

Macro-geographic dialects and changes with time in the song of the Splendid Sunbird *Cinnyris coccinigastrus*

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Summary

Song dialects of male Splendid Sunbirds recorded in seven West and Central African countries illustrate marked spatial variation throughout its range. Songs recorded at intervals of several years at fixed localities suggest that changes in local dialects are slight over intervals of up to 11 years but are more apparent over a 30-year interval. Males usually sing one dialect but one male sang two intermittently.

Résumé

Dialectes macro-géographiques et modifications dans le temps du chant du Souimanga éclatant *Cinnyris coccinigastrus*. Des dialectes dans le chant du Souimanga éclatant enregistré dans sept pays d'Afrique de l'Ouest et d'Afrique Centrale illustrent une variation spatiale marquée à travers son aire de répartition. Les chants enregistrés à intervalles de plusieurs années dans les mêmes localités suggèrent que des modifications dans les dialectes locaux sont peu marquées dans des intervalles allant jusqu'à 11 ans mais sont plus évidentes sur des intervalles de 30 ans. Les mâles chantent habituellement un seul dialecte mais un mâle en a chanté deux par intermittence.

Introduction

The Splendid Sunbird *Cinnyris coccinigastrus* occurs in West and Central Africa from Senegambia to Gabon and the Central African Republic. In some areas it is resident but in some northern savannas it is a wet-season visitor, May–October, returning south in the drier period, December–April (Fry *et al.* 2000, Cheke *et al.* 2001). Micro-geographic song dialects of neighbouring populations have been detected at Legon, Ghana (Grimes 2007). A male usually sings only one song type and his territorial singing is loudest and most prolonged at dawn, though song is heard at other times of the day. Usually males sing from within the canopy but will also use exposed perches.

In between songs, a male moves his head from side to side, as if to locate a singing neighbour, and occasionally sings in unison with a competing male, which often results in the omission of the first few notes of his normal song. The mean time difference between the start of consecutive notes in a song (the time difference pattern) together with the frequency-time profile of each note, made visible through spectrograms, define and distinguish dialects.

Macro-geographic song dialects, involving sunbird populations separated by distances large enough to prevent them from interbreeding, would be expected to occur, given the existence of micro-geographic dialects. This has not been previously investigated for any African sunbird and the results of such a study are presented in the first part of the paper.

In the 1970s, six populations of the Splendid Sunbird studied around the University of Ghana at Legon had stable dialects for at least two years and two were stable over three years, the duration of the study (Grimes 1974). A three-month study at Legon in 2004 also confirmed the short-term temporal stability of local dialects (Grimes 2007). Data collected over longer periods of time are now available and the changes observed are illustrated in the second part of the paper.

Most sunbirds invariably sang only one song type but during one recording session a male sang intermittently two distinct dialects: this is discussed in a final section.

Methods

Praat software (Boersma 2001) was used to obtain spectrograms from song sequences recorded on cassette, CD or videotape. Each song of a given male was analyzed as described in Grimes (2007) and the mean time difference between the start of consecutive notes in its song (the time interval pattern) obtained. Time interval data for songs recorded in Ghana in the early 1970s were abstracted from Grimes (1974). Time interval patterns of the various songs were created using Microsoft Excel. The number of songs recorded and data points used to calculate each standard deviation, with locality, date and recordist, are given in Appendices 1–5. It was not possible to measure the starting time of all of the notes because of background noises.

For the first part of the study (Appendix 1), songs of the Splendid Sunbird recorded in Guinea-Bissau (Cachau Forest, 11.80°N, 15.18°W), Gambia (Brufut Woods, 13.44°N, 15.31°W), Ivory Coast (Central Bouaké, 7.54°N, 5.54°W; North Dabakala, 8.35°N, 4.42° W), Ghana (Nkawkaw, 6.55°N, 0.77°W; Kwabenya, 5.68°N, 0.20°W; Shai Hills, 5.90°N, 0.06°E; Abrafo, 5.35° N, 1.38° W; Cape Coast 5.13° N, 1.28° W; Alouva, a district within Cape Coast), Nigeria (Agenebode, 7.10°N, 6.68°E; the International Institute of Tropical Agriculture (IITA), 7.49°N, 3.90°E; Leventis Guest House, 7.44°N, 3.89°E), Cameroon (Yaoundé, 3.87°N, 11.51°E) and Gabon (Libreville, 0.39°N, 9.45°E) have been used, mainly obtained from the British Library Sound Archive (BLSA), London. Most recordings were made by visitors and all

except one were one-off recordings of single males at each locality. In the recording by David Moyer at Cape Coast two males were recorded singing simultaneously.

For the second part of the paper (Appendices 2–4), the sunbird songs used were recorded at intervals of several years within and near the Tanji bird reserve in Gambia (13.36°N, 16.79°W: 1996, 1998, 2007), at N'Douci in Ivory Coast (5.86°N, 4.76°W: 1968, 1976) and within the campus of the University of Ghana at Legon, Ghana (5.65°N, 0.18°W: 1972, 2004). Tanji Quarry is within Tanji bird reserve and *c.* 300 m from Paradise Inn which is just outside its southern boundary. The distances apart of the recording sites at N'Douci are not known. The recording sites selected for Legon were those where sunbird songs had been recorded in the 1970s and in 2004: near bungalows Nos. 17, 18 and 19 in Little Legon, near the University Agricultural Department and within the University Botanical gardens. One was also recorded near bungalows Nos. 6, 8 and 9 in Little Legon in the 1970s, but at this site three were recorded in 2004 (dialects C, D and G in Grimes 2007). The distance between adjacent recording sites at Legon was in the range 400–1400 m (data taken from Fig. 2 in Grimes 2007). Any of the dialects C, D and G could have been used to illustrate temporal changes in the sunbird's song over 30 years near bungalows Nos. 6, 8 and 9 in Little Legon; dialect G was chosen because its time difference pattern was closer to the 1970s pattern than those of the others, and so illustrates the minimum change after 30 years. Different trees were used for territorial singing in 2004 near bungalows Nos. 17, 18 and 19 in Little Legon, Agricultural Department and Botanical Gardens, than in the 1970s, and were respectively *c.* 50 m, *c.* 150 m and *c.* 300 m from those used in the 1970s, which no longer existed due mainly to building development. The clump of trees used by sunbirds near bungalows 6, 8 and 9 in Little Legon in the 1970s was again used in 2004, but the trees were taller and had overlapping and interlocking canopies. These vegetation changes might account for there being three dialect populations in 2004 rather than the one in the 1970s. During several recording sessions at Legon more than one singing male was recorded, either by moving from one to another whilst the first continued to sing, or else by recording simultaneously two or more singing birds (Appendices 2, 3 and 4).

