PHYLOGENIES OF THE SUNBIRDS, SPIDERHUNTERS AND FLOWERPECKERS (NECTARINIIDAE) BASED ON ANALYSES OF VOCALISATIONS

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DECLARATION

I certify that this work has not been accepted in substance for any degree, and is not currently submitted for any degree other than that of Doctor of Philosophy (PhD) of the University of Greenwich. I also declare that this work is the result of my own investigations except where otherwise stated.

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ABSTRACT

The phylogeny and affinities of the flowerpeckers (sometimes separated from the Nectariniidae into the family Dicaeidae), sunbirds and spiderhunters (Family Nectariniidae) are controversial and have been much debated by ornithologists from the perspectives of both the biological species and phylogenetic species concepts. This study constructed phylogenies for the Nectariniidae from up to 20 parameters derived from quantitative analyses of their vocalisations and used these to test hypotheses on whether or not the origin of sunbirds is African or Asian. This is the first comparative study of bird songs for an entire large Family (294 taxa analysed) to derive a phylogeny. In addition to standard sonographic measurements, this study is the first to use entropy values derived directly from sonograms as an objective way of separating calls from songs and simple songs from complex songs.

Whilst some species have simple songs, those of others are complex with extensive repertoires. The complex vocalisations are more informative and provide good phylogenetic signals.

The affinities of the genera of flowerpeckers were firmly established on vocal grounds and concurred with their traditional taxonomy. The vocal phylogeny failed to separate sunbirds from spiderhunters but showed that the Asian group of sunbirds emerged as the basal clade and therefore the most primitive clade of the sunbird lineage. This is in agreement with the phylogenetic outcome of recent DNA studies. It is therefore concluded that sunbirds may have originated on the Indian subcontinent, reached Indian Ocean islands including Madagascar and then penetrated into Africa, with the possibility that some oceanic island species were later derived from secondary invasions from Africa. The results further suggest that the clade of the Gulf of Guinea group of species may have arisen from a common ancestor from the African continent. The Indian Ocean island species also separated as a distinct group.

Mean bill lengths and body sizes of different taxa were analysed in relation to the vocalisations. The results indicated significant relationships between bill length and body size and song complexity, with the latter higher in the more advanced genera. Song frequency was lower in forest species than those inhabiting open areas but no clear phylogenetic signals emerged from these data. Plumage dimorphism, nest structures and placements, habitat types and the breeding behaviour of the Nectariniidae were also examined.

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ABBREVIATIONS

AAH	Acoustic Adaptation Hypothesis
AVISOFT	Sound Analysis and Synthesis Laboratory
BAY	Bayesian
DNA	Deoxyribonucleic acid
FFT	Fast Fourier Transformation
FIR	Finite Impulse Response
Fmax	Maximum frequency
Fmin	Minimum frequency
HTUs	Hypothetical taxonomic units
Hz	Hertz
KHz	Kilohertz
NJ	Neighbour-joining
OTUs	Operational taxonomic units
PAUP	Phylogenetic Analysis Using Parsimony
Cda	Compact disk-Digital audio

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CHAPTER 1

INTRODUCTION

The first part of this thesis, Chapter 1, highlights the research issue. This summarises published literature on animal phylogenies in general and avian phylogeny, in particular. It also includes a synthesis of aspects of bioacoustics, DNA and morphology relevant to the description, discovery and classification of species. This is followed by a brief review of the auditory signal phenomenon and the associated constraints (song complexity, repertoire, environment, sound quality etc.) to its use in vocal phylogeny, a synopsis of the aims and objectives of the study and an outline of the thesis.

1.1 BACKGROUND TO THE STUDY

The evolution of animal communication is a complex subject that currently attracts much debate and research. Both birds and mammals continually rely on vocal communication to transmit information from a signaller to a receiver (Rowe and Skelhorn, 2004; Pytte *et al.* 2003; Peake, 2005) and allow for the recipient to process the information and respond to it (Bradbury and Vehrencamp, 1998). The main medium for the provision and utilisation of information amongst any group of animals is signal transmission but, in some environments, signal exchange can involve individuals that are not participating directly in the main transmission (McGregor and Dabelsteen, 1996; McGregor and Peake, 2000). However, in a situation of prey and predator interaction, a signaller may not benefit from the information emitted, which can be perceived as cues (Seeley 1989) or be termed eavesdropping when it is exploited by a receiver to the disadvantage of the emitter (Bradbury and Vehrencamp, 1998).

Communication is central to the social organisation of birds and plays a key role in reproduction, group cohesion and personal identity. A variety of sounds may be broadcasted to communicate with flock members, mates (or potential mates), neighbours and family members. These sounds vary from short, simple, call notes to surprisingly long, complex, songs, produced from the avian vocal organ, the syrinx (Garamszegi *et al.*, 2003; Bradbury and Vehrencamp, 1998).

Recent advances in studies of vocal signals have contributed to the debate on the significance of signalling in animal communication. Some experts argue that the burden of effective communication lies in the signaller's (male bird) ability to structure signals in a manner that would minimise transmission fidelity because acoustic signals lose amplitude and degrade while travelling to the receiver (Bradbury and Vahrencamp, 1998; Naguib and Willey, 2001; Blumstein and Turner, 2005). Also, in some species, amplitude regulation may be adaptive and serve to increase the efficiency and long distance signal transmission along with the established relationships between singing behaviour, acoustic structure and habitat (Pytte *et al.*, 2003).

Others are of the view that the perceptual abilities of the signal receivers (female bird) to identify and distinguish between conspecific and allospecific vocalisations of their males and those of their neighbours is crucial to understanding communication behaviour in birds (McGregor, 1989, 1991; McGregor and Avery, 1986; Lind *et al.*, 1996; Dawkins and Guilford, 1995; Beckers and ten Cate, 2003). The work of these authors marks the beginning of understanding about the origin of song complexity, comparable to the preferences female birds have for brighter colours or more elaborate plumage (Anderson, 1982, 1992). Consequently, how and why birds' songs differ in vocal repertoire size is unclear. Behavioural ecologists are still struggling to explain the sizes of vocal repertoires. Whereas some bird species have a single stereotyped song type, others have a repertoire that consists of several vocalisation types that vary in acoustic structure between different behavioural contexts, for example alarm calls, contact calls, flight calls and territorial songs (Hailman and Ficken, 1996; De Kort and ten Cate, 2003). A male White-crowned Sparrow *Zonotrichia leucophrys*, for example, sings only one song type while the male Brown Thrasher *Turdus rufus* has thousands of different song types and may even improvise its repertoire daily (De Kort and ten Cate, 2003; Gammon and Baker, 2004; Baker *et al.*, 2003; Irwin, 2001). There is also an observed linkage between sexual differences and the vocal ability of male and female birds, an observation that has recently been attributed to sex hormones, particularly the male hormone testosterone (Van Duyse *et al.*, 2002).

Pioneering studies of bird songs (Barrrington, 1773; Darwin, 1871) first attempted to uncover how birds acquire their songs and how acoustic signals diverged over time in speciation events. What is clear from these earlier studies is that young birds acquire their songs from their parents during a short imprinting period known as the sensitive or 'critical period' early in life. In an experiment conducted by Barrington (1773) and involving the songs of Linnet *Carduelis cannabina*, Chaffinch *Fringilla coelebs*, Skylark *Alauda arvensis* and Woodlark *Lullula arborea*, he discovered that each bird learned its tutor's song and that a young bird was not entirely without discrimination in its choice of tutors (Chilton, 1991). Although little is known about how learned vocalisations are acquired and maintained, song learning in many animals including rodents and primates has recently been linked to levels of dopamine (a hormone-like neurotransmitter synthesised in the midbrain) (Gale and Perkel, 2005; Sasaki *et al.*, 2006).

Extensive research has attempted to determine whether song discrimination by young birds could be responsible for dialects and whether or not dialects represent a reproductively isolated social system, with some individuals tending to spend their entire lives using a dialect (Anderson *et al.*, 2005). In many birds, song varies geographically as discrete or regional 'dialects' that link individuals or groups to a place of origin (Baker and Cunningham, 1985; Chilton *et al.*, 1996b; Catchpole and Slater, 1995). However, some dialects are thought to occur as a result of imperfect social learning perpetuated during the early stages of life (Kroodsma, 1982; Hafner and Petersen, 1985; Lougheed and Handford, 1992; Wright and Wilkinson, 2001). There is also evidence to suggest an evolutionary link between bird call notes and song and how mere call notes improved over time into melodious love songs (Darwin, 1871; Howard, 1920; Hartshorne, 1956; Nottebohm, 1972;

Neubauer, 1999).

1.1.1. Phylogeny

Phylogeny is the study of the evolutionary relatedness among various groups of organisms (species and populations) as understood by ancestor / descendant relationships (Blomberg *et al.*, 2003). Phylogenies contribute to our understanding of diversification and speciation in the patterns of evolution or the recovery of evidence of a series of unique events that comprise the history of life (Edwards and Cavalli-Sforza, 1964). Phylogenies further illustrate a species or a group connected over time through a lineage that enriches our knowledge of how evolution operates. Also, the taxonomic classification of organisms according to similarity and differences has been richly informed by the phylogenetic processes that have generated today's diversity and informs conservation decisions. Phylogeny is becoming a powerful tool for the conservation of biodiversity, playing a role in delimiting priority units for conservation and providing a good surrogate measure of biodiversity worldwide (Sinclair *et al.*, 2005; Williamson, 2006). Thus, the construction of phylogenetic trees serves to improve understanding of the relationships between taxa, and hence their evolution, and to define taxonomic units to aid conservation decisions.

It has long been recognised that bird songs contain evolutionarily conservative traits or elements that retain vital information about their evolutionary history, useful for reconstruction of the evolution and phylogeny of most bird species (Lanyon, 1969; Slabbekoorn *et al.*, 1998; Grant, 2001; Price and Lanyon, 2002).

Phylogenetically, all birds share a syrinx, indicating that this unique vocal organ evolved near the beginning of bird evolution (Fitch, 2006). However, because the vocal organs and structures such as the syrinx and vocal tract of most bird species do not fossilize, little is known about the phylogenetic history and timing of the origins of the vocalisations of most species (Fitch, 2005, 2006).

Historically, the use of comparative phylogenetic analysis (Sibley and Ahlquist, 1990; Johnson *et al.*, 2001; Livezey and Zusi, 2001; Mayr *et al.*, 2003) began as an attempt to resolve controversies about the classification of some bird species.

Until recently many phylogenetic inferences, other than classical ones based on morphology, were derived solely from molecular analyses such as DNA hybridisation (Houde, 1987; Sibley and Ahlquist, 1990; Lanyon, 1992; Mayr *et al.*, 2003), but it is becoming increasingly clear that vocal characters are also useful for deriving phylogenies.

In a few cases, vocal characters have been used to infer phylogenetic relationships among species either by refuting (Bretagnolle, 1995) or corroborating previous studies (Arctander *et al.*, 1996; Winkler and Shirt, 1978; Voelker, 1999b). In addition, it has been suggested that phylogenetic information is contained in the syntax structures of avian vocalisations. For instance, song syntax of all subspecies of North African and Canarian Blue Tits *Parus teneriffae* differs from the common syntax of continental Blue Tits, *P. caeruleus* and Azure Tits *P. cyanus* (Schottler, 1995; Martens, 1999). Jordan and Lanyon (2002) used song characters to estimate the phylogenetic affinities of *Psarocolius*, *Gymnostinops* and *Ocyalus*, of the Oropendola taxa, while Whitney and Pacheco (1994) used vocalisations to discuss the affinities of the little-known monotypic genera *Gyalophylax* and *Megaxenops*. Also, Miller (1996) used vocal characteristics to infer the relationships among Plovers *Pluvialis* and some Sandpipers *Calidris* while Winkler and Short (1978) inferred the relationships among Pied Woodpeckers *Picoides* and *Dendrocopo*s from the acoustic analysis of their vocalisations. Thus, bird songs have become models for investigating the evolution of animal signals, speciation and phylogeny, but they are also used in censusing and monitoring of bird populations (Beckers *et al.*, 2003; Bretagnolle and McGregor, 2006).

Some comparative studies involving DNA analysis seemingly suggest good congruence between acoustic and genetic divergence among species, e.g. in taxa of *Regulus* (Packert *et al.*, 2003), the various Old World warblers such as *Phylloscopus trochiloides* (Irwin, 2001; Irwin *et al.*, 2001); the *P. collybita* complex (Helbig *et al.*, 1996), *P. bonelli* (Helbig *et al.*, 1995); and in the Golden-spectacled Warbler *Seicercus burkii* complex (Martens *et al.*, 1999; Alstrom and Olsson, 2000; Martens and Eck, 2000).

Others strongly suggest considerable divergence between morphological and DNA-based classifications. Examples of such conflicting conclusions include studies on mammals such as African fruitbats (Megachipoptera; Cracraft, 1983), African shrews (Soricidae; Querouil *et al.*, 2001), amphibia such as treefrogs (Rhacophoridae; Wilkinson *et al.*, 2002), burrowing frogs (Sooglossidae; Biju and Bossuyt, 2003) and many avian taxa including both passerines such as pipits (Voelker, 1999a, b; Sibly and Ahlquist, 1983) and sunbirds (Warren *et al.*, 2003; Bowie, 2003) and non-passerines such as cranes (Krajewski and King, 1995), woodpeckers (Cicero and Johnson, 1995), Galliformes (Randi, 1996) and Pelecaniformes (Friesen and Anderson, 1997).

In some cases, a combination of morphology, DNA and / or vocalizations can be used to describe or discover species. For example, the population divergence of two Corvids, the Chough *Pyrrhocorax pyrrhocorax* and Alpine Chough *Pyrrhocorax graculus*, were determined by both species morphological differences and vocalisations (Laiolo *et al.*, 2004), whereas the monophyly or sister group relationship between Pici (woodpeckers and allies) and Galbulae (puffbirds and jacamars) was supported by both morphological and molecular analyses (Mayr *et al.*, 2003). Also, the speciation of warblers of the 'Chiffchaff complex' within the genus *Phylloscopus* found in Europe and Asia was elucidated with the help of DNA-sequence analysis and a review of plumage and vocal differences (Clement and Helbig, 1998).

The family Nectariniidae constitutes a very speciose and ecologically diverse group with 176 species, which are morphologically similar at genus and species levels. They remain relatively poorly differentiated on morphological grounds, despite the many attempts by several authors (Delacour, 1944; Beehler, 1953; Beehler and Finch, 1985; Sharpe, 1885; Sundevall, 1872; 1909; Wetmore, 1930, 1940, 1960; Sibley and Ahlquist, 1990; Sibley and

Monroe, 1990; Irwin, 1999; Fry *et al.*, 2000; Cheke and Mann, 2001; Bowie *et al.*, 2004) to redefine and classify the taxonomy and affinities of the family. Their evolutionary history remains convoluted and undefined.

Only a few of the above authors have attempted to trace the evolutionary lineages of members of the Nectariniidae (Delacour, 1944; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; Irwin, 1999; Fry *et al.*, 2000; Cheke and Mann, 2001; Bowie, 2003).

Indeed, it was Delacour (1944) who, in his revision of the morphological attributes of the family, sketched an evolutionary cladogram of the family aimed at reconstructing the history of successive divergences within it at the generic level. However, Delacour's (1944) evolutionary ladder was based on the strong belief that bright and or glossy colours are features that evolved late and that primitive species are mostly dull or without metallic colours. He therefore classed the most highly brightly coloured members of the family as the advanced genera.

Irwin (1999), supported by Fry *et al.* (2000), speculated that sunbirds were of African origin since African sunbirds have shorter bills than their Asian counterparts and constituted the dominant group (two thirds of sunbirds) as compared the fewer species (only about a third of sunbirds) from the Oriental region. They also assumed that the African continent is more primitive and has a longer evolutionary history than the oriental region. However, Irwin (1999) did not construct any phylogenetic tree to back his claim.

Bowie (2003) conducted a combined nDNA and mtDNA analysis on only 102 species of sunbirds and derived a DNA phylogeny of the Nectariniidae. Bowie's phylogeny indicated clearly that an Asian clade of 6 species was basal to the African and the Indian Ocean species and therefore represents the primitive group, or outgroup, of the taxa contrary to Irwin's claim that the sunbird lineage rather originates from Asia. Bowie's (2003) phylogeny is as yet unpublished.

Others such as Maclean (1985), Grimes (1974, 2007), Langrand (1990), Brieschke (1990, 1991) and Rasmussen and Anderton (2005) have attempted to investigate the voices and vocal structure of the family. However, the extents of these studies have been limited to the level of sonographic interpretation without evolutionary conclusions.

As the results in this thesis will show, the song attributes of this family are quite distinct even at subspecies level and therefore provide a diverse taxonomic base for comparative vocal analysis and the derivation of a more informed phylogeny.

1.1.2. Morphology

Although traditionally avian taxonomy has primarily relied on morphological characters for resolving relationships within and differences between genera, and between sibling and cryptic species, it has never been a panacea for resolving the systematics of bird species with uniform morphology (Martens *et al.,* 2004).

Morphological characters that are often used for morphometric analysis possess structural adaptations that tend to be conserved during evolution. In birds they include plumage (colour and pattern variation in individuals), weight, wing length, tail length, spur length, beak length, beak depth, beak width, body size and skeletal characters (Mateos and Carranza, 1997; David and Harper, 1999; Mayr *et al.*, 2003; Martens *et al.*, 2004; Huber and Podos, 2006).

Some morphological characters e.g. body size, beak length, beak depth and beak width correlate with some avian vocal parameters such as frequency, pulse rate, song and note durations (Martin, 1972; Crocroft and Ryan, 1995; Bradbury and Vehrencamp, 1998).

The morphological characters examined so far of this family by Delacour (1944), Beehler (1953), Beehler and Finch (1985), Sharpe (1885), Sundevall (1872,1909), Wetmore (1930, 1940, 1960), Sibley and Ahlquist (1990), Sibley and Monroe (1990), Irwin, (1999), Fry *et al.* (2000) and Cheke and Mann (2001) include plumage variations, the presence and absence of features such as pectoral tufts, tail length and structure and bill size. However the uniformity of these morphological characters amongst most members of the family (Cheke and Mann, 2001) allows only poor differentiating signals for clear systematics and morpho-phylogenetic characterisation. This study reviewed plumage variations, pectoral tufts, bill size, habitat and nest structures based on data in Cheke and Mann (2001) but could not derive any useful morpho-phylogenies from these poorly differentiated data either.

1.1.3. Vocalisations

Sonographic analyses of some taxa have supported the hypothesis that discrete acoustic traits evolved within the vocalisations of some birds and that these are often the most prominent or even the most diagnostic field characters (Payne, 1986; Cramp *et al.*, 1977; 1988; Clancey, 1990; Alstrom and Ranft, 2003; Ranft, 1997). The remarkable discovery of a new species, the Rock Firefinch *Lagonosticta sanguinodorsalis* in the Jos Plateau of Northern Nigeria, was based on analysis of the songs of its brood parasite *Vidua maryae* that revealed mimicry of an hitherto unknown bird (Payne, 1998).

Comparative vocal and phylogenetic methods are now well established in evolutionary research (Martins 1996; Cunningham *et al.*, 1998; Pagel 1999a) and the application of Fourier analysis and modern sonographic-based techniques (Nowick and Marler, 1988; Marler and Nelson, 1993) facilitates representation of the time-frequency domain structure of bird vocalizations and has made the study of vocal communication and differentiation an increasingly important part of bird taxonomy and phylogeny.

Vocal signals have been studied extensively and have become an integral part of the understanding of the evolutionary behaviour of most bird species and, in particular, species with poor morphological divergence (Kroodsma and Miller, 1982; Catchpole and Slater, 1995; Martens *et al.*, 2004). It has also been known from birdsong studies that songs have well defined acoustic structures that are highly characteristic of each species and therefore may be reliably used for interspecific and intraspecific species differentiation and identity (Catchpole and Slater, 1995; Miller, 1996; Doutrelant *et al.*, 2000).

