds, conditions related to captivity might have influenced the pattern of singing. There is evidence from one study of captive tropical bou-bou shrikes (*Laniarius aethiopicus*), that on occasions the normally antiphonal singing pattern can be switched to complete synchrony for a short time, e.g. when pair members were reunited after a period of separation (Thorpe, 1975).

Development of duet singing

The study of captive birds allowed drawing conclusions about the development of duet singing because the three pairs differed in duetting experience. This was reflected in a difference in temporal precision: continuous vocalisation in Pair 1 versus precisely timed duets in Pair 3. Surprisingly, repertoire sizes gradually declined from the most inexperienced to the most experienced pair but were always identical in pair members. During pair formation, both members might build up a pair-specific duet repertoire through learning from each other or a tutor. Further, syllables that are not shared after this learning period may be discarded. The latter mechanism would be compatible with the model of action-based learning proposed by Marler & Peters (1982) and (Marler, 1997) for song learning in males. The model proposes a developmental overproduction and a selective attrition of unused song types during crystallisation. The process of selection is mediated by social interactions and its timing varies considerably and can in some species be extended into the first breeding season (Marler, 1997). Pair 1 and 2 of our study species recorded in captivity was at the beginning of pair formation already sexually mature and produced duet syllables similar in structure to older pairs. Similar, African forest weavers, which acquire their full repertoire usually when 5 to 6 months old, are able to adjust their song type repertoire to conspecifics up to an age of two years (Seibt et al., 2002). It remains to be seen whether

duet repertoire composition of white-browed sparrow weaver pairs changes later in life after experimentally induced remating with different partners. There is evidence from a study of buff breasted wrens (*Thryothorus leucotis*) that newly established pairs build up a larger number of duet types from each individual's song type repertoire whereas old pairs minimise the number of duet combinations (Farabaugh, 1983).

Functions of solo and duet song

Previous studies on white-browed sparrow weavers have indicated that the male solo song is associated with the breeding season and that it is not affected by territorial challenges (Ferguson, 1988a; Wingfield & Lewis, 1993). Our own observations point in the same direction. In Zimbabwe, certain groups started dawn vocalisations throughout the study period with duets although males of neighbouring groups performed solo songs. Moreover, territorial challenges during the day were accompanied by intense duetting but never by solo singing. Similar patterns were observed in captivity (see below). Further, not all males performed solo song exactly at the same time of the year but did always when they engaged in breeding activities.

Thus, it seems reasonable that the solo song functions mainly in intersexual communication, i.e. in stimulating reproductive development of the mate ensuring reproductive synchrony between mates. Intrasexually, the solo song might be used to assess and establish social relationships between neighbouring males, because it is a long, simultaneous display.

Thorpe (1972) derived from extensive studies on several duetting species the conclusion that duetting functions primarily in mate recognition and maintaining contact thereby replacing visual displays in species living in dense tropical vegetation. Since then, this topic has attracted a large number of studies and many hypotheses have been proposed about its functions (for review, see Hall 2004). Territory defence is clearly one function of duetting (Seibt & Wickler, 1977). We hypothesise that duet vocalisations of white-browed sparrow weavers are directed towards territory neighbours. Pairs usually perform loud duets when in close proximity and frequently engage in counter-duetting or chorusing with neighbours at their territory boundaries. Moreover, in situations of instability, e.g. after invasions or after rearrangement of neighbours in captive pairs the intensity of duet song was much increased and remained high for several hours or even days. Further, simulated territorial intrusions elicited a significant increase in the frequency of

chorus singing performed by all group members (Wingfield & Lewis, 1993). These data strongly support the hypothesis that a major function of duets in this species is territory defence.

Next to the 'joint resource defence' hypothesis (see above), the present data support the 'signalling commitment' hypothesis (Hall, 2004) to explain duetting in white-browed sparrow weavers. The latter was proposed by Wickler (1980) on the basis of the highly synchronised duet songs of the African forest weaver. This hypothesis states that duet songs originate from territorial displays but that the evolution of highly complex and pair-specific duets cannot be explained by this function. Instead, elaborate and pair-specific duets require investment of time and energy from partners in learning such songs thereby signalling commitment to the partner and reducing the risk of desertion. In white-browed sparrow weavers, the existence of long-term partnerships (Lewis, 1982) as well as a learning period for duet songs, so far only shown in young captive pairs, supports this hypothesis.

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