Although only one spectrogram of the whistled notes in a song is used to illustrate each time difference pattern in the figures, each is representative of those included in the pattern (as shown by the relatively small standard deviations in most of the profiles). No attempt has been made to apply statistical tests to the data. Latitudes and longitudes were obtained using the web site <www.getlatlon.com>.

Results

Dialects recorded at locations visited only once

The range of dialects found throughout the sunbird's range in Africa is illustrated in Figs 1–5. All localities within a country are more than 3 km apart, a distance that is

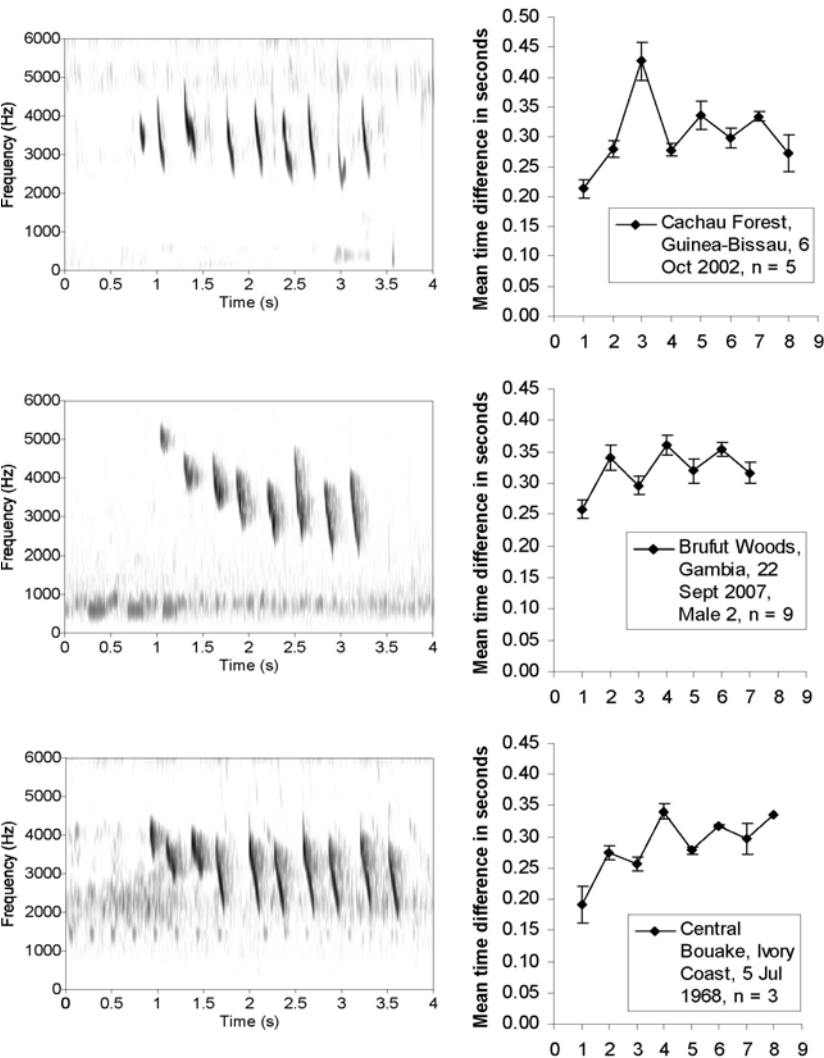


Figure 1. Songs of three Splendid Sunbirds, recorded in Guinea-Bissau, The Gambia and Ivory Coast. A spectrogram of a typical song of each bird is on the left and the time difference pattern (mean time difference between the start of consecutive notes \pm SD) on the right. The x-axis of the right-hand graphs identifies the note pairs from which the time difference was obtained (1 = first and second notes, 2 = second and third notes *etc.*); n = number of songs recorded at each location.