Differing acoustic characters have been used to derive vocal phylogeny in songbirds and these involve quantifying the varying patterns in song frequencies, durations, silent intervals, pitch / amplitude, entropy, bandwidth, position of syllable etc. While the use of these characters quantifies the auditory variations among bird vocalisations, they may be difficult to interpret (Tchernichoviski *et al.*, 2001). Also, the attempted quantification of these characters into single statistical units may obscure hidden dimensions within a song (d'Avella and Tresch, 2002). Homology is another important prerequisite when comparing traits across species and its definition is often considered as a constraint in evolutionary analysis of vocal traits (De Kort and ten Cate, 2003). Habitat and learning related modifications further compound the use of the above characters. Songs are usually modified by learning during development and thus some acoustic features vary dramatically between individuals of the same population (Baptista, 1996; Price and Lanyon, 2002). It is also evident that aspects of song features may be modified as signals travel through different environments, and these may create more variations in distantly related species inhabiting similar habitats than closely related species inhabiting different habitats (Morton, 1975; Wiley and Richards, 1978; Krebs, 1979).

Although the Nectariniidae are not among the well known bird songsters such as the finches (Fringillidae), sparrows (Passeridae), Old World warblers (Phylloscopidae), etc., their vocalisations include distinct forms such as trills, buzzes, whistles and complex syllables and phrases. All of these song forms contain acoustic features that are amenable to sonographic and statistical analyses thus enabling the use of character states such as the different levels of frequencies, durations, silent intervals, pitch / amplitude, entropy, and bandwidth and repertoires for species specific identity and studies of evolutionary history.

The characters that have been used in this study to analyse the vocalisations and which involve the application of both visual and the automated techniques include maximum frequencies, rhythm of frequency, note interval, note duration, amplitude, bandwidth, duration of phrase, number of notes in a phrase, size of repertoire, introductory rattle, click, squawk, song duration note percentage, pause rate and entropy. See Table 3.2. for examples of the data collected and used in the phylogenetic analyses.

The analysis of pre-recorded vocalisations is often constrained by poor quality recordings characterised by background noise from water currents, wind blow, songs / calls of other animals and birds in the background, buzzing of insects across the microphone, humans' voices, booming of cars or aircraft etc. which influence the quality of some sonographic output and statistical values derived from them.

In addition, duetting and choir singing and dialectal differences have been reported in some species (Brieschke, 1990; Grimes, 1974, 2007) but the extent to which these factors may have constrained the vocal analyses of the family and the phylogeny is unknown.

Although there is no known study on the constraints that song learning and song repertoire size or habitat signal attenuation effects might have on members of this family, it is possible that these may have had some effect on the results and the phylogenies, but, even so, are thought unlikely to have compromised the overall reliability of the outcome of this study.

1. 2. CONSTRAINTS IN STUDIES OF VOCAL PHYLOGENY

1.2.1. Behavioural attributes and function of vocal signals in songbirds

Some behavioural studies have examined signal form and content of auditory signals of animals from the function-based approach (Klump and Shalter, 1984; Gerhardt, 1991) and a majority of these studies have clearly shown that signals may convey lots of concurrent information to the intended recipients, but always contain a basic function and meaning (Bradbury and Vehrencamp, 1998).

In most songbirds, song serves two main functions, namely territory defence and mate attraction but other utterances include threat, alarm or alert calls. Territorial defence, mate attraction and courtship signals by males tend to be long-distance signals that are complex enough to contain structural patterns and are of frequencies that clearly distinguish them from similar signals of conspecifics with the main motives of attracting a mate (female), repelling competitors, identifying the boundaries of areas and defending the latter whilst conserving scarce resources for reproductive purposes (Bradbury and Vehrencamp, 1998). The complex nature of these signals encompasses a wide variety of vocal and behavioural phenomena including dialects and speciation (Baker *et al.*, 1981; Miller, 1996). In contrast threat, alarm, flight and feeding calls are mostly short range signals intended to alert assemblies and / or dispel individuals or groups in a social system (Bradbury and Vehrencamp, 1998).

Some authors have delved into the implications of signal functionality. Mate preferences have been tested extensively in captivity by measuring the response of copulation–solicitation displays to standardized playback experiments. For example, in White-crowned Sparrows *Zonotrichia leucophrys*, females show stronger responses to local dialects than to unfamiliar ones (Baker *et al.*, 1981; Baker, 1982, 1983; Lampe and Baker, 1994). The response of territorial males to playback of dialectal variation has also been tested extensively. In general, territorial males respond most strongly to familiar dialects, followed by foreign dialects, and heterospecific song. Species for which this has been shown include White-crowned Sparrow (Milligan and Verner, 1971, Baker *et al.*, 1981, Petrinovich and Patterson, 1981); Darwin's finches (Ratcliffe and Grant, 1985); Swamp Sparrow *Melospiza georgiana* (Balaban, 1988a) and Song Sparrow *Melospiza melodia* (Searcy *et al.*, 1997). Thus males may have more difficulty in establishing territories in areas with foreign dialects, thereby reducing gene flow among dialects (Baker *et al.*, 1981; Baker, 1982, 1983; Lampe and Baker, 1994).

Similarly, male Song Sparrows that share more songs with neighbours have been shown to be more successful in maintaining their territory (Beecher *et al.,* 2000; Wilson *et al.*, 2000). In another experiment, prospecting males were either repelled by playbacks of their species's songs or they provoked an attack by other males. In these playbacks, males responded with songs, launched an aggressive approach or attacked at the sound of their own song but retreated from songs of other species (Becker, 1982; Catchpole and Slater, 1995; Payne, 1986).

This is a clear indication that evolutionary divergence of mating signals is important in speciation. Two populations are essentially different species if they have diverged sufficiently so that members of one do not recognize members of the other as potential mates. Among closely related species, mating signals are often more divergent than morphological, genetic or other behavioural traits (Miller, 1996; Jones, 1997; Wells and Henry, 1998; Irwin *et al.*, 2001). Across a variety of taxa, experiments have demonstrated that females discriminate between conspecific and heterospecific male signals (e.g. Uetz and Stratton, 1982; Verrell and Arnold, 1989; Clayton, 1990; Ryan and Rand, 1993; Gerhardt, 1994; Wells and Henry, 1998). These observations suggest that divergence in mating signals occurs rapidly and can quickly generate reproductive isolation, as in the case of warblers of the 'Chiffchaff complex': *Phylloscopus canariensis* and *P. collybita* are morphologically similar to each other, differing slightly in colouration, wing structure, plumage and body proportions, but with clear distinctive and recognisable vocalisations. Also, individuals of the same species do not respond to the song or calls of the other species. There are also notable differences in the contact calls of different members of the 'Chiffchaff complex' (Clement and Helbig, 1998).

1.2.2. Song Repertoire

Song repertoire is another vocal phenomenon thought to either have evolved through the selection force of female mate choice or as an honest signal of male quality (Anderson, 1994; Searcy and Yasukawa, 1996; Spencer *et al.*, 2003). Song repertoire is the estimated number of unique song units each bird can sing (Irwin, 2000). It varies between different species with some species having only a simple stereotyped song repeated over and over again. The White-crowned Sparrow *Z. leucophrys* and the Splendid Sunbird *Cinnyris coccinigaster* are typical of species with this kind of repertoire of calls / songs. In contrast, the Mockingbird *Mimus polyglottos* and the Nightingale *Luscinia megarhynchos* have complex songs with many versions (Catchpole and Slater, 1995).

The display of repertoire by some species complicates the analysis of songs, particularly of species with large repertoires. To deal with large repertoires, it is necessary to obtain many recordings, as in the study of the brood-parasite indigo birds *Vidua* spp. that have many song versions and their study required refined song analysis of many recordings (Payne, 1998).

1.2.3. Song learning and dialects

Studies on song evolution have established parallels between song development and human speech development with their common attribute being that the behaviours are learnt (Doupe and Kuhl, 1999; Brenowitz, 2002). Young birds acquire and develop their songs by listening to adult conspecifics, producing stereotyped versions first that later crystallise into more structured songs (Thorpe, 1954, 1958).Young birds are not entirely without discrimination in their choice of tutors and may be able to filter the songs of other birds and to pick out the song to imitate. Hence regional 'dialects' can link them to a place of origin. Dialects have been recorded in Brown-headed Cowbirds (*Molothrus ater*), Corn Buntings (*Miliaria calandra*), elephants (*Loxodonta* spp.) and whales (Cetacea) among others (Chilton, 1991). However, the function of vocal dialects is still highly debatable and there two schools of thought that have attempted to explain the phenomenon.

Some behavioural ecologists believe that an individual's dialect represents a mark of birth place that can be used by others of the same species when choosing a mate and that females may avoid males with strange songs that have dispersed from distant populations. The second school of scientists consider that dialects are without function and are merely a by-product of song learning. A male learns from his father just as his father did before him. If a mistake is made and a bird learns a song incorrectly, the error is perpetuated by subsequent generations (Chilton, 1991).

Sunbirds with dialects include the Lesser Double-collared Sunbird *Cinnyris chalybeus,* the Splendid Sunbird *C. coccinigaster* and the Bronze Sunbird *Nectarinia kilimensis* (Brieschke, 1990) and whenever song dialects occur in a species, geographical variation of the song is expected (Grimes, 1974). Grimes (2007) also observed that the boundary between different dialects is very small and in some cases may occur within a distance of 50 metres.

Many species of birds learn their song from nearby singing males during a sensitive phase early in life (e.g. Kroodsma, 1982; Marler, 1997). Therefore, it is questionable whether males are still recognizable as being local or immigrant despite their developmental flexibility (Slabbekoorn *et al.*, 2002). Learned song can be an indicator of a natal population in several ways. An acoustic signature of the population may remain in the case of pre-dispersal learning from father or neighbour, with either restricted or no learning later in life. Well known examples of this type of learning are found in Zebra finches *Poephila guttata* (e.g. Clayton, 1990; Zann, 1997) and Darwin's finches (6 genera in the Geospizinae, e.g. Grant and Grant, 1996). However, many species are able to adjust their songs after dispersal (reviews in Krebs and Kroodsma, 1980; Kroodsma, 1982; Baptista and Gaunt, 1997; Payne and Payne, 1997). Although this may allow a male's song to partly converge to the songs of neighbours after dispersal, an acoustic signature of the natal population may still remain in at least two ways. First, post-dispersal adjustment to local song variants may take place via a process of selective attrition. In this process males learn a song repertoire before dispersal, from which they eventually select only the part that best matches the song of new neighbours (Marler and Peters, 1982; Nelson, 1992; Nelson *et al.*, 1996a). Second, even if a male is able to learn completely new songs after dispersal, an acoustic signature of the natal population may remain when song plasticity is constrained by genetically determined components. There is further evidence to suggest that components of highly plastic learned song may have a genetic basis. Despite intraspecific variation in learned song, species-specific characteristics such as duration, rhythm, frequency range or tonal quality are typically heritable (Marler and Pickert, 1984; Marler and Sherman, 1985; Baptista, 1996). Such heritable song characteristics are attributed to neural song templates or species-specific learning preferences with a genetic basis (Thorpe, 1958; Marler and Peters, 1977, 1988, 1989; Marler, 1990, 1991; Kroodsma and Canady, 1985; Eales, 1987; Nelson and Marler, 1993; Mundinger, 1995; Braaten and Reynolds, 1999; Soha and Marler, 2000). Recently, Nelson (2000) showed that White-crowned Sparrows not only inherently prefer learning from their own species, but even prefer their own subspecies's song. Acoustic variation may also have an indirect genetic basis, when song is affected by resonance characteristics inherently coupled to heritable variation in morphology (Slabbekoorn and Smith, 2000). Acoustic characteristics have been shown to be correlated with body size (e.g. Wallschlager, 1980; Tubaro and Mahler, 1998; Bertelli and Tubaro, 2002), vocal tract length (e.g. Suthers, 1994) and bill morphology (Palacios and Tubaro, 2000; Podos, 2001; Huber and Podos, 2006). Although empirical evidence for a correlation between heritable characteristics of song and ecological variables is limited, a convincing example is found in migratory and sedentary subspecies of the White-crowned Sparrow. Experiments in captivity showed that subspecies differ genetically in timing and flexibility of song learning. These differences are correlated with ecological aspects of their migratory mode and can be explained as adaptations to the length of the breeding season and the relative uncertainty over breeding location (Nelson *et al.*, 1995, 1996a, b; Slabbekoorn *et al.*, 2002).

A taxonomic study of antbirds (Passeriformes: Thamnophilidae) to establish species limits using vocal utterances has been attempted (Isler *et al.*, 1997, 1998). The study involved setting a methodology for taxonomic assessment of the antbirds and other sub-oscines using vocal characters. Also, differences in songs have been used in confirming the species distinctiveness of several species including the *Zenaida* doves and *Empidonax* flycatchers in the Neotropics (Payne, 1986).

As already mentioned, many bird songs are learned, which influences signal evolution and has to be controlled for or included as secondary variations during phylogenetic analysis.

1.2.4. Mimicry or imitation

Although vocal mimicry is an important phenomenon, little is known about why and how birds mimic other birds (Hamao and Fujiwara, 2004). An extensive investigation of the migratory Marsh Warbler *Acrocephalus palustris* revealed that males mimicked 102 and 113 species within their breeding and wintering areas, respectively (Lemaire, 1975; Dowsett-Lemaire, 1979). The common Starling *Sturnus vulgaris* is also recorded as mimicking birds belonging to as many as 11 orders, as well as sounds of Goat *Capra hircus*, frog species and the sound of a squeaking door and dripping water (Hausberger *et al.*, 1991). Stjernstedt (1996) noted that his recording of the White-bellied Sunbird *Cinnyris talatala* was an imitation of an unidentified bird.

1.2.5. Environmental and signal transmission

There is ample evidence that the environment can degrade vocal signals by causing frequency attenuation and contributing masking noise (Bradbury and Vehrencamp, 1998) and this has underlined the likelihood that habitat-dependent selection can lead to intraspecific divergence in vocalizations. There is also growing support for ecological gradients between different habitats being important in divergence and speciation (e.g. Endler, 1977; Bush, 1994; Smith *et al.*, 1997; Orr and Smith, 1998; Schluter, 1998; Schilthuizen, 2000). Song recordings from different parts of the habitat range are useful in delimiting biological species where the range is fragmented with populations in isolated regions or islands (Snow, 1973; Becker, 1982; Payne, 1986; Slabbekoorn and Smith, 2002). Habitats differ with respect to the density and type of vegetation, resulting in different selection pressures on acoustic signals as a consequence of the way in which sound attenuates and degrades as it penetrates the physical environment (e.g. Linskens *et al.*, 1976; Marten and Marler, 1977; Martens, 1980; Endler, 1992; Forrest, 1994; Brown and Handford, 1996, 2000). For example, lower frequencies transmit better in dense vegetation, which is associated with a lower average frequency used by forest species than species found in open habitats (Chappuis, 1971; Morton, 1975; Ryan and Brenowitz, 1985). In addition, reflective layers in dense vegetation lead to reverberations, and, depending on the acoustic structure of a song, this may be detrimental (e.g. Richards and Wiley, 1980; Wiley and Richards, 1978, 1982; Wiley, 1991; Dabelsteen *et al.*, 1993; Holland *et al.*, 1998) or beneficial to signal efficiency (Slabbekoorn *et al.*, 2002). However, habitats that drive song divergence may also lead to divergence in morphological, life history or behavioural traits (e.g. Endler, 1977, 1986; Lougheed and Handford, 1992; Smith *et al.*, 1997; Lambrechts *et al.*, 1997). If habitat-dependent selection is strong enough, divergence in a particular trait may evolve despite substantial gene flow (Slatkin, 1987; Rice and Hostert, 1993; Smith *et al.*, 1997) and may affect male fitness depending on whether a male disperses within or between habitats (Laland, 1994; Irwin and Price, 1999; Cate and Vos, 1999). It should, however, be noted that environmental constraints on evolution are more difficult to uncover and require comparative studies and phylogenetic analysis.

1.2.6. Vocal analysis

The analysis of sound is a complex phenomenon and often involves the breakdown of a continuous waveform into measurable quantities that provide a complete description of the signal components such as frequency, amplitude etc. and the technique commonly used to deal with signal measurements is Fourier analysis (Bradbury and Vehrencamp, 1998).

Describing the variation within a population is therefore a crucial first step towards understanding which aspects of the observed variation in a signal are meaningful in communication. Descriptive studies involving visual inspection of sonograms usually assess repertoire size or inter-individual differences in song output (Searcy and Nowicki, 2000). Parameters relating to structural differences between song types, for example the sequencing or presences of different elements have been described less systematically. However, such parameters could be an important means to assess variability, especially in species with small song type repertoires. However, the analysis of spectral characters such as maximum and minimum frequency, note duration and note interval can lead to acoustic characterization of calls / songs with respect to variation and structural differences between conspecifics (Leitao *et al.*, 2004). Vocal analysis involves the conversion of sound recordings on a magnetic tape or cda (compact disk-digital audio) into "wav" files, a format that can be processed by computer. Most avian vocalizations are within the range 1-8 kHz (www.avisoft.com).

1.2.7. Problems associated with sound quality

Background noise and poor quality recording of some species mar the usefulness of many recordings. Noise is sound lacking sufficient concentration energy within narrow margins of a principal frequency to give it a tone of identifiable pitch and it appears as broad band patches of energy encompassing the available spectrum (Cramp *et al.*, 1977). Many bird songs comprise a mixture of tones and noises. Background noise may arise from water currents, wind blow, songs / calls of other animals in the background, buzzing of insects across the microphone, humans' voices, booming of cars or aircraft etc. It impedes the output of sonograms and the export of statistical parameters for further analysis. In addition, poor recording and the problem of bird duetting and choir singing, further complicates editing bird song and quality and in most cases speckles sonograms.

1.3. AIMS AND OBJECTIVES

The aim of this research project was to re-examine the phylogeny of the sunbirds (Aves: Nectariniidae) by analysing their vocalisations. A particular aim was to test the hypothesis that the sunbirds originated in Asia. Sunbirds are restricted to Africa and Asia (apart from one species in each of Israel and Australia). They are the ecological equivalents of the Neotropical hummingbirds (Trochilidae) but are taxonomically unrelated, being passerines, unlike the non-passerine hummingbirds. Some taxonomists (e.g. Sibley and Monroe, 1990) have included the Flowerpeckers, an exclusively Asian group comprising two genera only, within the Nectariniidae whilst others separate them in the family Dicaeidae e.g. Dickinson (2003), so a subsidiary aim was to examine the affinities of the Flowerpeckers.

Phylogenies based on morpho-taxonomy and the biological species concepts are being challenged by results of cladistic studies on bird DNA and on their calls, which mostly use the phylogenetic species concept as a paradigm. Descriptions of new species now often include data on morphology, DNA and vocalisations or on at least two of these characteristics. Irwin (1999) concluded on morphological grounds that the sunbirds originated in Africa and thence radiated out to Asia. However, recent DNA studies have suggested that the lineage originated in Asia (Bowie, 2003). A principal aim of the proposed work is to test Bowie's hypothesis on the basis of sunbird vocalisations recorded from the Asian species and to compare these with the African recordings. The research was reliant on pre-recorded materials but as analyses using vocalisations depend on good quality recordings on tapes or mini-discs, not all the material available was usable.

1.4. OUTLINE AND STRUCTURE OF THE THESIS

The thesis is divided into three related parts and organised in seven chapters. The first part of the thesis contextualises the research issue in the preceding parts of this chapter (Chapter 1).

Chapter 2 provides a contemporary picture of the geographical distribution of flowerpeckers, sunbirds and spiderhunters including their preferred habitats, behaviours and affinities. This will form the foundation for the remainder of the thesis, which aims at determining the origins of sunbirds.

Chapter 3 provides short descriptions of the materials and methods and explains how the vocalisations were analysed, together with sections on morphological methods and the derivation of phylogenies of the flowerpeckers and sunbirds based on vocalisations. The discussion here focuses on issues relating to the measurement of acoustic features or characters, song and call structures such as trills, whistles and complex songs and sizes of repertoires and different ways of constructing phylogenetic trees.

Chapters 4 and 5 present detailed methods, the results of the analyses and findings of the research and discussions. Chapter 6 is a general discussion of the morphological predictions as against the DNA and vocal phylogeny of the Nectariniidae. It will draw conclusions and provide recommendations for future research.