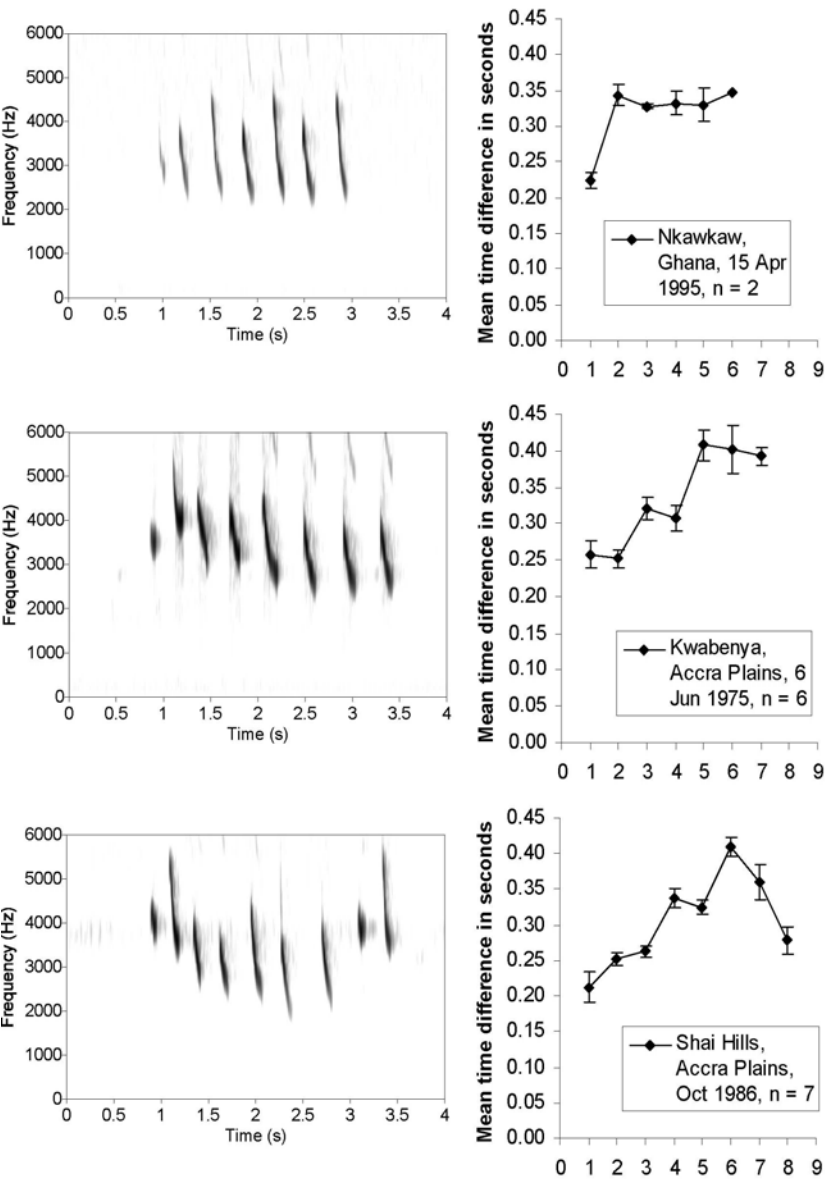


Figure 2. Songs of three Splendid Sunbirds recorded at three localities in Ghana. Details as in Fig. 1.

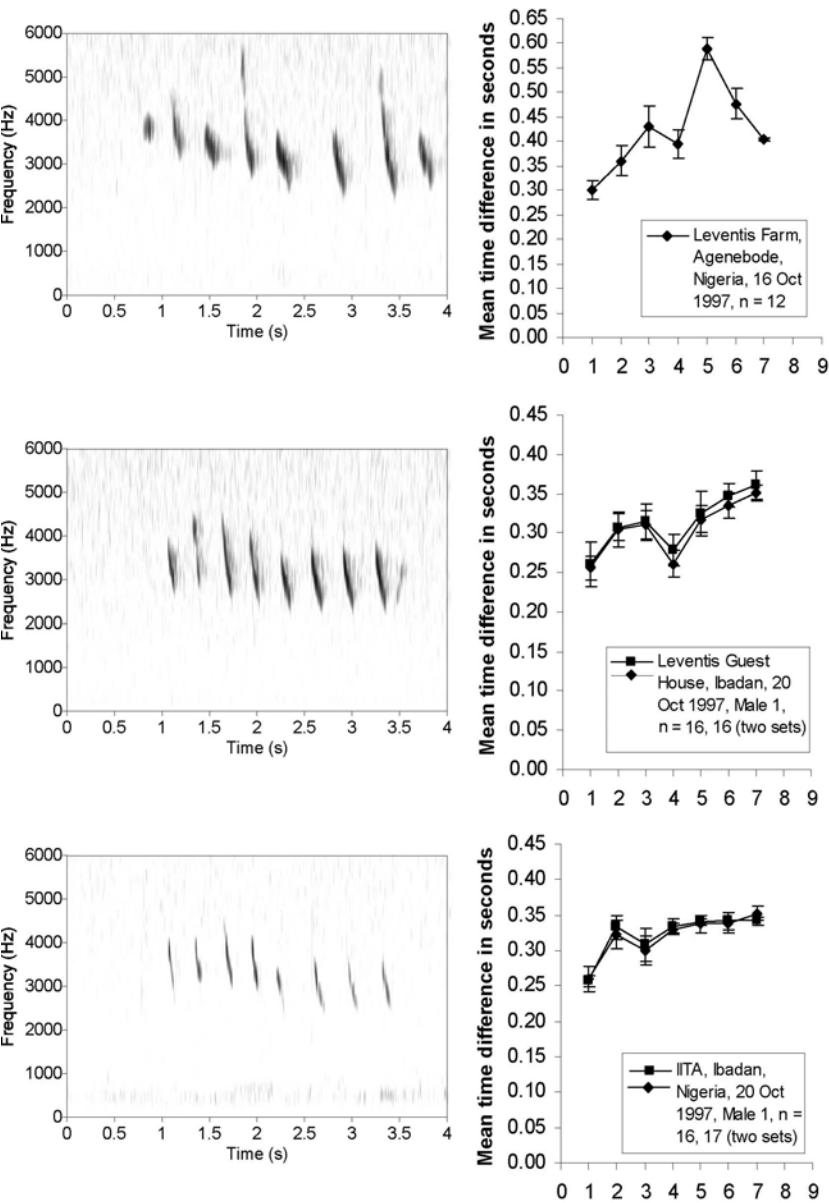


Figure 3. Songs of three Splendid Sunbirds recorded in Nigeria. Details as in Fig. 1.