CHAPTER 2

STUDY TAXA (NECTARINIIDAE): FLOWERPECKERS (DICAEINI) AND SUNBIRDS AND SPIDERHUNTERS (NECTARINIINI)

2.1. INTRODUCTION

This chapter presents the geographical distribution and associations among the species of flowerpeckers, sunbirds and spiderhunters comprising the Nectariniidae. It provides background on the study taxa and focuses mainly on systematic classifications, tracing the placements of family and generic groupings in the context of the Passeriformes as a suborder of the oscines. It describes the morphology, breeding habits, habitat and vocal characteristics of the Nectariniidae together with a brief examination of the conservation status of the family and its relationship with man.

Using the classification adopted by Cheke and Mann (2001) who followed Sibley & Monroe (1990), the family Nectariniidae is composed of two main Subfamilies: the Promeropinae (the sugarbirds) a group not considered in this study and the Nectariniinae (flowerpeckers, sunbirds and spiderhunters). The Subfamily Nectarininae is further classified on morphological grounds into two main tribes: the Dicaeini comprising the flowerpeckers and the Nectariniini composed of the sunbirds and spiderhunters. The presentation in this chapter has therefore been based on the categorisation of the two main tribes identified above. Some authors now treat the flowerpeckers as a separate family, the Dicaeidae (Dickinson, 2003; Gill and Wright, 2006; Mann and Cheke, 2008a).

The Tribe Nectariniini: sunbirds and spiderhunters are a well defined and uniform group of small or very small songbirds strongly associated with flowering trees and which feed mainly on nectar, insects and spiders. This has closely linked them ecologically but not taxonomically with other nectarivorous birds such as the honeyeaters (Meliphagidae) and the

American hummingbirds (Trochilidae). In some species there is sexual colour dimorphism with the males having most iridescent or metallic plumage. Some species possess pectoral tufts (in males only or in both sexes but never in females only) and some, but not all, moult into an eclipse or non-breeding plumage. Bills and tongues show remarkable variation and are of taxonomic significance (Delacour, 1944; Sibley and Monroe, 1990; Irwin, 1999; Cheke and Mann, 2001).

2.2. COMPOSITION AND GEOGRAPHICAL DISTRIBUTION

2.2.1. Flowerpeckers

The tribe of flowerpeckers (Dicaeini) is split into two genera. The *genus Dicaeum* is the largest genus with 36 species whereas *Prionochilus* is composed of only 8 species. Flowerpeckers are among the smallest of passerines. They are mostly forest and top canopy arboreal dwellers and feed mostly on small berries of mistletoes, nectar, pollen and spiders (Cheke and Mann, 2001). Flowerpeckers of the genus *Prionochilus* are found in Thailand, Vietnam, the Malay Peninsula, Indonesia and the Philippines and have 10 long primaries, whereas in species of *Dicaeum* the 10th primary is vestigial or very short. The genus *Dicaeum* occurs in the same areas as *Prionochilus* but also extends to the Indian sub-continent, Sri Lanka, Burma (Myanmar), Cambodia, Laos, south China, Hainan Island, Taiwan, Sulawesi, the Moluccas, New Guinea and its surrounding islands and one species reaches Australia (Figure 2.1).

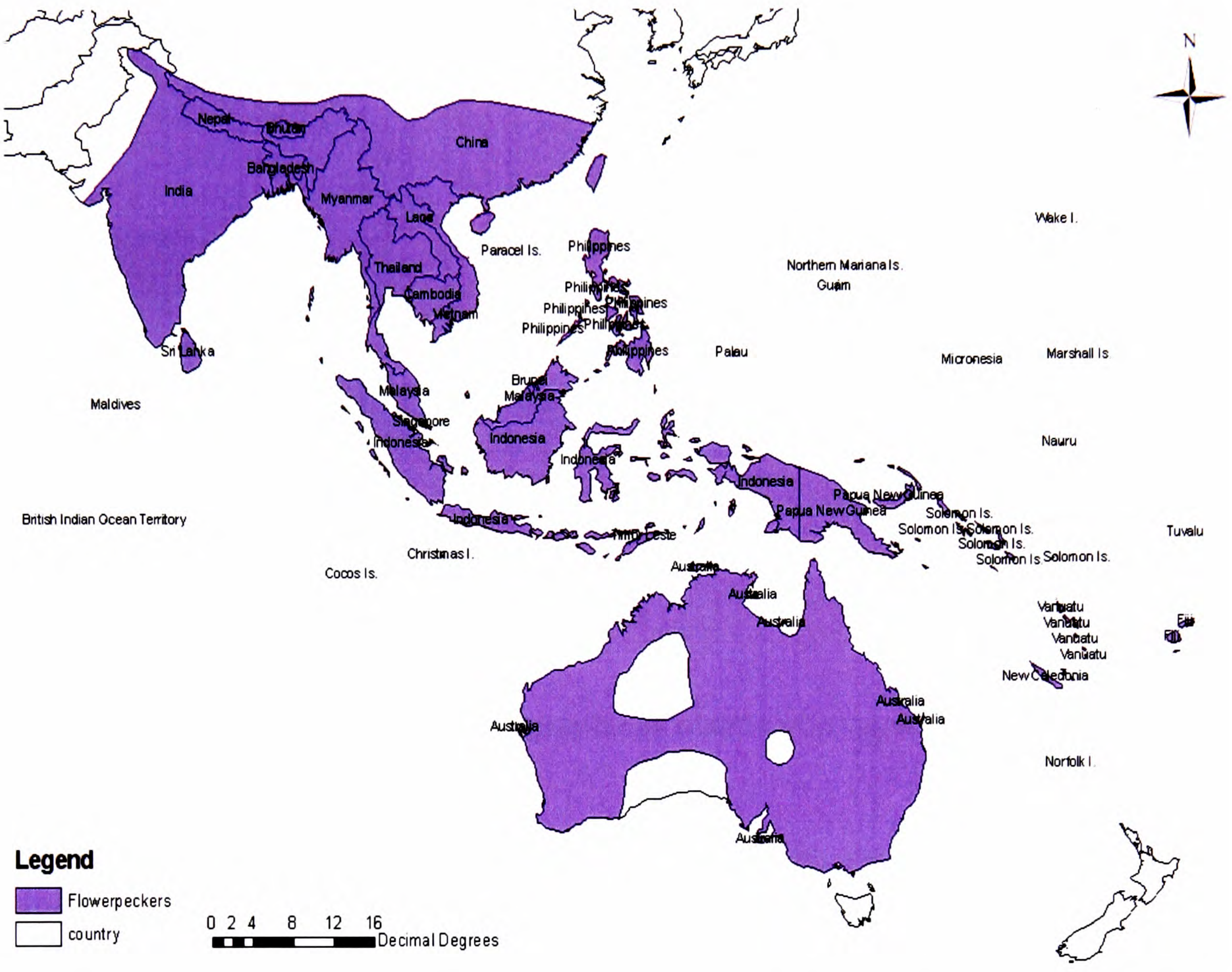


Figure 2.1. Map of the geographical extent (purple shading) of the flowerpeckers in the Oriental region, ranging from the Indian sub-continent to Australia.

2.2.2 Sunbirds and Spiderhunters

Sunbirds constitute a very large and ecologically diverse group and are classified into 176 species (Cheke and Mann, 2001) and so provide a diverse taxonomic base for comparative vocal analysis. Eleven out of 16 genera, consisting of 87 species, occur in Africa and the Indian Ocean islands while five genera of 31 species are found in Asia. However, species of two genera (*Anthreptes* and *Cinnyris*) are found in both Africa and Asia (Figure 2.2.).

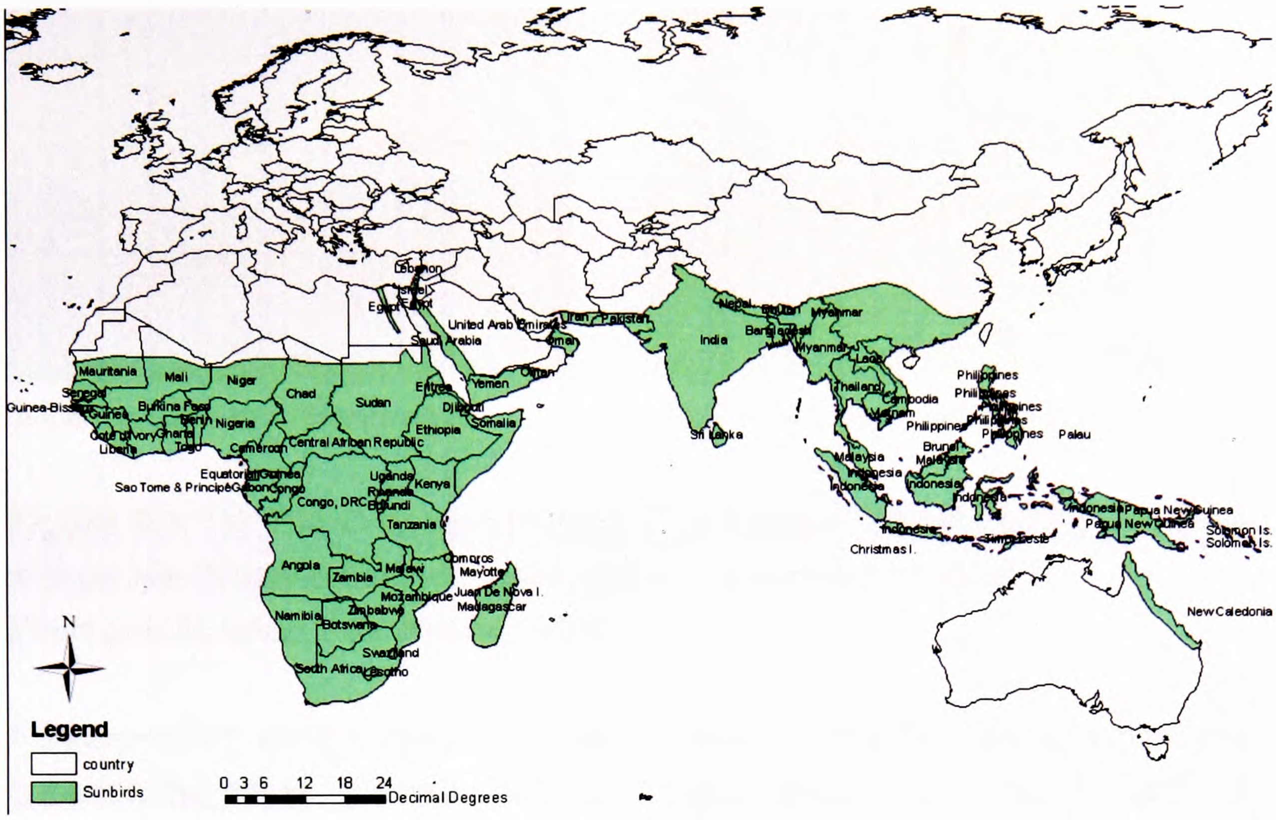


Figure 2.2. Map showing the geographical distribution (green shading) of sunbirds.

Sunbirds are widespread across the Afrotropical region, including the Indian Ocean islands, and southern parts of the Arabian Peninsula, extending northwards through north-eastern Africa into the Palaearctic region in the Levant, and then east and south through the Oriental region to Wallacea, New Guinea, the Solomon Islands and Australia. There is a high level of endemism. The 10 species of spiderhunters (genus *Arachnothera*) are all restricted to Asia.

2.3. APPEARANCE AND MORPHOLOGICAL CHARACTERS

2.3.1. Flowerpeckers

Flowerpeckers generally possess colourful plumage with short, stout and straight bills and very short tails (Figures 2.3a and b) and are noted for their elongated, flattened, slightly concave, tongues.

(a)Crimson-breasted Flowerpecker (b) Yellow-breasted Flowerpecker

Figure 2.3. (a) The Crimson-breasted Flowerpecker *Prionochilus percussus* and (b) the Yellow-breasted Flowerpecker *Prionochilus maculatus*. Photographs taken from Huang (2006).

Flowerpeckers exhibit much plumage variation both within conspecifics and between the sexes of some species. In some species, it is only a matter of contrasts between drab and brighter plumage differences while in others there is contrasting colouration. The drab or otherwise dull plumage is a common feature of females and this is typical of species such as the Scarlet-breasted Flowerpecker *Prionochilus thoracicus*. For some species such as the Golden-rumped Flowerpecker *Dicaeum annae* plumage is monomorphic and there are no gender differences. Twelve species (33.2%) of flowerpeckers are reported to possess mostly white lateral pectoral tufts in both sexes (Cheke and Mann, 2001).

2.3.2. Sunbirds and Spiderhunters

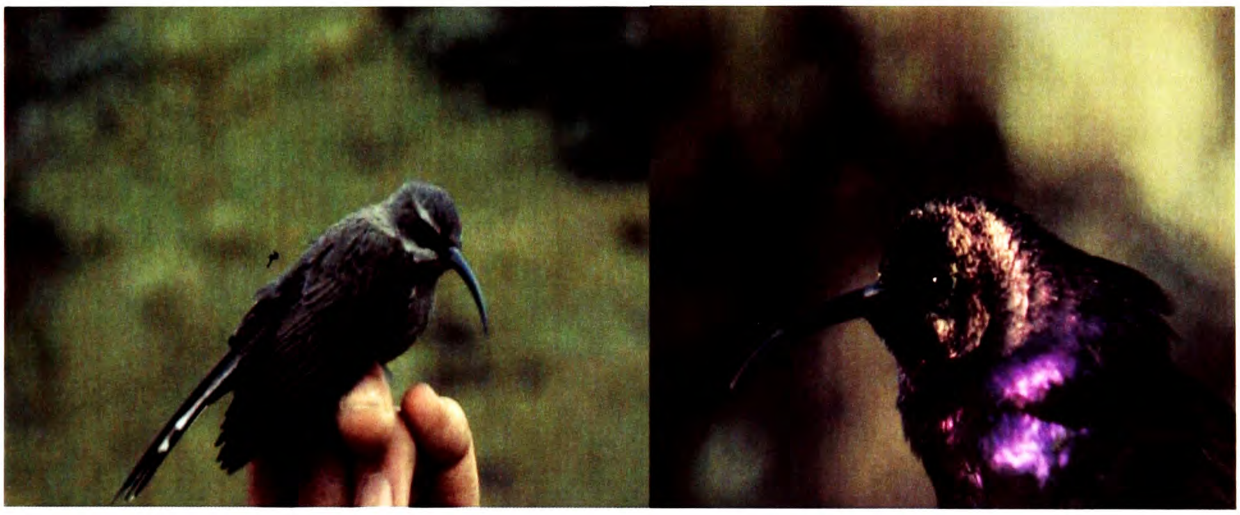
Sunbirds are often thought of as a relatively uniform group of small-sized birds, which are not highly diverged morphologically and behaviourally (Warren *et al.*, 2003). Some species are notably sexually dichromatic. Species thought to be closely related and morphologically similar can be distinguished by small variations in plumage colouration and by the sizes and lengths of their tails and shapes of their bills. Generally, the bills of sunbirds appear long, slender and curved (Grzimek, 1973; MacLean, 1985) (Figures 2.4. and 2.5).

(a) Male (b) Female

Figures 2.4 and 2.5.
Pictures showing the distinct long and slender curved bills of the Malachite Sunbird *Nectarinia famosa*; (a) male and (b) female. (Photographs: R. A. Cheke).

The long curved bills coupled with the tubular and serrated tongues of most sunbirds are adaptations for nectar feeding, whereas those with short bills are well adapted to insect feeding.

Many sunbirds are sexually dichromatic with males in about 96 (87.3%) species appearing more brightly coloured than the much drabber females of the same species.



(a) Female (b) male

Figures 2.6 and 2.7. Pictures showing (a) the dull female plumage and (b) the dazzling iridescent plumage of a male Tacazze Sunbird *Nectarinia tacazze* (Photographs: R.A. Cheke).

Only about 14 (12.7%) species of sunbirds appear similar morphologically in both sexes. The dull and less contrasting plumage of some species, especially the females, poses challenges for their identification (Farquhar *et al.*, 1996) (compare Figures 2.5 and 2.6).

Most species of sunbirds are also known to moult into brighter breeding plumage at the start of their breeding seasons. A few species, or some of their subspecies, moult into a distinct non-breeding plumage soon after the breeding season has ended. Some sunbirds possess or exhibit a yellow or red pectoral tuft. In some species it is found in both sexes while in other cases it can occur only in the male or only in one or other subspecies (Cheke and Mann, 2001).

The spiderhunters appear larger than sunbirds with more heavily built decurved and long bills, which are almost longer than the length of their heads (Cheke and Mann, 2001). The spiderhunters appear similar in plumage in both sexes and do not seem to moult into a non-breeding plumage. Only about 4 (40%) tend to display the pectoral tuft and then only in males (Cheke and Mann, 2001).

2.4. THE EVOLUTION AND SYSTEMATICS OF THE TAXA STUDIED

The convoluted history and classification of flowerpeckers (Dicaeini) remains controversial, debatable and less than clear-cut. The tribe Dicaeini (or family Dicaeidae) was traditionally classified by earlier studies on the basis of anatomy and other morphological characters (shapes of tongues and bill modifications) and was sometimes included with taxa that are now treated as separate such as the berrypeckers (Melanocharitidae) of New Guinea, the Hawaiian honeycreepers (Drepanidinae) of the Hawaiian Islands and the honeyeaters (Meliphagidae) of Australasia. The white-eyes (Zosteropidae) and the pardalotes (*Pardalotus* spp.) were also among taxa placed within the family Dicaeidae (Sundevall, 1872; Sharpe, 1885, 1909). At one stage, the flowerpeckers were placed among the Sylviidae (Beehler, 1953; Beehler and Finch, 1985).

Even though Delacour (1944) and others had recognised the close relatedness of flowerpeckers to sunbirds, it was Sibley and Ahlquist (1990) who identified this relationship on the basis of DNA hybridisation results and gave the Flowerpeckers the rank of a tribe (Dicaeini), composed of the genera *Prionochilus* and *Dicaeum* and placed them within the family Nectariniidae which included sunbirds, spiderhunters and sugarbirds. This position was followed by Cheke and Mann (2001).

Acoustic measurements of the vocalisations of the flowerpeckers as part of this study (Chapter 4 and see Iddi, 2005; Iddi *et al.*, 2006) further affirm the affinity of Dicaeini and provided evidence to support the view that most species of the genus *Prionochilus* constitute the most basal forms, within a clade separate from the genus *Dicaeum*.

Similarly, the evolutionary systematics of the sunbirds and spiderhunters is equally unsettled. The intricacy of the history of the placements of sunbirds and the ongoing attempts to replace or merge the generic grouping of some species renders the overall classification and systematic exercise as incomplete and far from resolved. Following Sibley & Monroe (1990), the family Nectariniidae includes two subfamilies, the Promeropinae comprised of two species of *Promerops* (sugarbirds, restricted to southern Africa) and the Nectariniinae which is further subdivided into two tribes, the Dicaeini, flowerpeckers (restricted to Asia and Australia), and the Nectariini, sunbirds and spiderhunters (Sibley and Monroe, 1990; Paynter, 1967). The sunbirds and spiderhunters currently consist of 16 generic groupings: *Chalcoparia*, *Deleornis*, *Anthreptes*, *Anthodiaeta* (formerly *Hedydipna*), *Hypogramma*, *Anabathmis*, *Dreptes*, *Anthobaphes*, *Cyanomitra*, *Chalcomitra*, *Leptocoma*, *Nectarinia*, *Drepanorhynchus*, *Cinnyris*, *Aethopyga* and *Arachnothera* (Irwin, 1993, 1999; Cheke and Mann, 2001, Mann and Cheke, 2006 and 2008a).

Earlier ornithologists have associated sunbirds with the non-passerine hummingbirds (Trochilidae) but sunbirds as passerines do not relate at all to the hummingbirds. Prior to the above classification by Sibley and Monroe (1990), sunbirds were further linked to the berrypeckers, pardalotes, Zosteropidae (White-eyes) and Meliphagidae (honeyeaters) on the basis of morphological characters and labelled insectivores (Wetmore, 1930, 1940, 1951, 1960). However, Delacour (1944) reviewed the family Nectariniidae and reduced the number of genera of sunbirds to five but accepted and reintroduced some subgenera, including *Deleornis* and *Rhizophorornis*.