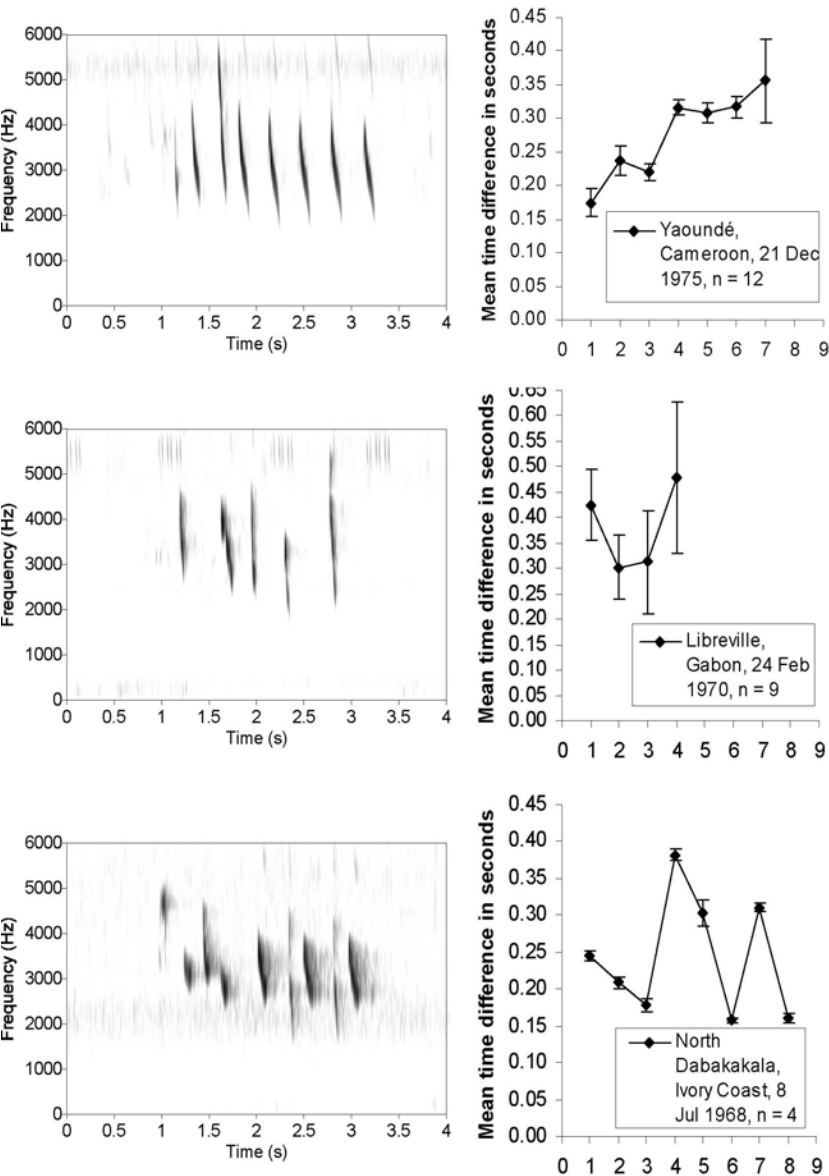


Figure 4. Songs of three Splendid Sunbirds recorded in Cameroon, Gabon and Ivory Coast. Details as in Fig. 1.

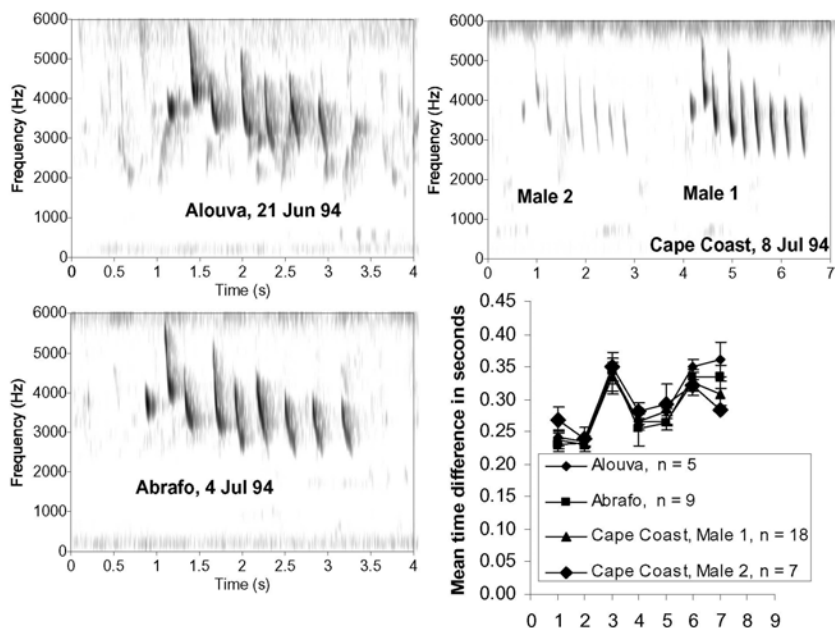


Figure 5. Songs of four Splendid Sunbirds recorded in the Cape Coast area, Ghana. Details as in Fig. 1.

assumed large enough to prevent sunbird populations from mixing. Visual inspection of each figure reveals that the spectrogram and the time interval pattern of each song are distinctive for each locality and taken together define a macro-geographic dialect. The chosen spectrogram illustrating the song of the Shai Hills sunbird (Fig. 2) is unusual as the last two notes are similar to the first two. This only occurred in two of its seven songs recorded and has not been found in any other sunbird song examined so far. The data obtained from the recordings made at IITA and the Leventis Guest House, which are c. 6 km apart, have been split into two consecutive sets for analysis (Fig. 3). The songs from Libreville, Gabon (BLSA reference 3182) and North Dabakala, Ivory Coast (BLSA reference 3180) (Fig. 4) are markedly different from other dialects. Audibly they are unlike the usual song of a Splendid Sunbird and neither the spectrogram nor the mean time difference pattern of each song is typical (compare Fig. 4 with Figs 1–3). There are no field notes to indicate whether the birds were visible during these recordings but both recordists are familiar with the species' song. Of the four sunbirds recorded in the Central Region of Ghana, three were at Cape Coast and the fourth at Alouva some 30 km north of the others, but all unexpectedly sang the same dialect.

Dialects recorded at locations visited more than once

The time difference patterns and spectrograms of sunbird songs recorded on three occasions over an interval of 11 years at Tanji bird reserve, The Gambia (Fig. 6) and over an interval of 8 years at N'Douci, Ivory Coast (Fig. 7) are remarkably similar and suggest that the dialects at these two locations changed little during these periods. Although data collected at Legon suggest that time difference patterns for songs recorded near staff residence No.18 in Little Legon (Fig. 8), near the Department of Agriculture (Fig 9) and near staff residence No. 8 in Little Legon (Fig. 10) are similar to those recorded 30 years later, there are differences in the frequency-time profiles of certain notes. Thus the first three notes in songs recorded in the 1970s at both the Agricultural Department and near staff residence No. 8 in Little Legon differ from the corresponding notes in songs recorded in 2004 (Fig. 9 and 10). Moreover, the differences in Fig. 10 would have been greater if the other two dialects (C and D) detected in the neighbourhood of staff residence No. 8 in Little Legon in 2004 had been used. In contrast the song dialect recorded within the Botanical Gardens at Legon in the 1970s (Fig.11) has a markedly different time difference pattern and spectrogram from those of the dialect recorded in 2004. In preparing Fig. 11, I have corrected the value of the mean time difference between the start of the fifth and sixth notes; this is 0.356 s not 0.311s as plotted erroneously in Fig. 6 of Grimes (2007).

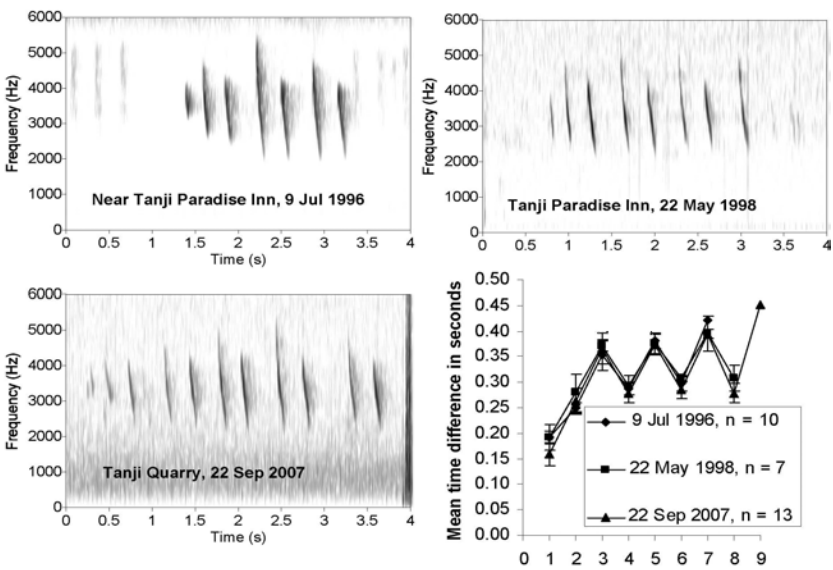


Figure 6. Songs of Splendid Sunbirds recorded over a period of 11 years at three sites within the Tanji bird reserve, The Gambia. Other details as in Fig. 1.

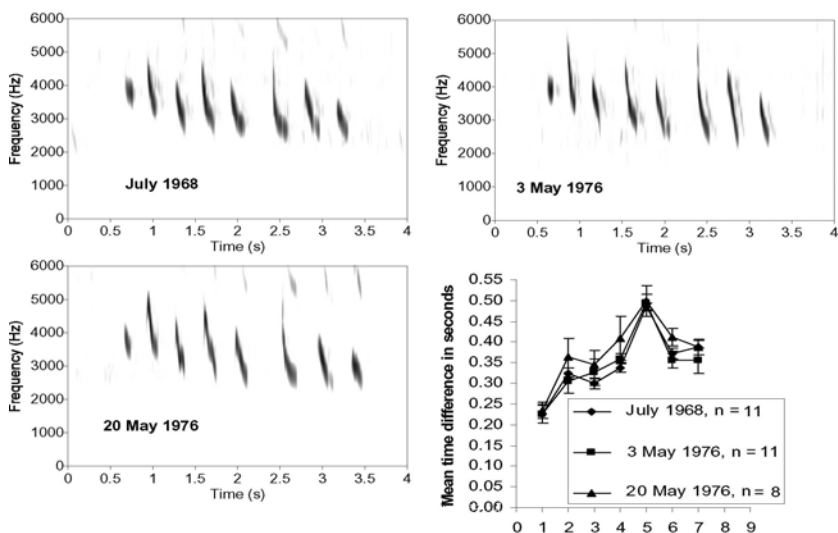


Figure 7. Songs of Splendid Sunbirds recorded over a period of eight years near N'Douci, Ivory Coast. Details as in Fig. 1.

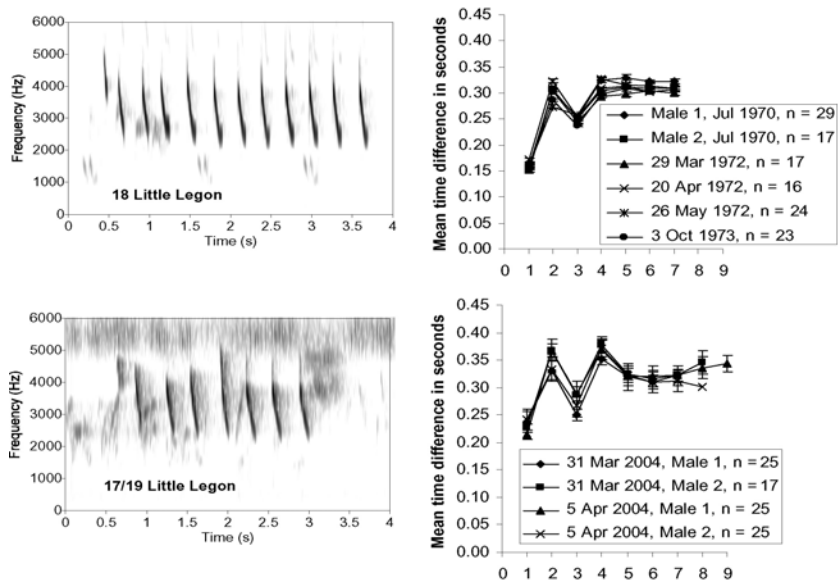


Figure 8. Songs of Splendid Sunbirds recorded near bungalows 17, 18 and 19 in Little Legon, Ghana in the 1970s and in 2004. Details as in Fig. 1.

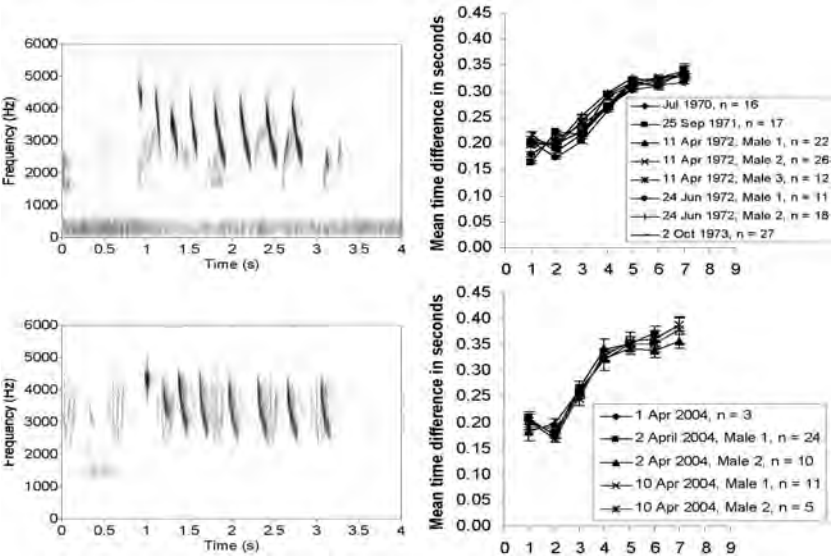


Figure 9. Songs of Splendid Sunbirds recorded around the Agricultural Department, Legon, Ghana in the 1970s and in 2004. Details as in Fig. 1.