In another revision exercise, Irwin (1993, 1999) decided to exclude two genera of the Nectariinidae and instead accepted 14, listing them as *Anthreptes, Deleornis, Anabathmis, Dreptes, Anthobaphes, Cyanomitra, Chalcomitra, Leptocoma, Nectarinia, Hedydipna, Cinnyris, Hypogramma, Aethopyga* and *Arachnothera*. To this list, Cheke and Mann (2001) added *Chalcoparia* for (*Anthreptes*) *singalensis* and *Drepanorhynchus* for (*Nectarinia*) *reichenowi* and elevated the Nectariniidae to its current 16 genera.

Irwin (1999) supported by Fry *et al.* (2000) further proposed that sunbirds are of African origin based on the fact that they have shorter bills than their Asian counterparts and would perhaps be mostly insectivorous rather than nectar feeders. The genera *Deleornis* and *Anthreptes* were classed as the most primitive and *Cinnyris* the most derived genera of the subfamily Nectariini. However, Cheke and Mann (2001) argued on the basis of tongue structure and concluded that *Chalcoparia* is rather the most primitive of all sunbirds.

Currently the status of the Olive Sunbird *Cyanomitra olivacea / obscura*, one of the most widely distributed sunbirds in Africa, is in a state of flux. On morphological grounds the species was split into the Eastern Olive Sunbird *Cyanomitra olivacea* and the Western Olive Sunbird *Cyanomitra obscura* (Smith, 1840; Jardine, 1843; Clancey, 1992, 1993). This split was supported by Fry (2000) and Cheke and Mann (2001). However, based on mtDNA evidence Bowie *et al.* (2004a) suggested that the divergence levels were too low to support the split. In another DNA study, Bowie *et al.* (2004b) also confirmed the validity of Moreau's Sunbird *C. moreaui* and concluded that it is a sister species to Loveridge's Sunbird *C. loveridgei*.

Mann and Cheke (2006) reviewed the genus *Hedydipna* on the basis that Cabanis (1850), Shelley (1876, 1880), Roberts (1931, 1932) and Skead (1967) had used *Anthodiaeta* in place of *Hedydipna*, and concluded that *Anthodiaeta* should replace *Hedydipna* if *collaris*, *platura, metallica* and *pallidigaster* are treated as congeneric.

Vocal analyses of 195 sonograms of 65 species of Afrotropical sunbirds provided some general support to Irwin's conclusions (Maina 1999, L.W. Maina and R.A. Cheke, unpubl; Cheke and Mann, 2001). In specific findings, the calls of *Chalcomitra* spp. were generally found to be similar to each other as were most songs of *Cyanomitra* spp. They consisted of trills with complex as well as simpler parts at the start or end and differed from the songs of *Cinnyris* spp. Tongue structure lends further support to the acceptance of the above generic classification (Mann and Cheke, 2008b; Cheke and Mann, 2001).

2.5. REPRODUCTIVE BEHAVIOUR

There have been few reports on the breeding behaviour and general biology of flowerpeckers, for which more extensive investigation is required. There is, however, a reasonable amount of information, summarised by Cheke and Mann (2001) and Mann and Cheke (2008a), on various aspects of the parental care, the positioning and style of nest-building, clutch size and egg colouration, sexual differences in plumage, breeding plumage and presence or absence of pectoral tufts. Although limited to only few of the species, territorial behaviour has also been reported among the Flowerpeckers.

Whereas some species appear to be polygamous and exhibit cooperative parental care, when either sex or neighbours partake in building nests and other breeding activities as in the case of the Plain Flowerpecker *Dicaeum concolor,* species such as the Mistletoebird *D. hirundinaceum* leave the burden of nest-building and incubation to the female with males supporting only with feeding the young (Mann and Cheke, 2008a). For over half (23; 52%) of the species of flowerpeckers, the nests remain undescribed and of the 21 (48%) species whose nests are described, most descriptions are restricted to the structure and positioning of the nest. The nests are predominantly pouched, spherical, oval or pear-shaped, pocket- or purse-shaped and mostly surreptitiously disguised under bushes and trees. The design of the nest incorporates mostly a side entrance as in the case of the Orange-bellied Flowerpecker *D. trigonostigma*. The location of the side entrance can vary and in some species it is located at the top of the nest as, for example, is that of the Red-capped Flowerpecker *D. geelvinkianum*. The construction materials may include assorted matter from vegetation, cobwebs, feathers and caterpillars. In some species, inner decoration and lining of the nest is extensive, as for example in nests of the Pale-billed Flowerpecker *D. erythrorhynchos*, while for others such as the Yellow-vented Flowerpecker *D. chrysorrheum* the external finishing is remarkable (Cheke and Mann, 2001).

The clutch size varies from two to four but two to three is typical of most species. However, for 22 (50%) species the eggs of flowerpeckers are as yet unknown or not described. Those known are usually white, but a few are speckled, blotched or spotted with red, brown, grey and purple colouration.

Contrarily, much more is known of the reproductive attributes of sunbirds. Some species form small social groupings in which males display by exhibiting a form of dance in a male courtship arena usually known as a lek. Examples include the Blue-throated Brown Sunbird *Cyanomitra cyanolaema*. Some species are territorial and defend breeding territories with varying tactics.

Whereas the males of some species lead their territorial campaign with song repertoire skills as in the case of Reichenbach's Sunbird *Anabathmis reichenbachii*, others such as the Orange-breasted Sunbird *Anthobaphes violacea* adopt the more physical and aggressive attacking approach (Mann and Cheke, 2008b). Others such as the Eastern Double-collared Sunbird *Cinnyris mediocris* rather prefer the more gentle approach involving courtship displays with pectoral tufts displayed (Figure 2.8).

Figure 2.8. Male Eastern Double-collared Sunbird *Cinnyris mediocris* displaying pectoral tuft. (Photograph: R.A. Cheke).

Almost all sunbirds exhibit their breeding plumage as an additional mechanism for attracting females during the breeding season, an example being the Superb Sunbird *Cinnyris superbus.* Thirty-three (27.5%) species, such as the Palestine Sunbird *Cinnyris oseus*, moult into a non-breeding plumage shortly after the breeding regime.

Most species are monogamous and may pair for life. Such species' breeding activities are mostly carried out by both males and females, but sometimes adult helpers are involved in co-operative breeding systems. Examples include the Purple-rumped Sunbird *Leptocoma zeylonica* (Ganguly, 1986; Cheke and Mann, 2001). Polygamy has also been reported in some species including amongst the spiderhunters. Nest construction, incubation and parental care are often the sole responsibility of the female. In some species such as the Palestine Sunbird *Cinnyris oseus*, cloaca pecking by males, suggestive of extra-pair copulation behaviour is known.

The construction and structures of nests is diverse and elaborate amongst sunbirds and spiderhunters (Figure 2.9). Shapes and structures of nests include presence or absence of "beards" (trailing sections below the nest), pouch- and pear-shaped nests and, almost invariably, side entrances. Most species tend to hang their nests on trees while others disguise the nest in bushes. Some spiderhunters may construct cup-shaped nests, whereas others construct very long nests consisting of structures stuck under palm fronds (Cheke and Mann, 2001) (Figure 2.9e and h).

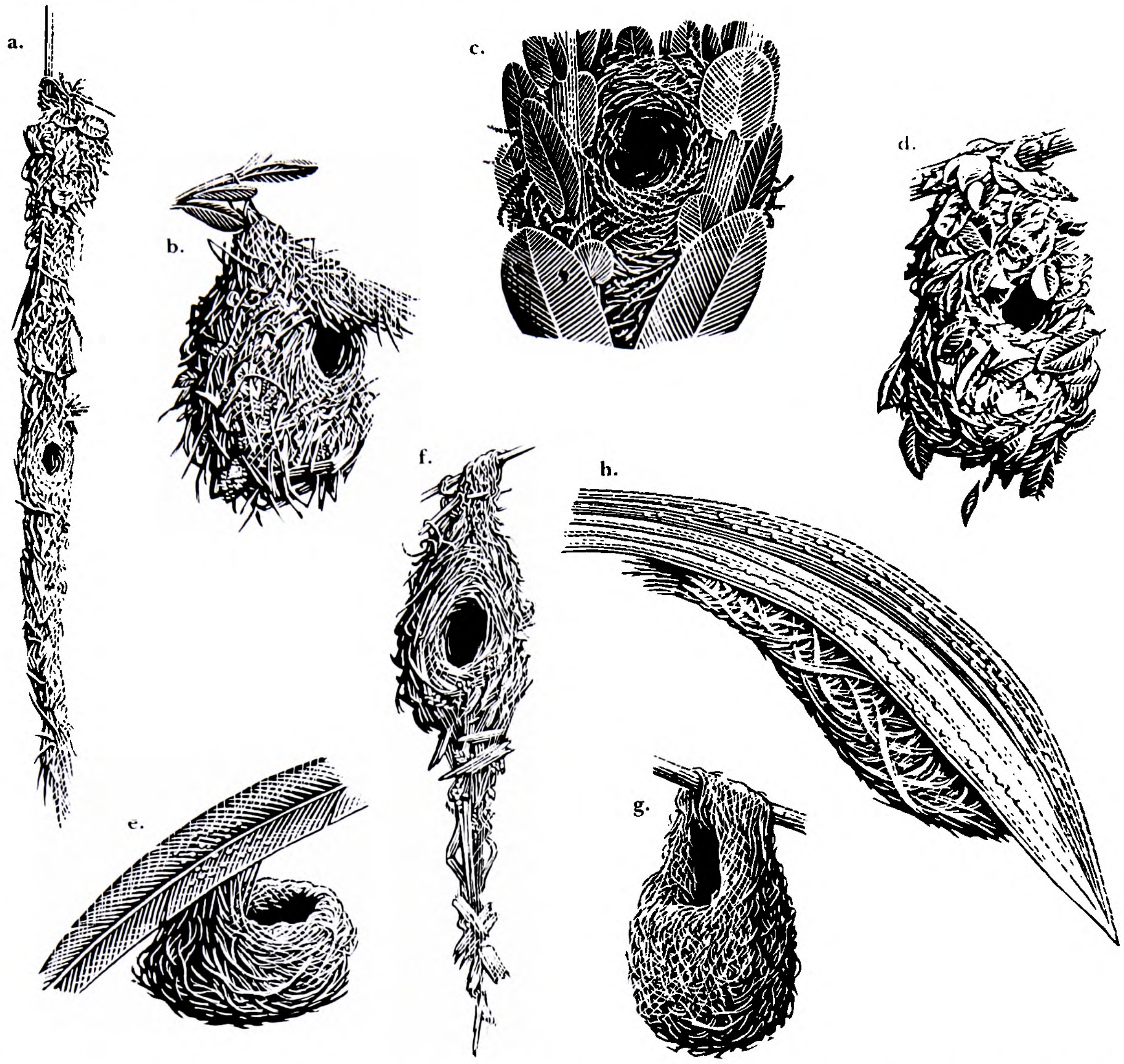


Figure 2.9. Types of nests of the Nectariniidae (from figure 19 in Cheke and Mann, 2001). (a) Blue-throated Brown Sunbird *Cyanomitra cyanolaema*; (b) Collared Sunbird *Anthodiaeta collaris*, showing porch over entrance; (c) Orange-breasted Sunbird *Anthobaphes violacea* not suspended; (d) Western Violet-backed Sunbird *Anthreptes longuemarei*; (e) Streaked Spiderhunter *Arachnothera magna*; (f) Olive-backed sunbird *Cinnyris jugularis*, showing long bear; (g) Midget Flowerpecker *Dicaeum aeneum*; and (h) Yellow-eared Spiderhunter *Arachnothera chrysogenys*.

The clutch size may also vary from one to four, with two eggs being the most common per nest. Some species may have two broods in a season, while others may triple-brood or even have up to five consecutive broods within a year.

The egg colouration of sunbirds and spiderhunters varies considerably among species with about 39.2% of eggs being plain and ranging from pure white to greyish-white whereas 43.3% of others are spotted with markings ranging from greyish-white spots or streaks to pink and olive or dark brown patterns. About 17.5% of species have eggs that are undescribed (Cheke and Mann, 2001).

2.6. VOICE

2.6.1. Flowerpeckers

The one to two syllabled call notes and songs of flowerpeckers are much simpler than the usually elongated complex strings of notes or phrases uttered by the well-known songsters among passerines. The repetitive nature of the identical call notes of most species, for example the repeated call note *'tswik'* of the Yellow-breasted Flowerpecker *P. maculatus* and the '*ship-ship-ship*' notes of the Yellow-rumped Flowerpecker *P. xanthopygius* assist in field identifications (Cheke and Mann, 2001).

However, there are a few species that are capable of varying the syllables of their call notes, with some species constructing up to three different call notes as in the case of the White-throated Flowerpecker *D. vincens* with its '*twee-see-see, tzee tzee tzee'* call notes. There are also some species whose songs may appear complex and comprise a combination of a string of notes and phrases with either a distinct click or a rattle at the beginning or end of the song. Examples include the most well known mimicry by a Flowerpecker, that of the Mistletoebird *D. hirundinaceum* with its staccato notes and phrases *'wit-wissweet' 'wit-wissweet'* '*witsoo witsoo witsoo'* (Cheke and Mann, 2001; Mann and Cheke, 2008a). On the whole, analysis of the vocalisations of the flowerpeckers places them in the basic category of song types consisting mainly of trills and whistles with some species exhibiting some interludes of complex notes or phrases in their vocalisations.

2.6.2. Sunbirds and spiderhunters

The sunbird vocalisations are varied and comprise trills, whistles and some very complex songs. There is a wide range of call notes and phrases, with considerable intraspecific variation. Some species repeat fairly simple notes, usually high and metallic ones, while others utter a complex mixture of notes and phrases and are occasionally very melodious (Rasmussen and Anderton, 2005). The call notes and songs of some species are predictable and highly recognisable, as for example the high pitched chirps '*seep*' of the Plain Sunbird *Anthreptes simplex* and *cheewit-cheewit-cheewit* of the Long-billed Sunbird *Cinnyris lotenius*. Those with varied syllables are more difficult to recognise, including species with loud and high pitched chattering warbles, rasping, sharp, harsh, buzzing notes interspersed with whistles and wheezes. Examples include the Purple-rumped Sunbird *Leptocoma zeylonica*, which utters a mix of metallic upstroke chirp notes *Sit-sit/tseet-tseet-tseet/tsut sweety-swee, sweety swee.*

The species with more complex patterns of syllables and large repertoires appear to have very complex songs (Cheke and Mann, 2001; Rasmussen and Anderton, 2005). Examples include Anchieta's Sunbird *Anthreptes anchietae*, whose usual call is *tseu-werr, tsoo-wit, tser-wit-tsui-tsi, chip-choo-chip, witchoowitchoo, chip chip, chipyoo* and the Mariqua Sunbird *Cinnyris mariquensis* also utters very complex songs intermingled with trills, whistles and melodic warbles, *chur-chur, tser-tser, chip-chip-chip, tsi-tsi, b-r-r-r-zi.* Some species have different dialects e.g. the Splendid Sunbird *Cinnyris coccinigaster* (Grimes 1974, 2007; Payne, 1978) and others are known to mimic the songs of other birds e.g. the White-breasted Sunbird *Cinnyris talatala* (Cheke and Mann, 2001).

Although voice descriptions of most members of *Arachnothera* consist mostly of calls with little information on song vocals of most species, the vocalisations of these spiderhunters are equally as varied as those of sunbirds. Their vocalisations range from simple repetitive call notes as in the case of the Little Spiderhunter *Arachnothera longirostra* with its *chee chee chee* call notes and Yellow-eared Spiderhunter *Arachnothera chrysogenys* with its *twit-twit-twee* notes. However, descriptive songs of some members of the group indicate a mix of simple and complex utterances and examples include the Long-billed Spiderhunter *Arachnothera robusta* with its *choi choi choi* song notes and the *chee-wee-dee-weet* complex song pattern of the Streaky-breasted Spiderhunter *Arachnothera affinis*.

2.7. HABITAT

Flowerpeckers are adapted to a wide range of habitats from forests, woodlands, scrub, forest edges and clearings, at sea level and up mountains and plantations and gardens within human settlements. Forests appear to be their stronghold with close to 70% dependent on closed habitats and they mostly live within the canopy level of trees. Examples of forest-restricted species include The White-throated Flowerpecker *D. vincens*. Others such as the Scarlet-backed Flowerpecker *D. cruentatum* are well adapted to open habitats ranging from sea level to the tops of mountains and within human cultivations. About 25% of flowerpecker species are found in closed and open habitat types ranging from forests to arid areas. A typical example of this group of flowerpeckers is the only Australian member of the group, the Mistletoebird *D. hirundinaceum* (Cheke and Mann, 2001).

Whereas Spiderhunters are exclusively forest birds and can occasionally be associated with plantations, sunbirds occupy a variety of habitats. A wide range of species (51; 43%) inhabits a number of differing habitat types including forests, forests edges, woodlands, savannas, semi-arid areas and from sea level to higher altitudes of the Afro-alpine moorlands. Examples include the Plain-throated Sunbird *Anthreptes malacensis*, a species from Asia with 17 subspecies occupying various types of forests, woodland, scrub, swamps and modified habitats such as plantations and gardens.

Hunter's Sunbird *Chalcomitra hunteri*, for instance, is among 35 species (29%) that occur in open habitats, with some species extending their habitat range to include semi-arid areas, e.g. the Nile Valley Sunbird *Anthodiaeta metallica*. Some species (34; 28%) are restricted to closed habitats and are therefore exclusively forest dwellers; the Crimson-backed Sunbird *Leptocoma minima* occurs in all types of forest, including plantations (Cheke and Mann, 2001).

2.8. STATUS AND CONSERVATION

The major threat to flowerpeckers is habitat loss and since few species occur in very restricted ranges, very few flowerpeckers (18.2% of species) are considered either critically endangered, vulnerable or near threatened. Therefore, species with varied habitat types or of wider geographical distribution such as the Mistletoebird are capable of withstanding man's perturbation of their habitats to a reasonable extent. Others such as the Orange-bellied Flowerpecker *D. trigonostigma* appear to be common in some parts of their distribution and uncommon in the more sensitive habitats.

The species considered critically endangered or close to extinction are those with very restricted ranges or those which are incapable of adapting to different types of habitats. Examples of this category of species include the Cebu Flowerpecker *D. quadricolor*, The Black-belted Flowerpecker *D. haematostictum* and the Scarlet-collared Flowerpecker *D. retrocinctum* (Mann and Cheke, 2008a).

Two species of sunbirds have been designated as endangered, five as vulnerable and nine as near threatened (including one spiderhunter). The endangered species include the Amani Sunbird *Anthodiaeta pallidigaster* and the Elegant Sunbird *Aethopyga duyvenbodei*. The vulnerable species are: Banded Sunbird *Anthreptes rubritorques*, São Tomé Sunbird *Dreptes thomensis,* Rockefeller's Sunbird *Cinnyris rockefelleri* and Rufous-winged Sunbird *Cinnyris rufipennis*. The species under the near threatened category include Plain-backed Sunbird *Anthreptes reichenowi*, the Red-throated Sunbird *Anthreptes rhodolaema*, Ursula's Sunbird *Cinnyris ursulae*, Neergaard's Sunbird *Cinnyris neergaardi*, Moreau's Sunbird *Cinnyris moreaui,* the Grey-hooded Sunbird *Aethopyga primigenius*, the Apo Sunbird *Aethopyga boltoni*, Lina's Sunbird *Aethopyga linaraborae* and Whitehead's Spiderhunter *Arachnothera juliae* (Cheke and Mann, 2001).

The threat posed to these species can primarily be attributed to habitat loss. Many countries in the tropics have undergone extensive deforestation and in some areas it is so severe that many wildlife species, including some sunbirds, are either displaced or restricted to remnants of their habitats. Most of these species are predominantly forest dependent species that have been relegated to fragmented patches of their forest habitats owing to human developmental activities and, in particular, tree felling.