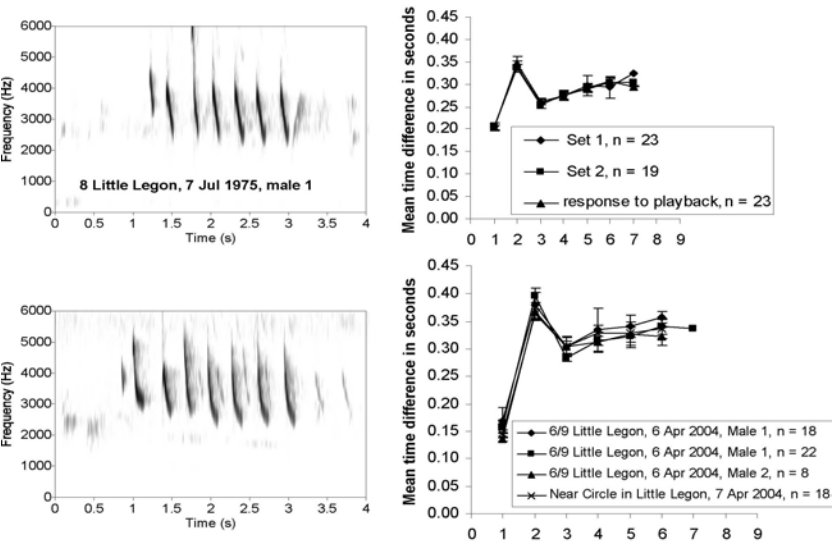


Figure 10. Songs of Splendid Sunbirds recorded near bungalows 6, 8 and 9 in Little Legon, Ghana in the 1970s and in 2004. Details as in Fig. 1.

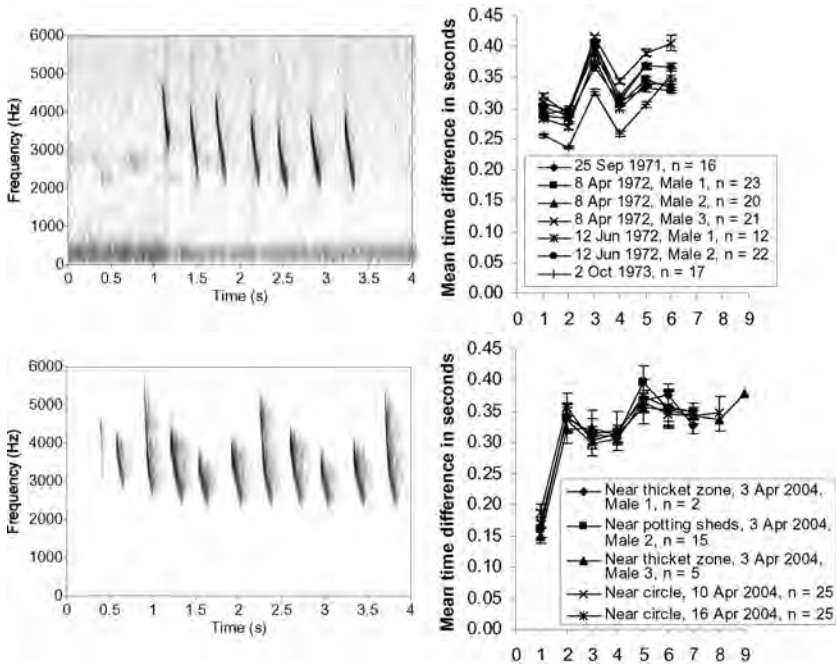


Figure 11. Songs of Splendid Sunbirds recorded in the Botanical Gardens, Legon, Ghana in the 1970s and 2004. Details as in Fig. 1.

Individual with two song types

The spectrograms illustrating the two song types of the bird recorded at 7 Lower Hill appear in Fig. 12. The dialects (108 of type A and 45 of type B, each easily distinguished by ear) were sung intermittently, in no apparent order, before the male flew away. Singing order of the dialects was: A (7); B (6); 8A (10,9,11,10,10,9,9,9); 3B (9,10,9); 2A (9,9); 2B (9,10); A (10); B (3); A (10); 6B (9,9,8,9,9,7); 3A (10,9,10); B (8); 3A (8,9,9); B (9); 3A (9,10,10); 5B (8,8,9,9,10); 3A (8,9,10); B (8); 3A (9,11,10); 3B (9,8,9); 7A (10,10,10,10,10,10,9); B (10); 3A (9,10,9); 3B (10,9,9); 15A (10,10,10,10,9,9,9,9,9, 10,10,9,10,10,9); B (9); 6A (10,9,10,10,11,10); B (8); 2A (6,10); B (9); 8A (9,10,9,9, 10,8,9,9); B (9); 2A (9,10); B (9); 5A (9,9,10,9,11); 3B (8,9,8); 2A (9,9); B (9); 2A (9,9); B (9); 2A (9,10); B (9); 2A (11,8); B (9); 2A (9,9); B (9); A (9); B (8); 11A (10, 9,9,9,8,8,9,10,9,10,9); B (8); A (9); B (7); 2A (9,7); B (8), where the number(s) within brackets for each dialect represent the number of notes sung in each song. Thus the fourth entry above “3B (9,10,9)” means that three B type songs were sung sequentially after eight type A songs and were followed by two A type songs, and the notes in each B song were 9, 10 and 9 respectively.

During the first 5 min of the recording, Common Bulbuls *Pycnonotus barbatus* were vocal and their songs often overlapped with those of the sunbird, making the measurement of time differences between start of consecutive notes in the sunbird's song difficult. As a result data from only 95 of the A type songs and 39 of type B songs have been used in Fig. 12.