2.9. RELATIONSHIP WITH MAN

The association between man and flowerpeckers is weak and there is very little information available on this small-bodied and uninspiring group of passerines. They appear worthless in terms of what they can provide man in terms of food, aviculture or recreation. They are not known to be major pests and do not pose any serious threat to man in the area of agriculture, although the Scarlet-backed Flowerpecker *D. cruentatum* and the Yellow-vented Flowerpecker *D. chrysorrheum* have been implicated in the spread of economically important mistletoes. The only harmonious relationship is the significant role Flowerpeckers play as pollinators or dispersers of plant seeds useful to man.

On the other hand, the relationship between sunbirds and humans could be described as quite harmonious. Sunbirds, perhaps, are too tiny to be of any use to man in terms of meat or for products such as feathers for magico-religious purposes. However, sunbirds still play a role in making human existence more valuable. Perhaps their greatest significance lies in their role as pollinators of many flowering plants, including those of economic value. Another is the inviting aesthetic value of sunbirds, which raises the spirit, and pleasures of many in the wilderness areas for recreation and tourism. One most often unnoticed usefulness of sunbirds to humans is that they are predators of some nuisance insects. However, some species have been categorised as pest birds and often implicated in attacks on some fruiting and flowering plants. Examples include the Scarlet-chested Sunbird *Chalcomitra senegalensis* and Purple Sunbird *Cinnyris asiaticus* (Fry *et al.*, 2000; Irwin, 1999; Cheke and Mann, 2001).

CHAPTER 3

MATERIALS AND GENERAL METHODS

This chapter provides an overview of the research design. The chapter is divided into two sections. The first section introduces how and where the recordings were gathered and used in the analyses, the number of elements measured and the resulting differing features used to derive the quantitative measures of variation in vocalisations amongst the Nectariniidae that were used in the subsequent phylogenetic analyses. In this section there is also a series of descriptions of techniques and definitions of parameters adopted for the analysis and issues relating to their particular applications. The second section provides a review from secondary sources of some morphotaxonomic features of the Nectariniidae, summarizing key similarities and differences, and explaining the origins of those used in attempts to derive correlations with the vocal phylogenies.

The study applied a mixed methods approach in measuring the acoustic characters of bird songs. The mixed method approach refers to a combination of (1) the visual inspection and scoring of avian vocalisations from sonographic printouts (Thorpe 1954) and (2) the automated derivation of quantitative values from spectrographs (Clark *et al.* 1987; Tchernichovski *et al.* 2000). Both of these approaches have become the focus of emerging signal science research and combining them capitalises on each of their strengths, compensates for their respective weaknesses and facilitates a comparison between similarity and variability scores obtained from each (Kroodsma, 1982; Catchpole and Slater, 1995; Nelson *et al.*, 1995; Tchernichovski *et al.,* 2000).

Although the visual scoring approach has been the most widely used method for vocal characterisation for decades, its subjectivity and arbitrariness limits its applicability (Zann, 1996; Tchernichovski *et al.,* 2000). The automated approached, however, is a recent phenomenon, generally perceived as a robust method capable of objective characterisation of vocal structures.

Invariably, the approach also suffers from problems such as high dimensionality, and is best suited for species such as the Zebra finch *Taeniopygia guttata* with songs lacking silent intervals (Tchernichovski *et al.,* 2000).

The study also adopted the note frequency and rhythmic song structure approach to separate the different recordings of species vocalisations into trills, whistles and complex songs (Myron *et al.*, 2003).

This research followed the genus, species and subspecies nomenclature of Cheke and Mann (2001) to categorise the vocalisations taxonomically because it provides the most comprehensive recent checklist of the Nectariniidae.

The songs of different taxa of sunbirds, spiderhunters and flowerpeckers were mostly obtained from the Library of Wildlife Sounds of the National Sound Archive at the British Library, Euston, London. The recordings were classified according to taxon, place, date of recording and recordist. Where possible, the recordings were further separated as far as possible on the basis of information provided by the recordists on the British Library Sound Archive Catalogue into functional and behavioural context as alarm calls, begging calls, mating calls or territorial songs. Full details are given in Appendix 1. On a coarser scale for use in evolutionary interpretations, they were also grouped into whether they originated from Africa, Asia or Atlantic or Indian oceanic islands). Appendix 1 lists them separately according to their origins.

All the species' recordings including the number of vocal measurements (notes / elements per song type), mean and variability at generic level are summarised in Table 3.1.

Table 3.1. Numbers of recordings and measurements from different genera of Nectariniidae analysed and details of variability in numbers of elements per recording.

Genus	**No. of species in genus**	**No. of recordings including from different subspps.**	**Total no. of measured elements**	**Range (min-max) of element per recording**	**Mean no. of elements per recording**	**St.Dev**
Prionochilus	6	6	207	13-72	34.5	20.97
Dicaeum	38	36	1,606	21-80	42.3	14.32
Chalcoparia	1	2	80	25-55	40.0	21.21
Deleornis	2	2	123	60-63	61.5	2.12
Anthreptes	13	15	740	28-97	52.8	20.60
Anthodiaeta	4	9	424	45-95	70.6	18.05
Hypogramma	1	1	40	-	40.0	-
Anabathmis	3	3	150	35-60	50.0	13.22
Dreptes	1	1	50	-	50	-
Anthobaphes	1	1	40	-	40	-
Cyanomitra	8	26	1,331	35-99	55.5	18.29
Chalcomitra	7	17	877	35-90	58.5	17.59
Leptocoma	5	15	530	34-99	53.0	19.14
Nectarinia	6	14	644	34-80	53.7	16.71
Drepanorhynchus	1	2	85	40-45	42.5	3.53
Cinnyris	50	98	7,962	50-125	87.5	20.13
Aethopyga	17	28	1,697	40-90	65.3	16.23
Arachnothera	10	18	1,268	40--110	70	23.16
Total	**174**	**294**	**17,854**	**13-125**		

The primary goal of this study was to analyse the variations that exist within the song characters of the available recordings of the Nectariniidae and to use the scores of the discrete character states to construct a vocal phylogeny of the family. The song types were classified broadly into calls, simple songs and complex songs based on visual inspection of sonograms. From each category, scores were obtained from 20 character states some of which were derived from automated analyses (see list on page 48). The results from these measurements were used as the raw data in the phylogenetic analyses. Examples of such measured vocalisations of three species' calls, three species' simple songs and three species' complex songs are given in table 3.2. The examples are provided in each category for one flowerpecker species, one spiderhunter species and one sunbird species. Calls were taken from Yellow-rumped Flowerpecker *Prionochilus xanthopygius* (Appendix **2.6**), Thick-billed Spiderhunter *Arachnothera crassirostris* (Appendix **3.140**) and Flaming Sunbird *Aethopyga flagrans guimarasensis* (Appendix **3.72**). Examples of simple songs are provided for Blood-breasted Flowerpecker *Sanguinoletum wilhelminae* (Appendix **2.57**), Little Spiderhunter *Arachnothera longirostra longirostra* (Appendix **3.117**), Scarlet-tufted Sunbird *Deleornis fraseri* (Appendix **4. 191**) and for complex songs for Mistletoebird *Dicaeum hirundinaceum hirundinaceum* (Appendix **2.67**), Little Spiderhunter *Arachnothera longirostra prillwitzi* (Appendix **3.118**) and Johanna's Sunbird *Cinnyris johannae johannae* (Appendix **4.127**).

The scores of the song characters varied across the taxa, but as shown in the table, only the Johanna's Sunbird *Cinnyris johannae johannae* scored positively on all characters (compare its data with those of the Yellow-rumped Flowerpecker *Prionochilus xanthopygius*) depicting the level of variability among the complex vocalisations.

Typically, the frequency shift from 8.4 kHz of the call notes of the Yellow-rumped Flowerpecker *Prionochilus xanthopygius* to 6.8 kHz of the simple song notes of the Little Spiderhunter *Arachnothera longirostra longirostra* and to the 6.0 kHz of the complex song notes of the Johanna's Sunbird *Cinnyris johannae johannae* and the rhythm of frequency fluctuation from 1 kHz, 3 kHz and 5 kHz, respectively (see table 3.2), indicate a big frequency slope and fluctuation as the vocalisations shift from calls to simple songs and to complex songs.

	Characters															
Types of vocalisations	Freq. kHz (a.d.)	Note duration (a.d.)	Note interval (a.d.)	Peak ampl. (a.d.)	Bandw (a.d.)	Entropy (a.d.)	Phrase duration (v.i.)	No of notes in a phrase	Size of repertoire (v.i.)	Intro. rattle (v.i.)	Click (v.i.)	Squawk (v.i.)	Note % (v.i.)	Pause rate (v.i.)	Song duration (v.i.)	Rhythm of freq. (v.i.)
Calls																
Yellow-rumped Flowerpecker	8.4	0.02	0.91	22.0	8.2	0.78	2	0	1	0	0	0	0.8	3	2	1
Thick-billed Spiderhunter	8.2	0.03	0.62	24.0	8.6	0.66	3	5	1	0	0	0	0.8	5	2	2
Flaming Sunbird	6.3	0.04	0.25	26.0	8.5	0.65	3	0	1	0	1	0	0.7	4	3	2
Simple song																
Blood-breasted Flowerpecker	7.2	0.06	0.31	27.0	7.0	0.33	3	0	2	0	1	0	0.8	4	2	3
Little Spiderhunter	6.8	0.06	0.24	28.0	6.8	0.32	3	0	1	0	0	0	0.7	5	3	3
Scarlet-tufted Sunbird	6.6	0.07	0.23	29.0	6.0	0.31	4	0	1	1	0	0	0.6	5	2	3
Complex song																
Mistletoebird (Flowerpecker)	7.0	0.02	0.25	25.0	6.8	0.30	4	5	3	1	0	0	0.5	5	2	3
Little Spiderhunter	6.2	0.05	0.24	28.0	6.2	0.22	0	0	3	0	0	0	0.5	5	3	4
Johanna's Sunbird	6.0	0.06	0.20	30.0	6.0	0.15	6	7	7	1	1	1	0.6	6	3	5

Table 3.2 Examples of the vocal measurements of three species taken from each the three vocalisation types; calls, Simple songs and complex songs, a.d. = data on character states derived from the automated analyses and v.i. = visual inspections of sonograms.

The range of mean entropy values for calls (0.78, 0.66, 0.65), simple songs (0.33, 0.32, 0.31) and complex songs (0.3, 0.22, 0.15) decrease between categories revealing increasing complexity in the evolution from simple calls to complex songs.

The two main Fourier techniques used in the characterisation of sound are the time domain (measure of period) and the frequency domain (measure of frequency). The measurement of either time or frequency is common in published studies but a combination of the two is a normal requirement in any sound analysis in order to attain a better understanding of the sound structure (Bradbury and Vehrencamp, 1998; Tchernichovski *et al.*, 2001). Since the bulk of the recordings obtained for this study were directly from the field and mostly dominated by environmental masking noises, this study adopted the settings in the software used (Avisoft) that relate more to the frequency based Fourier measurement because it is more capable of handling low quality (noise masked) recordings or harmonic interferences than the time domain measurement (Kroodsma, 1982; Catchpole and Slater, 1995). However, the frequency domain technique is often susceptible to the phenomenon of 'period doubling' (a situation where a harmonic stack increases its periodicity twice that of the original stack, filling intervening frequencies) (Tchernichovsky *et al.*, 2001).

There are several different sound analysis software packages available such as Canary, Wild Spectra, Sigview and Micro LAB. The Avisoft SASlab is one of the most widely used packages (De Kort and ten Cate, 2003; Spencer *et al.*, 2003; Brumm and Slater, 2006) and was used for the vocal analysis in this study. The Hamming window and other parameters (see table 3. 2) were selected for the generation of sonograms.

Table 3.3. Spectrogram settings used for analyses in Avisoft.

Frequency resolution:	**Parameter**
Bandwidth	323 Hz
FFT-Length	256
Frame [%]	100
Window	Hamming
Overlap [%]	50
Time Resolution	5.80 ms
Floating point arithmetic	Checked

The Hamming window in Avisoft has a smoothing function that enhances sonogram quality, remedies spectrum distortion and delivers the best results in most cases.

Sonograms of all the available recordings of each taxon were created (see examples in Appendices 2, 3, 4 and 5). Sonograms are simple graphs of vocalisations that show time in seconds(s) on the x-axis and frequency or pitch in kilohertz (kHz) on the y-axis and therefore display distinctive sound renditions of all the features of vocalisations and present the simplest spectra for the interpretation of songs.

The song types were also further categorised into calls, simple songs and complex songs to reduce biases. For instance, recordings from some species whose recordings appear simple, but are capable of uttering complex songs were made when they were performing simple acts. As reported by the recordists, these included birds in flight, perched, feeding or making alarm calls. Complex songs were recorded when the birds were in excited states e.g. during territorial displays.

Whenever the recordist's commentary confirmed two or more recordings at the same location and on the same date, the best recording was chosen for analysis. An attempt was also made to use one representative of the song and or call of each individual species and of the clearest recording for analysis. When more than one bird was recorded on a single track, one song or call was selected for each individual. When necessary all recordings were converted from cda (compact disk-digital audio) to ".wav" files by means of the "Roxio-SoundStream" utility conversion software (www.roxio.com), for subsequent analysis using Avisoft, SASlab (www.avisoft-saslab.com).

Measurements of acoustic features within songs and calls were performed by first generating spectrograms and visually scoring variability among song notes and measured values derived directly from Avisoft, SASlab. The real time spectrograph facility of Avisoft allows spectrogram display of recorded signals that can be visualized on the spectral window.

The spectrogram window menu allows for the variation of parameter options for the generation of sonograms of each available vocalization and the analysis of the sound spectra. The spectrogram parameters include Frequency resolution which corresponds to the filter bandwidth, the Fast Fourier Transform (FFT)-Length, Frame size, Evaluating window, Overlap and Floating point arithmetic.

After loading in Avisoft, all sound tracks were first filtered using the Finite Impulse Response (FIR) filter to remove any sounds with frequencies that fell below 1.0 kHz. The menu 'edit' provides different functions (cut, trim, delete, filter, etc.) for the removal of such undesired signals or noise. The Hamming window option was selected and used when generating sonograms of each available vocalization and to analyse the sound spectra. Parameters derived from the sonographic analyses such as maximum frequencies, rhythm of frequency, note interval, note duration, amplitude, bandwidth, duration of phrase, number of notes in a phrase, size of repertoire, introductory rattle, click, squawk, song duration note percentage, pause rate and entropy were chosen to form a classification system. Measurements of acoustic features within songs and calls were performed by (1) generating the spectrograms of each track of a taxon and (2) deriving values of each note / element of the various parameters measured directly on the spectrogram.

Many authors have adopted visual inspection to discriminate between discrete calls and songs but this study has, in addition, used values derived directly from the entropy parameter of the spectrograms to distinguish between calls and songs and between simple and complex songs.

Measurements of parameters derived from the sonographic analyses such as maximum frequencies, rhythm of frequency, note interval, note duration, amplitude, bandwidth and entropy are automatically detected in Avisoft. In addition, their numeric values were automatically computed for each element from start to finish in the automatic parameter measurement windows of the spectrogram for export to Microsoft EXCEL for further computations. The first line of separation of recordings was according to the thresholds of entropy values derived from sonograms. If entropy was > 0.34, vocalisations were classed as calls, if > 0.3 but < 0.34 as simple songs and if < 0.3 as complex songs. For data justifying these thresholds and for further details see the detail methods section in chapter 4.

Values of the parameters that could not be generated directly from Avisoft were determined by visual inspection of sonograms. A particular element was scored as present or absent in the song / call of each taxon. Also, the relative positions of some elements, possible similarities and differences between the structures of syllables, the nature of the start and end of a song or phrase, the size of the repertoire and the overall pattern of sonograms of individual taxa were also scored. The present attribute state was represented by one and the absent as zero and further coded in a character matrix as 1, for duration of phrase; 2, number of notes in a phrase; 3, size of repertoire; 4, introductory rattle; 5, click; 6, squawk; 7, song duration; 8, note percentage; 9, pause rate and 10, rhythm of frequency (Table 4.1 of chapter 4).

3.1. DESCRIPTION OF ACOUSTIC PARAMETERS

3.1.1. Frequency:

In sonographic analyses, the frequency is the number of oscillations per second measured in Hertz (Hz). Frequency has, however, been defined using a variety of forms of words related to pitch (Sondhi, 1968). Whereas Bradbury and Vehrencamp (1998) defined frequency as the number of cycles per unit time (cycles per second), Cramp *et al.* (1977) defined frequency as the speed of oscillation (cycles) or vibration per unit of time. Although the two definitions use different terminology they do not differ in meaning. However, the examples used to explain frequency by these authors differed. Bradbury and Vehrencamp (1998) explained frequency in line with the pressure medium and view frequency and wavelength as inversely related for any given medium and therefore are of the opinion that higher frequencies have short wavelengths, while lower frequencies have long wavelengths. Cramp *et al.* (1977) on the other hand, explained frequency by a physical example and stated for instance, that when a hollow tube is hit, a fairly constant sound is heard because hitting the tube produces a shock-wave which oscillates (travels up and down within the tube) and moves at a constant speed in the tube. This oscillation or vibration is what we hear as pitch. The length of the hollow tube determines the frequency: the longer the tube, the further the shock wave has to travel, and hence the lower the frequency.

The acoustic application of the above explanations to bird song analysis is that sound attenuates and degrades as it penetrates the physical environment (Linskens *et al.*, 1976; Marten and Marler, 1977; Marten *et al.*, 1977; Martens, 1980; Endler, 1992; Forrest, 1994; Brown and Handford, 1996, 2000). This ‘degradation effect’ explains why lower frequencies transmit better in dense vegetation, which is associated with the lower average frequencies used by forest species in comparison with species found in open habitats (Chappuis, 1971; Morton, 1975; Ryan and Brenowitz, 1985). Differences in frequency changes can be an important parameter in determining variability among taxa (Catchpole and Slater, 1995).

3.1.2. Note interval and note duration

A single tone of a definite pitch, which describes a musical frequency, is referred to as a Note. Notes are usually classified as “#” sharp or “b” flat (Cramp *et al.*, 1977). In songs of most species, the interval between notes is important. In the Nightjar *Caprimulgus europaeus* and Field Sparrow *Spizella* *pusilla,* there are reports of reduced male reaction to songs with irregular pauses, while the Swamp Sparrow *Melospiza georgiana* and the Robin *Erithacus rubecula* show no change of reaction when the song's note interval is modified (Payne, 1986). Also, in the Goldcrest *Regulus regulus* the rhythm or the alternation between long and short elements is species specific and is an important characteristic.

Note duration of most species is relatively constant but can change under excitement or stress. Note duration is an important species specific parameter when assessed in combination with other characteristics such as syntax and the structure of the note (Catchpole and Slater, 1995).

3.1.3. Note percentage

Note percentage refers to the overall duration of all notes in a song divided by the song duration.

3.1.4. Rhythm

The rhythm is an "envelope of intensity" and pattern of note frequency over time.

3.1.5. Song duration

Song duration is the time from the beginning to the end of a song or call.

3.1.6. Repertoire

The term repertoire has been used in the literature as the entire range and distinct functions of vocal classes that an individual of a species uses (Bradbury and Vehrencamp, 1998). Repertoire here is used as the estimated number of unique song units each bird can sing (Irwin, 2000).

Sonograms were examined for each species and distinct types of song elements classified on the basis of unique syllable composition and arrangement to determine individual repertoire size. Scored as 1 for single repertoire, 2, 3, 4 etc, according to the different sizes of the repertoire of individual species.

3.1.7. Entropy

Entropy is a measure of randomness, which can be represented by the ratio of the geometric mean to the arithmetic mean of a spectrum (Ho *et al.*, 1998; Tchernichovski *et al.*, 2000). This measure is known as Wiener entropy and is defined by the formula:

$$W = \log \left[\frac{(\ \exp[\int df Log(S(f))]}{\int df S(f))} \right]$$

Where *f* denotes a probability density function. Entropy is thus measured on a logarithmic scale from 0 to minus infinity which represents 'white noise' or equivalent to log (1) = 0 and the complete ordered form of log (0) = minus infinity. This means that entropy from the pure tone end of a sound scale approaches minus infinity, but at the other end of the scale approaches 1 if characterised by white noise (Tchernichovski *et al.*, 2000). The above formula expresses a model based on continuous or differential entropy. However, Shannon (1948) was of the view that differential entropy is not in general a good measure of uncertainty or information based on the fact that differential entropy can be negative and also not invariant under continuous co-ordinate transformations. Shannon (1948) further suggested that it could be more useful in a continuous case to use the relative entropy of a distribution, defined as the Kullback-Leibler divergence from the distribution to a reference measure *m*(*x*),

$$D_{KL}(f(x)\,||m(x)) = \int f(x) \log \frac{f(x)}{m(x)}\, dx$$

Which expresses relative entropy as it carries from discrete to continuous distributions and is invariant under co-ordinate representations.

The application of Wiener entropy in birdsong analysis is still in its infancy and only a few authors (Ho *et al.*, 1998; Tchernichovski *et al.*, 2000; Lombardino and Nottebohm, 2000; Gabriel *et al.*, 2003) have so far used Wiener entropy as a characterisation criterion for the vocalisation of the Zebra finch *Taeniopygia guttata*. The above authors derived their entropy values from the time domain setting and performed their characterisations using the continuous wave approach and by omitting silent intervals, but in this study entropy values were derived from the frequency domain setting and measured single wave forms by capitalising on the silent intervals as a natural partitioning criterion for categorising the birdsongs into component notes/ syllables. The technique adopted here stems from the fact that vocalisations of the Nectariniidae are of well defined syllables with distinct silent intervals between notes and phrases. The values derived from this approach indicated less disorder for the simpler songs and therefore generated higher entropy values than the pieces of notes measured in larger blocks as in the case of the complicated vocalisations.

The technique used in this study involved using an activated cursor for sequencing individual notes and phrases of the vocalisations (calls, simple songs and complex songs) as they appeared on the spectrogram window to clearly measure and derive the entropy values (see figure 3.1) for the three song categories.

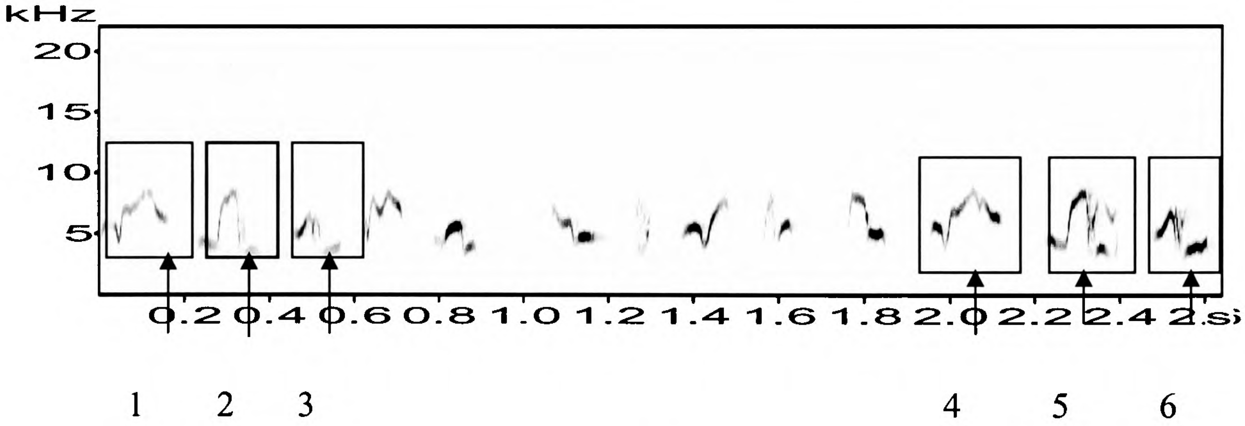


Figure 3.1. Depiction of measurements of 6 notes as examples from the note by note derivation of entropy values from the frequency domain setting used in this study.

The above method, as used in this study differs from that of Tchernichovski *et al.* (2000). They omitted the silent intervals between the notes of a vocalisation, and thus analysed continuous waves (see figure 3.2). The wave appearing on the spectrogram in fig. 3.2 conforms to the technique adopted by Tchernichovski *et al.* (2000). The entropy characterisation estimated by this technique records higher entropy values for the more wavy portions (1 and 2) as indicated by the arrows on the spectrogram.

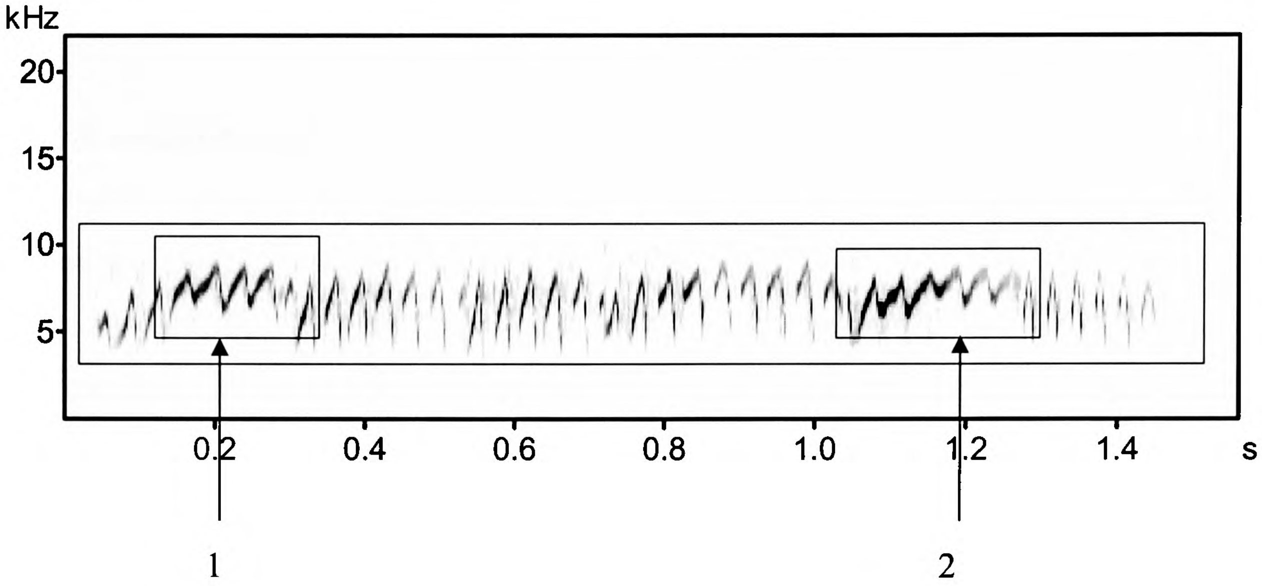


Figure 3.2. Spectrogram showing wave forms similar to the type suited for the measurement of entropy using Tchernichovski *et al.*'s (2000) approach.

It is clear from the above that the technique adopted in this study is quite different from wave measurement technique used by Tchernichovski *et al.* (2000) to derive the entropy values.

The entropy concept draws its foundation from Boltzmann's view of the second law of thermodynamics as the law of disorder. Entropy (the subject of the second law) and energy (the subject of the first law) and their relationship are fundamental to the understanding not just of physics, but life in terms of biology, evolutionary theory, ecology and psychology (Swenson 1990). Boltzmann's (1974, first published 1886) conclusion that 'a system will almost always be found either in a state of maximum disorder or moving towards it' provides the basis for the entropy values generated from calls (high entropy values) and songs (low entropy values) in the AVISOFT software. The entropy parameter (Wiener entropy) is computed as follows: as already mentioned, Wiener entropy is defined as the ratio of the geometric mean to the arithmetic mean of the spectrum W = {exp[SS df Log(S(f))]}/[SS df S(f)] (SS is the integration operator) or in the discrete domain (in the SASLab Pro implementation): W = sqrt(sum(sqr(m(f)))/n) / (sum(m(f))/n) where m(f) is the magnitude of the spectrum and n is the number of spectral lines that have been summed. It does not have units. White noise has a value of 1, a pure tone a value of 0. Amplitude does not affect the value.

3.1.8 Negentropy

Negative entropy (Negentropy) is a concept first introduced by the Nobel laureate physicist Schrödinger (1944) when explaining that a living system exports entropy in order to maintain its own entropy at a low level. Negentropy in information theory has been adapted as a measure of distance to normality. Negentropy is therefore always positive and invariant by a linear invertible change of coordinates and vanishes if the signal is Gaussian.

Negentropy is therefore defined as $J(p_x) = S(\Phi_x) - S(p_x)$, where $S(\Phi_x)$ stands for the Gaussian density with the same mean and variance as p_x and $S(p_x)$ is the deferential entropy: $S(p_x) = -\int p_x(u) \log p_x(u)du$. Negentropy is used in statistics and signal processing (Comon, 1994) and this study has drawn from this concept of converting the entropy values (measures of degree of disorder) derived from the sonograms to negentropy values (measures of degree of order, equivalent to 1 - mean entropy) for the analysis of the relationships between song complexity and vocalisation frequency, bill length and body sizes of the Nectariniidae. While entropy is a measure of disorder, negentropy is a measure of order, thus the latter can also be used in phylogenetic studies on the expectation that negentropy (order) will tend to increase with increasing evolutionary development.

3.1.9 Amplitude

The amplitude of a sound or vocalisation defines its loudness. Amplitude is normally expressed in decibel levels or dB. The significance of amplitude in vocal analysis is based on the fact that as a sound wave travels from one point to another, it will, on its way, dissipate due to attenuation (lessening of the amplitude of the signal over distance / time). Amplitude values reflect the overall loudness pattern of a song based on the temporal positions of the instantaneous peak amplitudes along the entire spectrum of a song.

3.1.10. Bandwidth

There is no single universal precise definition of bandwidth. Whereas it is often applied to mean the measure of the capacity of a communication signal or the difference between the highest and lowest frequency components of a signal measured in Hertz (cycles per second), it is also understood to mean the measure in Hertz of a frequency range in which the signal's Fourier transform is nonzero or the measure of how rapidly a signal fluctuates with respect to time. Hence the greater the bandwidth, the faster the variation in the signal may be.

3.1.11. Pause rate

The pause rate is the number of pauses in a song divided by the song duration.

3.1.12. Squawk

A squawk is a rapidly modulated tone more than 15msec long, scored as 0: absent; 1 Present.

3.1.13 Click

Clicks are short pulses of broadband sound (less than 15msec long) with peak energy above 1 kHz. They are produced individually but not as part of a trill. Scored as 0 absent; 1 present.

3.1.14 Rattle

A rattle was recorded whenever a rattle of any type in a call or song was present. A rattle is defined as a series of short (less than 15msec long), repeated pulses of sound with most or all energy below 1 kHz. and scored as 0 absent; and 1 present.

3. 2. DESCRIPTION OF MORPHOTAXONOMIC MEASUREMENTS

The morphotaxonomic information was taken from Cheke and Mann (2001), who collected and collated their data from unpublished field notes, published literature and measurements of museum specimens. Cheke and Mann's classification of the Nectariniidae used in this thesis was based primarily on morphological data and plumage characteristics. The systematics of the Nectariniidae based on the above data, has greatly assisted in providing an insight into the phylogenetic patterns and the evolutionary history of the morphological and behavioural traits within the lineage.

The data used for the analyses of the morphotaxonomic features were therefore derived from secondary material. Thus published data were used when seeking correlations between the vocal culture of the Nectariniidae and the sexually related morphological ornaments such as non-breeding plumage, plumage brightness and drabness, pectoral tufts and behavioural attributes such as habitat choice and 'nest architecture'. A further analysis was done to seek the linkages between vocalisation and beak morphology and whether or not habitats have any influence on the song type of species of the Nectariniidae.

3.2.1. Plumage

Plumage variation analyses focus on specific colouration at certain plumage regions among species. Each plumage character was scored for similarity and differences or the presences and absences of a character state of the species.

3.2.2. Non-breeding plumage

The non-breeding plumages were scored as 0 for absent and 1 for present.

3.2.3. Pectoral tuft

The pectoral tuft is a sexual plumage characteristic that is erected during mating displays. Some species lack it altogether and in those species with a pectoral tuft it usually occurs only in males, but in some species it is present in both sexes. Scored as 0; absent, 1; present in male only 2; present in both sexes. In no case were pectoral tufts present in females only.

3.2.4. Bill and body size

The data on measurements of the bill length and wing length of the entire family were compiled from Cheke and Mann (2001). Wing length was used as a measure of body size and to standardise other measurements e.g. by dividing the bill length by the wing length.

3.2.5. Nest structure and placement

The different nest shapes (pear- or pocket-shaped) and the presences and absences on the nests of a porch or a beard were scored as 0, absent, 1, present, and 2 for the presence of any two.

3.2.6. Habitat

The habitat analysis was preceded by the classification of the vegetation types in which a particular species may occur and using categories such as primary forests, deciduous or secondary forest, mangrove or coastal forest or montane forest, woodlands or the different types of savannahs, bush country, or grassy vegetation and open montane vegetation above the tree-line, swamp edge and lakesides, oases, desert fringes, plantations, areas partly cleared for agriculture, parks, tree-lined roads, gardens and all forms of secondary growth. The actual level of classification was the grouping of the various vegetation types listed above into major habitat types such as 1, closed habitat (including riverine forest, montane forest, secondary and primary forest); 2, open habitat (grasslands, woodlands, secondary growth and cultivations) and 3, general habitat type (referring to species occurring in both closed and open habitats). See appendix 7 for details of the habitat classifications for all species.

3. 3. STATISTICAL ANALYSIS

Statistical analysis with Microsoft EXCEL was used to analyse measured values derived from all the parameters; minimum frequency (Fmin), maximum frequency (Fmax), entropy, note interval and note duration. When the standard cross hair cursor is activated and a Microsoft EXCEL spreadsheet is opened, the Avisoft-sonograph automatically allows for the export of the cursor readings to an opened EXCEL spreadsheet by enabling the Dynamic Data Exchange (DDE) module. The cursor readings of all parameters at any given cursor point are then recorded under a parameter measurement legend for further analyses. Also, beak morphology and body size data were analysed with SPSS 12.0.0. (www.spss.com). The variability within each taxon was then calculated and all available data used to construct phylogenetic trees.

3. 4. PHYLOGENETIC ANALYSIS

This section presents a brief introduction to the software and methods used in the phylogenetic analyses with emphasis on the main approaches and limitations of the chosen methods. It also includes a brief outline of how phylogenetic trees are bootstrapped and rooted.

PAUP* version 4b10 (Swofford, 1998), was used in the construction of the phylogenetic trees. PAUP is highly flexible software that allows for the estimation of bootstraps or statistical estimates to assess the reliability and the level of confidence of the branching and groupings on a tree. The trees displayed and printed by PAUP* provide the perfect tools for understanding evolutionary distances and how several taxa descend from a common extant ancestor, visualised as nodes and branch lengths (Hall 2004).

PAUP is amenable to several methods but making a choice with respect to the best method to use for phylogenetic studies can be contentious and should be made based on the situation or, specifically, on the type of data at hand, size and complexity of the dataset and computer speed available.

The three main methods that were adopted in these analyses and used to generate the consensus trees were the Neighbour-joining (NJ), the Maximum parsimony (MP) and Bayesian (BAY) methods.

3.4.1. The Neighbour-joining (NJ) method

The method originates from the Distances methods in which the construction of trees is primarily based on the calculation and expression of deviant distances of pairs of taxa to the node that joins them. From the algorithmic approach, the NJ manipulates a distance matrix by first calculating for each taxon its net divergence from all other taxa as the sum of the individual distances from the taxon (Hills *et al.*, 1996) and then uses the net divergence to calculate a corrected distance matrix. It then finds the pair of taxa with the lowest corrected distance and calculates the distance from each one of them to the node that joins them (Hills *et al.*, 1996; Swofford *et al.*, 1996; Hall, 2004). Although the NJ method is fast and yields only a single tree from a given dataset, it is usually impeded by speed and sometimes underestimates the actual distances or the amount of change along lineages.

3.4.2. Maximum parsimony

(MP) or the minimum change method constructs its trees by generating several trees from the same set of data and selecting from amongst them the tree (or trees) that minimises the number of evolutionary steps by scoring and grading each tree to ensure the tree with most parsimony is the one with the lowest score (Hall and Barlow, 2003; Hall, 2004). The MP constructs its tree from the tree searching approach and uses an algorithm to determine the minimum number of steps necessary for any given tree (any given branching order) to be consistent with the data. The Parsimony approach is based on assumptions that the most likely tree is the one that requires the fewest number of changes to explain the data in the alignment. It also assumes that a character is more likely to be common to two taxa because it was inherited from a common ancestor than it is to be common because of homoplasy (when two taxas' characters are similar but were not derived from a common ancestor but from convergent evolution) (Graur and Li, 2000; Hall, 2004).

Although MP is fast, unlike NJ, Maximum Parsimony is capable of generating and evaluating a number of trees from which it chooses the best and most reliable tree. The MP is, however, disadvantaged by its inability to handle large datasets.

3.4.3. Bayesian (BAY) trees

The Bayesian approach, according to Rannala and Yang (1996), Mau and Newton (1997) and Mau *et al.* (1999), has an outstanding capability of handling very large phylogenies and can be quickly calculated. The method executes data files by evaluating the tree that better fits the model and then conducts many generations to select the best tree. Further calculations are conducted by consensus of the tree branch lengths and the groupings or clades as equivalents of bootstrap values (Hall, 2004).

The Bayesian method is character-based and is applied to each site along the alignment. It begins with a tree (either a user-specific tree or a randomly chosen tree) with a combination of branch lengths, substitution parameters, and a rate variation across parameters to define the initial state of the chain. A new state of the chain is then proposed and the probability of the new state, given the old state, is calculated. A random number between 0 and 1 is drawn, and if the number is less than the calculated probability, the new state (new tree) is accepted; otherwise the state remains the same (Huelsenbeck and Ronquist, 2001). This constitutes a single generation of the chain (Hall, 2004). The Bayesian method has several advantages and these include its ability to maximise the probability of a given tree's data and its evolutionary lineage. It also searches for the best tree as in the case of the MP and will often consider the same tree many times to ascertain reliability of the tree. It is, however, incapable of calculating posterior probabilities and not widely used (Mau and Newton, 1997; Mau *et al.*, 1999; Hall, 2004). The phylogenetic analyses were conducted by loading the grouped data matrix into the PAUP input file using NEXUS, a format that is most convenient and directly read and written by PAUP.

3.4.4 Bootstrapping a tree

Bootstrapping is a widely used method for providing statistical estimates in support of the reliability of the groupings and the order in which different taxa diverge in a phylogenetic tree (Graur and Li, 2000; Hall, 2004). 'Reliability' in this sense is measured as the probability that the members of a given clade are indeed members, and always are members, of that clade. Although several bootstrap cycles are initiated on each clade during a tree construction, bootstrap samples of 100 to 1000 repetitions are used to estimate tree reliability and a minimum of 2000 replicates are required to obtain a 95% confidence level. Since 90% bootstrap is normally accepted as an upper level of confidence for a clade and 25% bootstrap value rejected as lacking confidence, a threshold of 50% bootstrap value is usually set to mark the level of confidence for all the clades. So that clades with 50% and above are generally accepted confidently while those below the threshold of 50% are regarded as not significant. The values of the bootstrap are usually placed at the nodes or sometimes along branches (Swofford *et al.*, 1996; Hall, 2004). Several authors such as Voelker (1999b), Irestedt *et al.* (2001), Grant (2001), Bowie (2003) and Douady *et al.* (2003) have adopted the 50% bootstrap technique. All bootstraps in this study were based on the 50% confidence threshold.