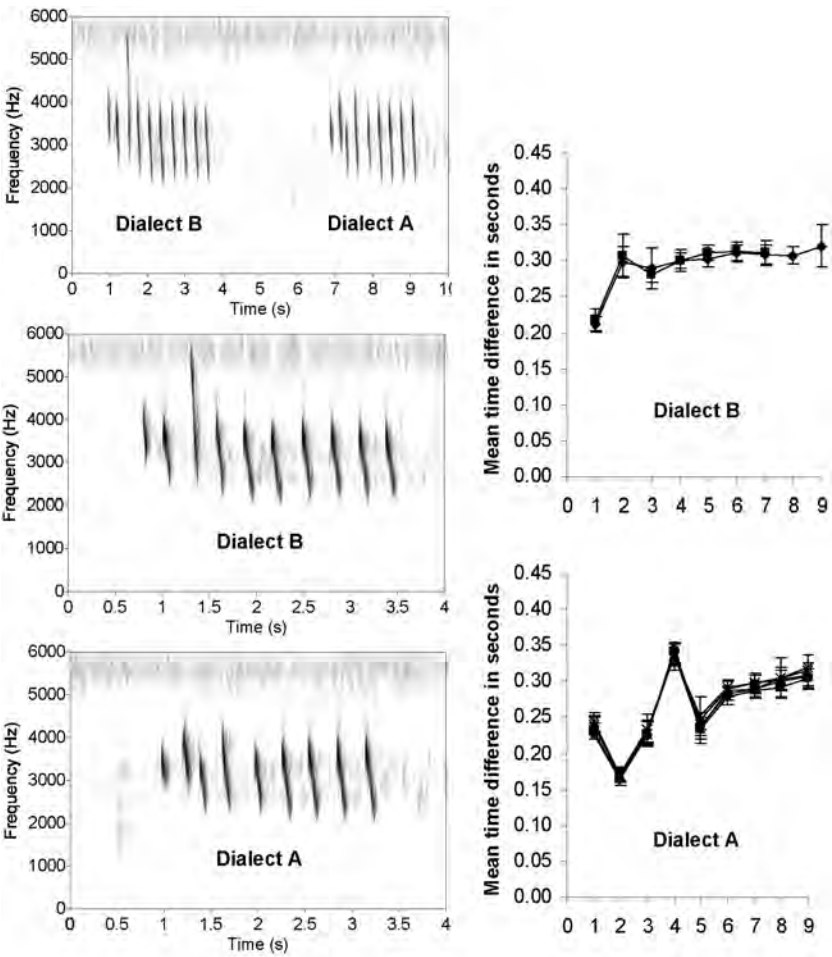


Figure 12. Two song dialects (A and B) of a Splendid Sunbird recorded at 7 Lower Hill, Legon, Ghana, 27 Oct 1974. Details as in Fig. 1.

Discussion

Although dependent on *ad hoc* recordings and therefore not fully comprehensive, these results draw attention to the Splendid Sunbird as an ideal candidate for research into song dialects. Its dialects vary considerably over its range and their structural simplicity makes them ideal for obtaining comparable quantitative data.

The existence of macro-geographic dialects was not unexpected. The similarity of the dialects recorded at two localities some 30 km apart in the Central Region of Ghana was not anticipated and contrasts from the data collected at Legon (Figs 8, 9 and 10) where dialects changed over distances of < 1 km. These data also contrast with the songs recorded by Payne (1978) on the campus of the University of Cape Coast in 1975. He sampled the songs of most sunbirds on the campus but found that, although local song variation occurred, variations in space were not grouped into discrete dialects.

Song dialects of male Orange-tufted Sunbird *Nectarinia osea* occur throughout Israel and have been studied in detail using a colour ringed population near Ramat-Aviv, Israel, where two dialects occur side by side and dispersal from natal areas is low (Leader *et al.* 2000). Males of both dialects responded more positively to playback of their own dialect than to playback of the other and Leader *et al.* (2002) concluded that the stability of discrete dialects in the sunbird was partly due to the acoustic properties of the environment.

Catchpole & Slater (2008) and Marler & Slabbekoorn (2004) discuss the wide variety of dialect types that exist and review suggestions as to how and why dialects develop. Whether or not dialect boundaries act as barriers to dispersal, and whether or not genetic differences exist across dialect boundaries are crucial questions. The latter has now been answered for the Orange-tufted Sunbird population at Ramat-Aviv, where Leader *et al.* (2008) found that dialects did not restrict gene flow.

We do not know when and from whom a juvenile Splendid Sunbird learns his song and whether or not an individual is sedentary. These are important pieces of information when asking how dialects may have developed and how they are maintained. The picture is further complicated if songs are recorded where the sunbird is a migrant. It is not known what songs (if any) described in this paper involved migratory sunbirds, but those recorded in Gambia, Ghana and Nigeria and probably in Ivory Coast were at localities where the sunbird is resident. The wide range of macro-geographic dialects recorded may reflect changes in the sunbird's habitat which ranges from wooded savannas through farm bush, scrub and forest edge to gardens and residential areas (Fry *et al.* 2000), but this remains speculation.

It remains a puzzle why only one sunbird has been recorded singing two distinct dialects but this is unlikely to be due to brevity of the recordings of the other sunbirds. Several were long enough to have included more than one dialect if switching times between dialects recorded at bungalow 7 Lower Hill were typical. Following the discovery by Chilton *et al.* (1990) that White-crowned Sparrows *Zonotrichia*

leucophrys occasionally sing more than one dialect when at a dialect boundary, a possible answer to the puzzle is that the sunbird might have been singing at its dialect boundary.

The data presented suggest that temporal changes in song dialects of the Splendid Sunbird at a given locality over an interval of 8–11 years are slight. The changes detected over an interval of 30 years range from minor to major (Fig. 11) differences in the frequency-time profiles of the notes and/or in the time difference patterns of the songs. The major changes in the dialects at the Botanical gardens at Legon may have been due to an emigration of the original population followed by an immigration of a new one but this is not known. Alternatively the changes may simply reflect a shift with time of a dialect boundary as occurred in a study of the Puget Sound White-crowned Sparrow (Chilton & Lein 1996). Temporal changes in songs of Chaffinch *Fringilla coelebs* and Indigo Bunting *Passerina cyanea* recorded some years apart were considered to result from simple random processes (Ince *et al.* 1980, Payne *et al.* 1981).