3.4.5 Placing the root of a tree

The root of a tree is a representation of the common ancestor of all of the taxa being considered. Generally, every set of taxa has some common ancestor but the problem in phylogeny is where to place the node that represents the ancestor which is the root (Hall and Barlow, 2003; Hall, 2004). To root a tree therefore means choosing a point on the tree that represents the earliest time in the evolutionary history of the taxa. To avoid arbitrary placement of the root, two main approaches (1) Midpoint rooting and (2) outgroup have been adopted to help resolve the rooting of phylogenetic trees. (1) The Midpoint rooting places the root at the middle of the longest path between the two most distantly related taxa. Such a placement implies that the rate of evolution has been the same along all branches but this is not always the case. Unless it is certain that the evolutionary rates have been constant across the taxa being considered, using the midpoint could be risky and inapplicable (Hall and Barlow, 2003). The alternative and most widely used approach is the outgroup technique. An outgroup (primitive) is a taxon that is more distantly related to each of the ingroup (derived) taxa than any of the ingroup taxa are to each other. Finding the outgroup taxon involves a search through the scores of all taxa and the legitimate outgroup(s) assigned and used to root the tree. The outgroup technique is sufficiently reliable if the outgroup(s) are actually homologous to the study taxa and phylogenetically informative (Graur and Li, 2000; Hall, 2004). This study and others such as those by Grant (2001), Irestedt *et al.* (2001), Bowie (2003) and Douady *et al.* (2003) adopted the outgroup technique for rooting the trees.

CHAPTER 4

ACOUSTIC ANALYSES AND ACOUSTIC-BASED PHYLOGENIES OF THE STUDY TAXA

4.1 INTRODUCTION

Phylogenies derived from the acoustic characters of bird songs are becoming increasingly common in studies of avian evolution and systematics. Vocal phylogenies are now contributing to a better understanding of the evolutionary histories of many bird species and helping to resolve controversies about the classification and placement of some species (e.g. Whitney and Pacheco, 1994). The vocalisations of the Nectariniidae were categorised into three main vocalisation types, calls, simple songs and complex songs, using unbiased criteria, and used to derive phylogenies. The family is poorly differentiated on morphological grounds and all attempts at deriving the evolutionary histories based on revision and examination of their morphology and vocalisation remain convoluted and, in some cases, without evolutionary conclusions or constructive phylogenies. Even the only constructed DNA phylogeny remains unpublished.

The purpose of this chapter is to present the results of the acoustic measurements of all the vocal recordings collected and collated during the course of the research and the resulting phylogenies of the study taxa. It details the approaches used in the acoustic analyses and how the vocal variability that emerged from the analysis was used to derive the phylogenies. It also includes sample trees from Delacour (1944) and the combined nDNA and mtDNA tree derived by Bowie (2003) earmarked for discussion in chapter 6. A brief discussion of the affinities of the Flowerpeckers and Spiderhunters and the origin of Sunbirds is presented in this chapter.

4.2 DETAILED METHODS

This section details the vocal and phylogenetic approaches used for the analysis. It outlines the sonographic-based techniques for quantifying bird vocalisations i.e. the visual inspection of sonogram printouts and the automated derivation procedures. It also explains the steps used to derive the phylogenetic trees of the study taxa.

4.2.1 Visual scoring by inspection of sonograms

The visual scoring and quantification of song units was conducted on printed sonograms (see Appendices 2, 3, 4 and 5) and the partitioning of units was based on silent intervals within the different species' vocalisations. Three quarters of the parameters adopted in this study were analysed by this technique. The varying number and lengths of silent intervals between notes and phrases were parameters used for distinguishing between different species' songs.

Presented below are the attribute states of the parameters scored, determined by visual inspection of sonograms coded in a character matrix (see table 4.1) which was based on inspecting and scoring the number and types of different syllables and how they occur in the sonograms of each species.

A representative of a sonographic data matrix of 10 acoustic characters, for a sample of 30 randomly selected species of Nectariniidae is given in table 4.1. This depicts the number of song units, or repertoire size, of all taxa derived from visual inspection of sonograms of their vocalisations. The units range from a 0 score, representing the absence of a particular song unit, to 8 for different song units and coded in the character matrix as follows: 1, for duration of phrase; 2, number of notes in a phrase; 3, size of repertoire; 4, introductory rattle; 5, click; 6, squawk; 7, song duration; 8, note percentage; 9, pause rate and 10, rhythm of frequency. Each of these was subdivided using the following codes for different attributes:

1. Duration of phrase; 1 = 0-2 seconds, 2 = 2-3 seconds, 3 = 3-4 seconds, 4 = 4-5 seconds, 5 = 5-6 seconds, 6 = 6-7 seconds, 7 = 7-8 seconds and 8 = 9 or more seconds.

2. Number of notes in a phrase; 1 = 3 notes, 2 = 4 notes, 3 = 5 notes, 4 = 6 notes, 5 = 7 notes, 6 = 8 notes, 7 = 9 notes, 8 = 10 or more notes.

3. Size of repertoire; 1 = 2 different types of syllables, 2 = 3 different types of syllables, 3 = 4 different types of syllables, 4 = 5 or more different syllables.

4. Introductory rattle; 0 = no introductory rattle, 1= presence of introductory rattle.

5. Click; 0 = no click, 1 = presence of a click.

6. Squawk; 0 = no squawk, 1 = presence of a squawk.

7. Song duration; 1 = 10-25 seconds, 2 = 26-35 seconds, 3 = 36-45 seconds, 4 = 46-55 seconds, 5 = 56-65 seconds, 6 = 66-75 seconds, 76 or more seconds.

8. Note percentage: this is a measure of the summed duration of all notes in an individual species song divided by the total song duration and scored as: 2 = 20%, 3 = 40%, 4 = 60%, 5 = 80%, 6 = 80-100%.

9. Pause rate; 2 = 3 pauses per song, 3 = 4 pauses per song, 4 = 5 pauses per song, 5 = 6 or more pauses.

10. Rhythm of frequency; 2 = notes fluctuating within 2 frequency levels, 3 = notes fluctuating within 3 frequency levels, 4 = notes fluctuating over 4 frequency levels.

The scores of each taxon were further computed by the mean and standard deviations of all the characters and grouped by error bars into four main categories (A, B, C and D), see appendices 10 and 11. The categorisations were made after ranking all the mean and standard deviation scores and grading them by high and low scores. An example of the note percentage score and grouping is as follows (0-0.3 = A, 0.4-05 = B, 0.6-0.7= C, > 0.8 = D). Note that values of A and B groupings represent call vocalisations, C for simple songs and D for complex songs. See appendix 9 for sample grouping of all characters used for the construction of the phylogenies.

Table 4.1. Sonographic data derived from visual inspection of sonograms of 23 randomly sampled species or subspecies. For explanation of codes see text.

	Character numbers									
Species name	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Prionochilus o. olivaceus	2	2	1	0	0	0	2	2	4	2
P. maculatus oblitus	3	3	1	0	0	0	3	3	3	2
P. thoracicus	3	3	1	1	0	0	3	3	2	2
D. a. australe	4	4	1	1	0	0	3	3	2	2
D. a. agile	3	3	2	0	0	0	2	3	3	2
D. t. trigonostigma	4	5	2	0	0	0	4	3	2	2
D. celebicum celebicum	3	3	1	0	0	0	3	4	2	2
Anthreptes reichenowi reichenowi	4	6	2	1	0	0	4	4	3	3
Anthodiaeta pallidigaster	1	1	1	0	1	0	1	5	4	2
Leptocoma minima	3	2	2	0	0	1	2	4	4	2
Cinnyris asiaticus asiaticus	4	6	4	1	1	1	6	5	3	4
Nectarinia kilimensis kilimensis	4	5	3	1	1	1	6	6	3	4
Anthodiaeta collaris zuluensis	6	8	5	1	0	1	5	4	3	3
Cinnyris jugularis bruensis	5	8	5	1	0	1	5	4	3	3
Cyanomitra o. oritis	6	8	3	1	1	1	6	5	2	4
Chalcomitra rubescens crossensis	4	5	3	1	0	1	7	4	3	3
Chalcomitra senegalensis cruentata	6	8	3	0	0	1	6	4	3	3
Aethopyga nipalensis koelzi	7	7	3	1	1	1	7	5	3	4
Cyanomitra olivacea olivacea	4	7	3	1	0	0	4	4	3	3
Cinnyris chloropygius chloropygius	4	8	4	1	1	1	7	6	4	4
Cinnyris manoensis manoensis	4	7	3	1	0	1	5	5	4	3
Cinnyris p. preussi	6	5	3	1	1	1	6	5	3	3
Cinnyris mariquensis mariquensis	5	6	3	1	0	0	5	4	4	3

For each taxon, the variations in scores of the ten parameters listed in Table 4.1. were summarised by calculating their means and standard deviations. The scores under each parameter for each taxon were then grouped in terms of closeness, as a grouping criterion for use in deriving the phylogenies. The species with the highest mean scores in terms of the variability of syllable types were classed as complex vocalisations e.g. Olive-bellied Sunbird *Cinnyris chloropygius chloropygius* (Appendix **4.59**). Below is a list of all species chosen for inclusion in Table 4.1 and the reference codes for their sonograms as used in Appendices 1-5 for ease of comparison between the data in the Table and the appearance of the corresponding sonogram. *Prionochilus o. olivaceus* (Appendix **2.2**); *P. maculatus oblitus* (Appendix **2.3**); *P. thoracicus* (Appendix **2.9**); *D. australe* (Appendix **2.21**); *D. a. agile* (Appendix **2.11**); *D. t. trigonostigma* (Appendix **2.27**); *D. celebicum celebicum* (Appendix **2.45**); *Anthreptes reichenowi reichenowi* (Appendix **4.19**); *Nectarinia kilimensis kilimensis* (Appendix **4.218**); *Anthodiaeta collaris zuluensis* (Appendix **4.197**); *Anthodiaeta pallidigaster* (Appendix **4.203**); *Aethopygya nipalensis koelzi* (Appendix **3.93**); *Leptocoma minima* (Appendix **3.20**); *Cyanomitra o. oritis* (Appendix **4.180**); *Chalcomitra rubescens crossensis* (Appendix **4.37**); *Cyanomitra olivacea olivacea* (Appendix **4.178**); *Cinnyris jugularis bruensis* (Appendix **3.44**); *Chalcomitra senegalensis cruentata* (Appendix **4.48**); *Cinnyris chloropygius chloropygius* (Appendix **4.59**); *Cinnyris manoensis manoensis* (Appendix **4.66**); *Cinnyris p. preussi* (Appendix **4.77**) *Cinnyris mariquensis mariquensis* (Appendix **4.101**).

4.2.2. Automated derivation and statistical analysis

The automated derivation technique involved using the cursor to carefully encircle each syllable to derive values under a chosen parameter's legend in the spectrogram window of the Avisoft software. The data were then exported directly into a Microsoft EXCEL spreadsheet for further computations for use in the construction of the phylogenetic trees. The automated approach was used for a quarter of the parameters measured. These included frequency, entropy, peak amplitude, note/syllable start time and end time, interval, duration and bandwidth (see Tables 4.2 - 4.4) All values of the above parameters were obtained simultaneously from the cursor on each measured syllable.

Entropy values were used to separate calls from simple and complex songs using the threshold values given in section 4.2.3. (below). Examples of measured values exported from the spectrograph of a call (Mean entropy 0.6, Yellow-breasted Flowerpecker *Prionochilus maculatus oblitus*, Appendix **2.3**), of a simple song (Mean entropy 0.33, Forked-tailed Sunbird *Aethopyga christinae sokolovi*, Appendix **3.97**) and from a complex song (Mean entropy

0.2, Pygmy Sunbird *Anthodiaeta platura*, Appendix **4.207**) are given in Tables 4.2, 4.3 and 4.4.

Table 4.2 Statistical computations from a call.

Yellow-breasted Flowerpecker *Prionochilus maculatus oblitus*								
function	**duration**	**interval**	**start time**	**end time**	**peak ampl**	**Max freq (kHz)**	**bandwidth**	**entropy**
min	0.04	0.13	0.2	17.9	21.4	7.2	7.4	0.3
max	0.07	0.23	0.3	41.2	25.2	7.5	7.9	0.9
mean	0.05	0.23	0.03	29.4	23.0	73	7.6	**0.6**
stdev	0.02	0.02	0.16	0.17	0.76	12.1	11.5	0.05

Table 4.3 Statistical computations from a simple song.

Forked-tailed Sunbird *Aethopyga christinae sokolovi*								
function	**duration**	**interval**	**start time**	**end time**	**peak ampl**	**Max freq (kHz)**	**bandwidth**	**entropy**
min	0.05	0.17	0.2	19	20.4	6.0	5.4	0.2
max	0.06	0.28	0.5	44.1	28.2	7.2	6.9	0.5
mean	0.55	0.22	0.04	46.4	24.3	6.6	6.2	**0.33**
stdev	0.03	0.08	0.16	0.17	0.76	10.1	9.55	0.04

Table 4.4 Statistical computations from a complex song.

Pygmy Sunbird *Anthodiaeta platura*								
Funtion	**duration**	**interval**	**start time**	**end time**	**peak ampl**	**max freq (kHz)**	**bandwidth**	**entropy**
min	0.01	0.04	0.2	21.9	22.4	5.6	5.1	0.1
max	0.13	0.21	0.3	23.5	35.1	8.0	7.7	0.3
mean	0.04	0.09	0.03.	22.7	28.3	6.7	6.4	**0.2**
stdev	0.03	0.05	0.41	0.42	4.19	8.32	9.91	0.05

Variability (mean and standard deviation) within each taxon was then calculated for all available data exported from spectrographs of recorded species for future use in the construction of phylogenetic trees and other analyses.

4.2.3 Thresholds for separating vocalisation categories

The thresholds for distinguishing between calls and songs and between simple songs and complex songs were initially obtained by visual inspection of the signal images on the spectrogram windows as they were listened to. This involved finding sequences of vocalisations that were clearly calls, simple songs or complex songs and comparing their respective mean and standard deviation scores for the entropy variable calculated by the software. Then the entropy values were ranked and the cut-off points of separation in each of the two cases (1) of calls versus songs and (2) simple songs versus complex songs were identified as the thresholds. The technique required the following steps:

(A) The first step was to activate the automatic parameter measurement set-up on the spectogram window and then activate the means and standard deviation boxes for entropy, under the subsidiary parameter measurement statistics window. The bandwidth was also adjusted from 111Hz to 323 Hz to improve on the cut-off points of the wavelengths of the signal spectrum in the spectographic window.

(B) An activated cursor was used to interlock with the different types of the vocalisations as the cursor advanced from calls to songs and or from simple songs to complex songs within the spectogram windows. Arbitrary thresholds were set by comparing the mean and standard deviation values with the syllable images displayed on the spectograms.

(C) Setting the upper and lower limits defining the range of entropy values (0-1) as displayed in the spectographic window for all the vocalisations analysed.

(D) The cut-off points of the entropy values (0.3 and 0.34) were identified by visual comparison between the syllabic imagery of the varying vocalisations and the entropy mean scores from the cursor at the points of transition from calls to songs and from simple songs to complex songs, respectively.

A plot of the mean entropy values of the vocalisations of the Nectariniidae shows that their core concentration zone had entropy values in the range 0.2-0.6 (Figure 4.1), thus the majority of the vocalisations were above the threshold of 0.34 and so were mainly calls or simple songs.

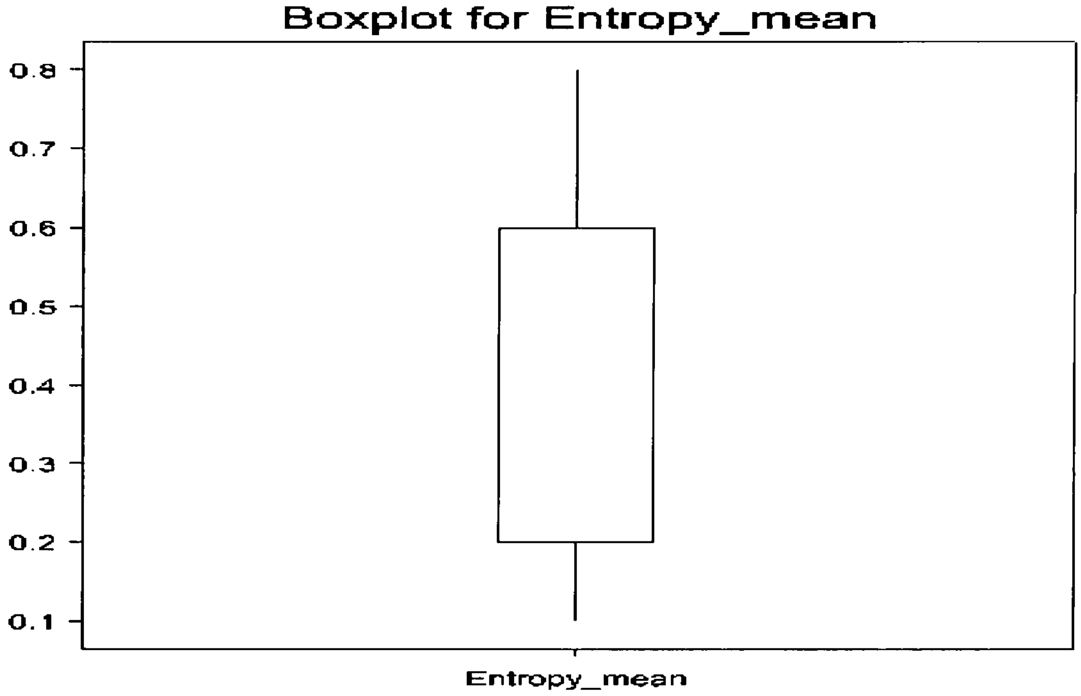


Figure 4.1. Box-plot for mean entropy values of the Nectariniidae. Note that the core concentration zone was between 0.2 and 0.6.

The mean entropy values of all the vocalisations were further computed for each genus and converted to mean negentropy values and used to plot each of the distribution curves (Figures 4.2 - 4.5) for calls, simple songs and complex songs based on the threshold values converted to negentropy (1 - 0.3 and 1 - 0.34, i.e. 0.7 and 0.66. Thus all vocalisations with mean negentropy values <0.66 were classified as calls, those between 0.66 and 0.7 as simple songs and those > 0.7 as complex songs.

Figure 4.2 depicts the mean negentropy values according to genus studied of vocalisations of every taxon within each genus for which data were available, in relation to the thresholds (0.7 and 0.66) of the negentropy values of different vocalisation types.