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Appendix 1

Numbers of data points used to obtain the mean time intervals in note pairs of songs of Splendid Sunbirds illustrated in Figs 1–5.

Locality & indiv. ¹	Recordist ²	Date	Note pair							
			1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9
Guinea-Bissau										
Cachau Forest	CB	6 Oct 2002	5	5	4	4	4	4	2	2
Gambia										
Brufut Woods	CB	22 Sep 2007	9	9	9	8	8	7	5	
Ivory Coast										
Central Bouaké	CC	5 Jul 1968	3	3	3	3	3	3	2	1
North Dabakala	CC	8 Jul 1968	4	4	4	4	4	4	4	
Ghana										
Nkawkaw	C	15 Apr 1995	2	2	2	2	2	1		
Kwabanya	LG	6 Jun 1975	6	6	6	6	6	6	5	1
Shai Hills	CW	Oct 1986	7	7	7	7	7	7	2	2
Alouva	DM	21 Jun 1994	5	5	5	4	4	4	2	
Abrafo	DM	4 Jul 1994	9	9	9	9	8	8	7	2
Cape Coast ♂1	DM	8 Jul 1994	18	18	18	18	17	13	9	6
Cape Coast ♂2	DM	8 Jul 1994	7	7	7	7	7	5	2	
Nigeria										
Agenebode	CB	16 Oct 1997	11	12	12	10	5	5	3	
IITA Ibadan Set 1	CB	20 Oct 1997	16	16	16	15	15	14	4	
IITA Ibadan Set 2	CB	20 Oct 1997	16	17	17	16	13	7	2	
Leventis GH Set 1	CB	20 Oct 1997	16	16	16	16	15	15	12	
Leventis GH Set 2	CB	20 Oct 1997	16	16	16	16	16	15	6	
Cameroon										
Yaoundé	CC	21 Dec 1975	12	12	12	12	12	10	5	
Gabon										
Libreville	CC	24 Feb 1970	9	9	9	9	8	5		

¹Each line refers to an individual male except that the two entries each for IITA Ibadan and Leventis Guest House refer to consecutive song sets for one male at each site.

²Recordists: CB = Clive Barlow; CC = Claude Chappuis; C = Clive Carter; LG = Llew Grimes; CW=Chris Watson; DM = David Moyer.

Appendix 2
Numbers of data points used to obtain the mean time intervals in note pairs of songs of Splendid Sunbirds illustrated in Figs 6–8.

Locality & indiv. ¹	Recordist ²	Date	Note pair									
			1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Gambia												
Tanji Paradise Inn	CB	9 Jul 1996	10	10	10	9	9	8	1			
Tanji Paradise Inn	CB	22 May 1998	3	3	3	7	7	7	4	2		
Tanji Quarry	CB	22 Sep 2007	13	13	12	9	8	5	3	3	1	
Ivory Coast												
N'Douci	CC	Jul 1968	11	11	11	11	8	7	4			
N'Douci	JV	3 May 1976	11	9	8	6	4	2	2			
N'Douci	CC	20 May 1976	8	8	8	8	7	4	2			
Ghana												
18 Little Legon ♂1	LG	Jul 1970	29	29	29	29	29	29	29			
18 Little Legon ♂2	LG	Jul 1970	17	17	17	17	17	17	17			
18 Little Legon	LG	29 Mar 1972	17	17	17	17	17	17	17			
18 Little Legon	LG	20 Apr 1972	16	16	16	16	16	16	16			
18 Little Legon	LG	26 May 1972	24	24	24	24	24	24	24			
18 Little Legon	LG	3 Oct 1973	23	23	23	23	23	23	23			
17/19 Little Legon ♂1	LG	31 Mar 2004	25	25	25	25	24	23	8			
17/19 Little Legon ♂2	LG	31 Mar 2004	14	14	15	17	17	17	17	11		
17/19 Little Legon ♂1	LG	5 Apr 2004	24	24	25	25	25	25	25	20	8	
17/19 Little Legon ♂2	LG	5 Apr 2004	24	24	25	25	25	25	13	1		

¹Each line refers to an individual male.
²Recordists: CB = C. Barlow; CC = C. Chappuis; LG = L. Grimes; JV = J. Vieillard.

Appendix 3
Numbers of data points used to obtain the mean time intervals in note pairs of songs of Splendid Sunbirds in Ghana, recorded by L. Grimes and illustrated in Figs 9 and 10).

Locality	Date	Individual ¹	Note pair							
			1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9
Agriculture Dept	Jul 1970		16	16	16	16	16	16	16	
	25 Sep 1971		17	17	17	17	17	17	17	
	11 Apr 1972	♂1	22	22	22	22	22	22	22	
		♂2	26	26	26	26	26	26	26	
		♂3	12	12	12	12	12	12	12	
	24 Jun 1972	♂1	11	11	11	11	11	11	11	
		♂2	18	18	18	18	18	18	18	
	2 Oct 1973		27	27	27	27	27	27	27	
	1 Apr 2004		3	3	3	3	3	3		
	2 Apr 2004	♂1	22	22	23	24	24	24		
		♂2	10	10	10	10	10	10	3	
	10 Apr 2004	♂1	11	11	11	11	11	7	3	
		♂2	5	5	5	5	5	4	2	
8 Little Legon ²	7 Jul 1975	Set 1	22	23	23	23	23	18	1	
		Set 2	19	19	19	19	17	14	1	
		After playback	23	23	23	21	20	16	2	
6/9 Little Legon ²	6 Apr 2004	♂1 Set 1	20	20	22	22	22	18	1	
		♂1 Set 2	18	18	18	18	16	3		
		♂2	7	7	8	8	8	6		
Near Circle ²	7 Apr 2004		18	17	17	17	17	13		

¹Each line refers to a different male except that the three entries for 8 Little Legon and the first two for 6/9 Little Legon refer to consecutive song sets for one male at each site; the third entry for 8 Little Legon was obtained after playback of that male’s song.
²These three locations were within 30 m of each other.