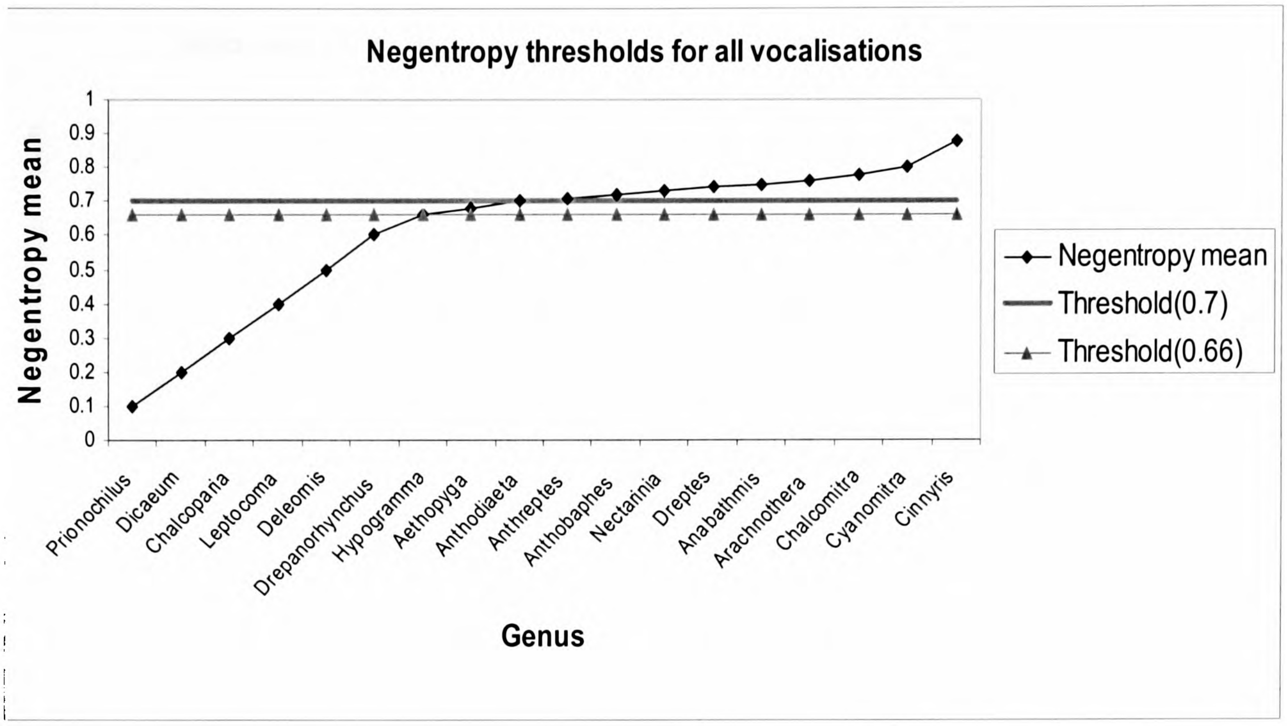
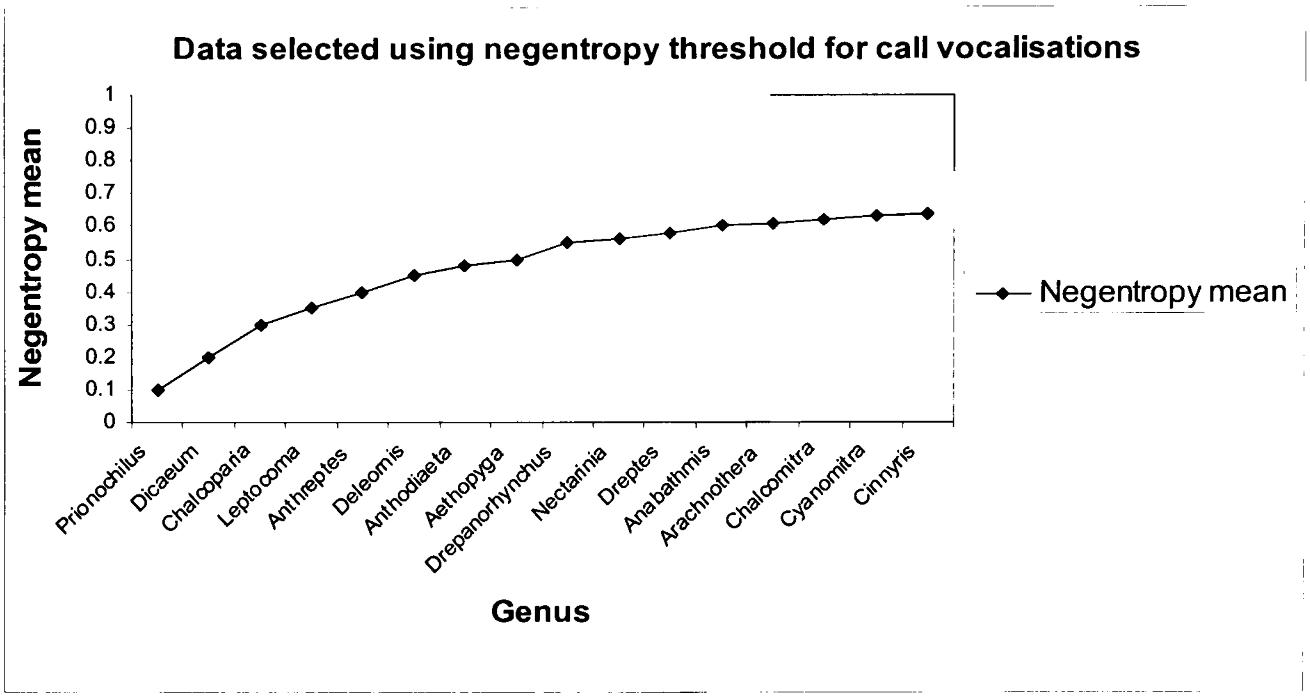


Figure 4.2. The mean negentropy values of all vocalisations (negentropy thresholds 0.7 and 0.66) for all species within different genera for each genus from the entire set of vocalisations analysed.

However, to show intergeneric variation for calls alone, songs (both simple and complex) alone, simple songs only and complex songs only, the data were re-analysed using the threshold values to separate vocalisations into each of the four categories first (Figures 4.3 - 4.6).

All the genera with the exceptions of *Hypogramma* and *Anthobaphes* had call recordings analysed in this study (Figure 4.3).



Figures 4.3. The mean negentropy values of call vocalisations (negentropy < 0.66) for all species within different genera for each genus with calls analysed. No recordings of calls were available for *Hypogramma* and *Anthobaphes*.

Figure 4.4 shows the mean negentropy values at the genus level for all songs (negentropy above the 0.66 threshold). All genera had some song recordings analysed.

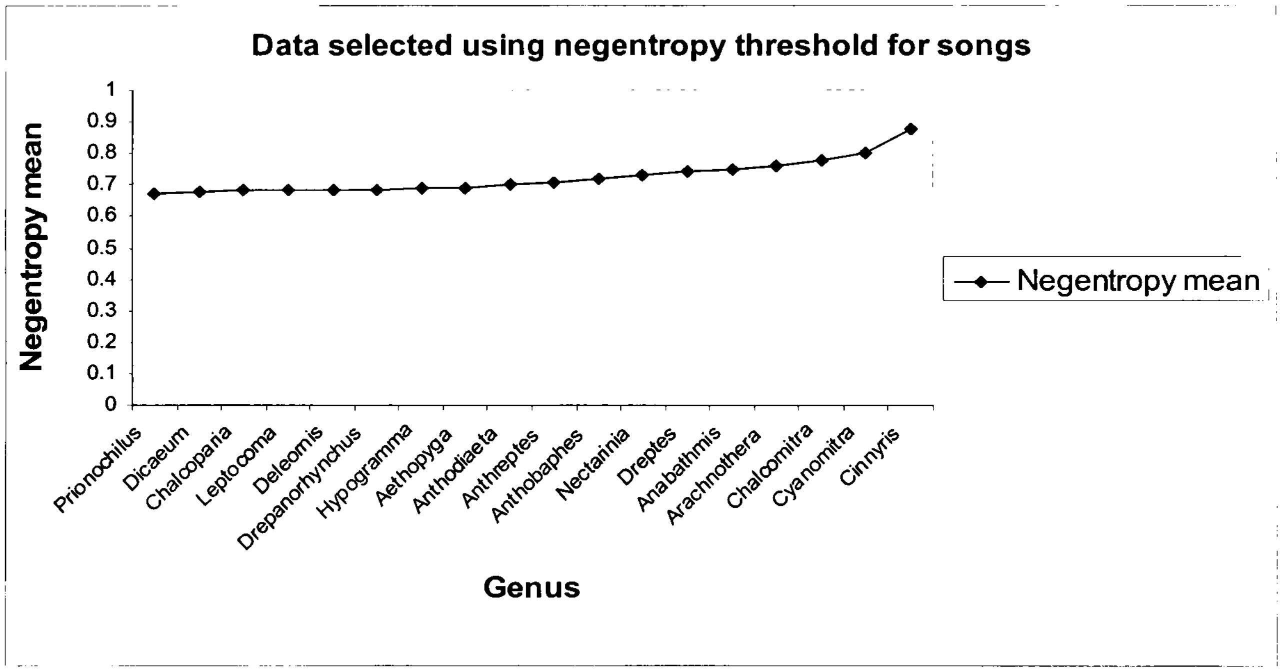


Figure 4.4. The mean negentropy values of song vocalisations (negentropy >0.66) for all species within different genera for each genus.

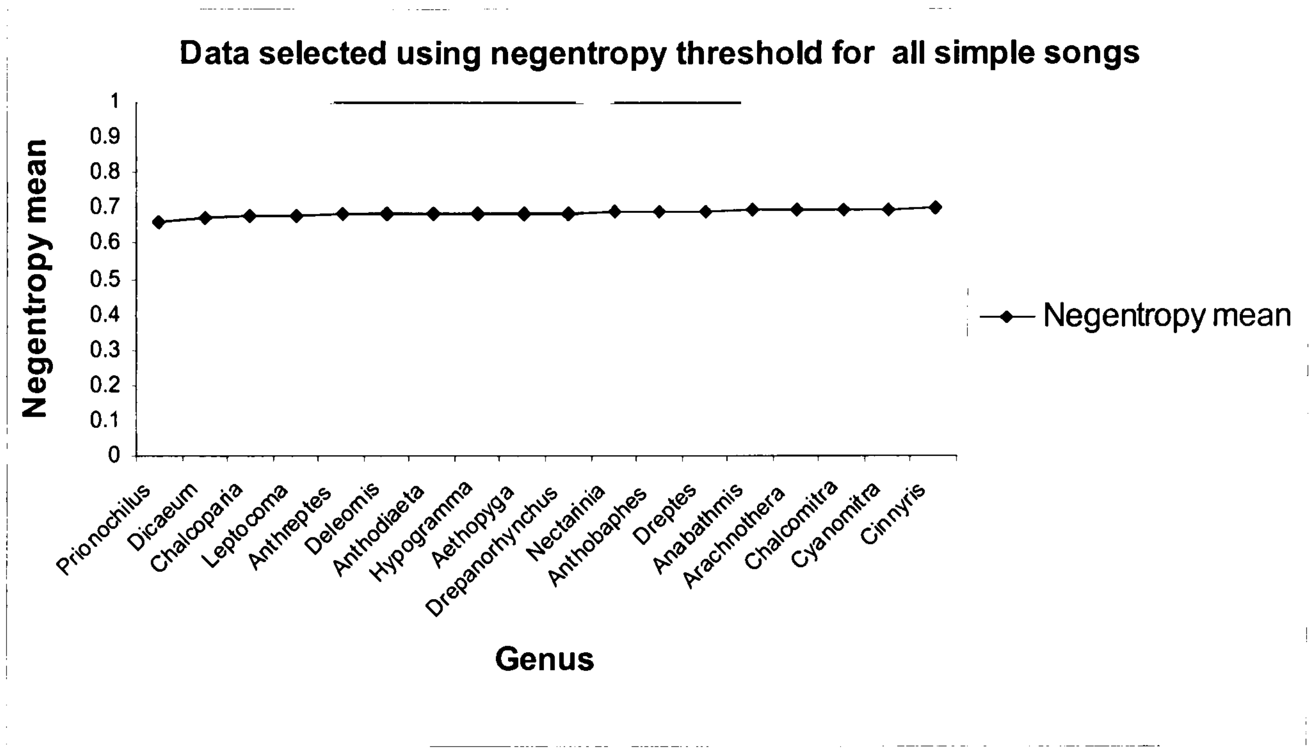


Figure 4.5. The mean negentropy values of simple song vocalisations (mean entropy (≥ 0.66 and ≤ 0.7) for all species within different genera for each genus.

Figure 4.6 illustrates the results for the fourth category of the vocalisations, the complex songs with negentropy values above the 0.7 threshold.

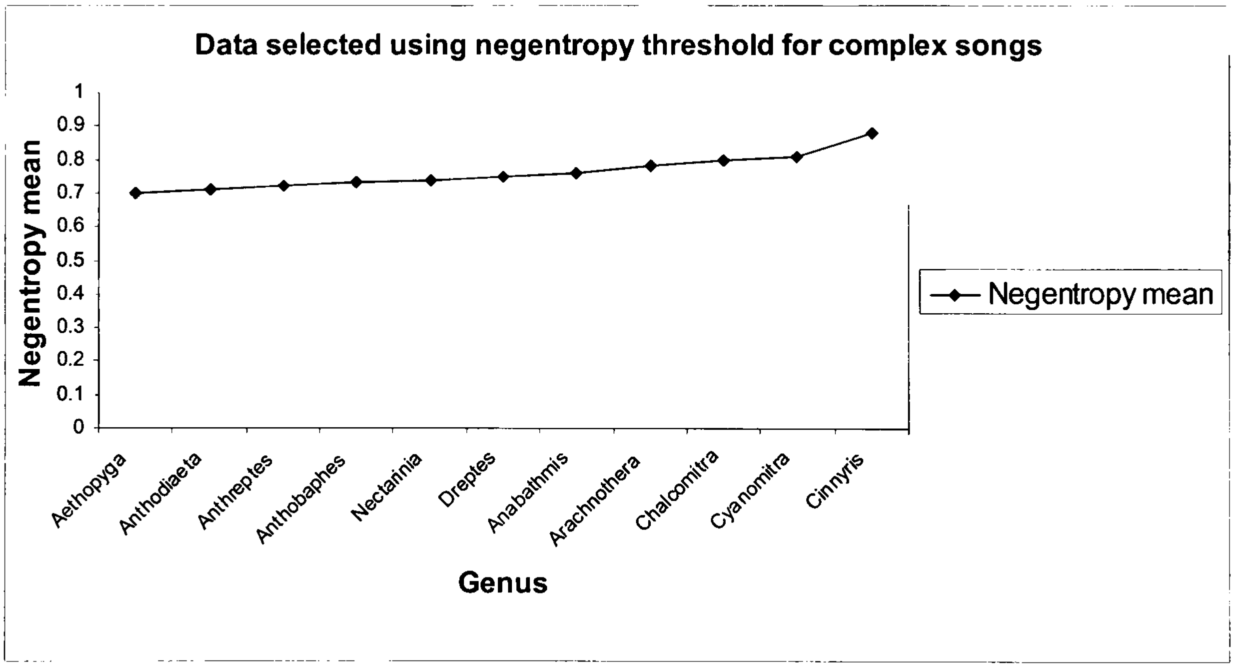


Figure 4.6. The mean negentropy values of complex song vocalisations (negentropy >0.7) for all species within different genera for each genus.

4.3. RESULTS OF ACOUSTIC ANALYSIS

4.3.1. Acoustic measurements

The songs analysed of the Nectariniidae range from call vocalisations (Figure 4.7) to very simple songs (Figure 4.8) to very complex songs (Figure 4.9), which, as described in section 4.2.3, were separated using thresholds of entropy values derived from spectrograms.

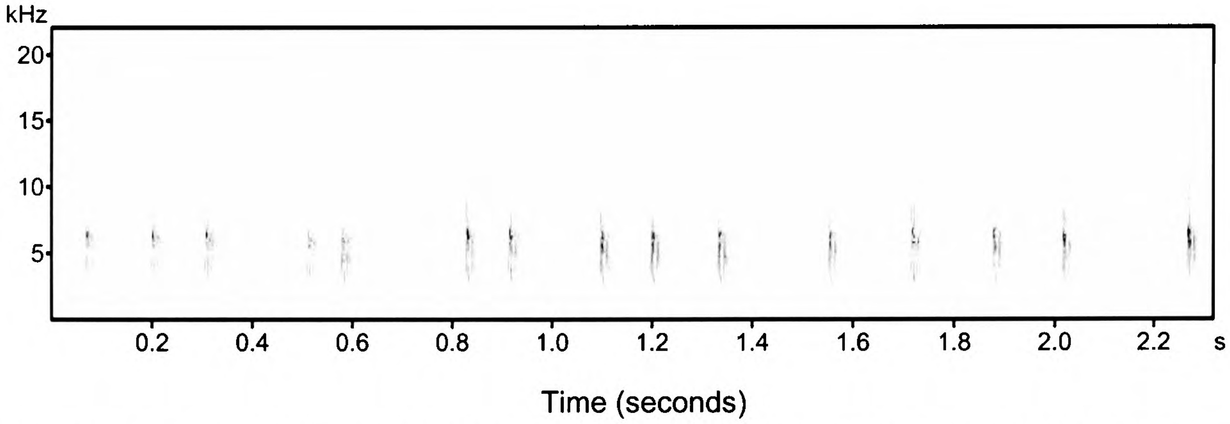


Figure 4.7. A sonogram showing a series of calls from a Yellow-breasted Flowerpecker *Prionochilus maculatus oblitus* (Appendix **2.3**).

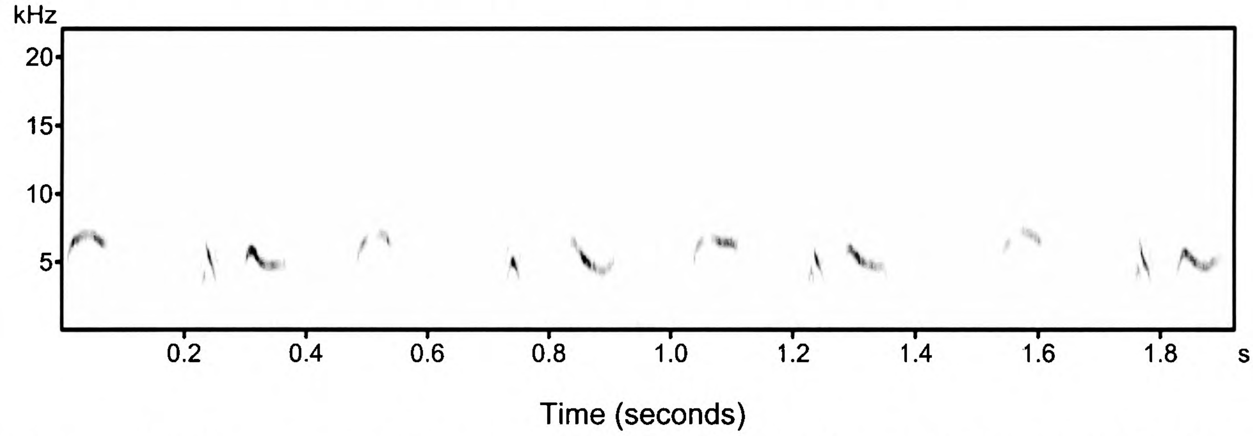


Figure 4.8 Sonogram of a very simple song of the Forked tailed Sunbird *Aethopyga christinae sokolovi* (Appendix **3.97**)

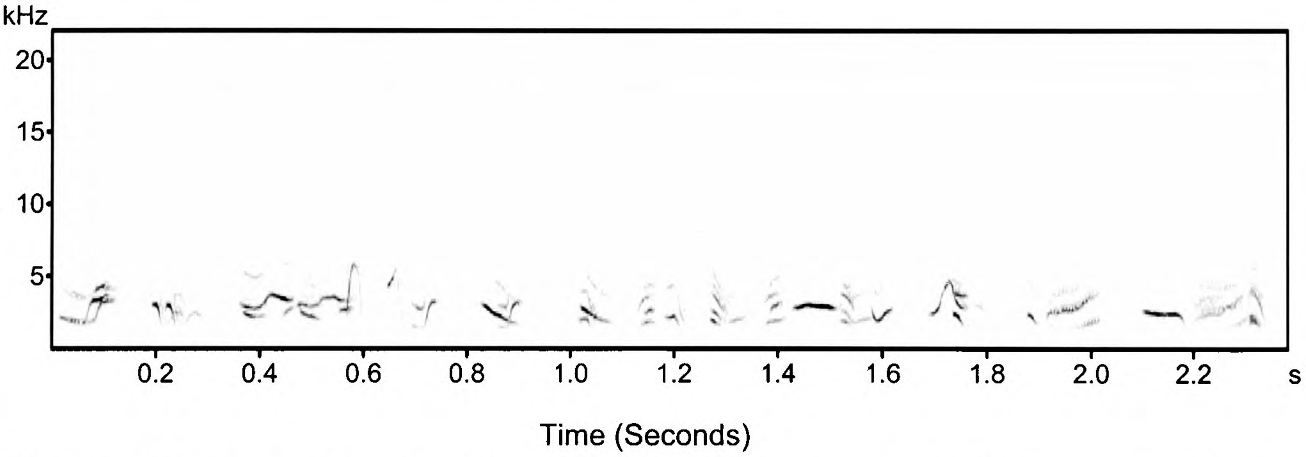


Figure 4.9. Sonogram depicting the very complex song of the Carmelite Sunbird *Cyanomitra fuliginosa aurea* (Appendix **4.35**).

4.3.2. Categorisation of song types

The main groupings were calls, simple songs and complex songs and these have been further calibrated by mean entropy values and the rhythm of frequency notes of individual species' vocalisations derived from the respective sonograms (Figures 4.10a and b; 4.11a and b; 4.12 a and b).

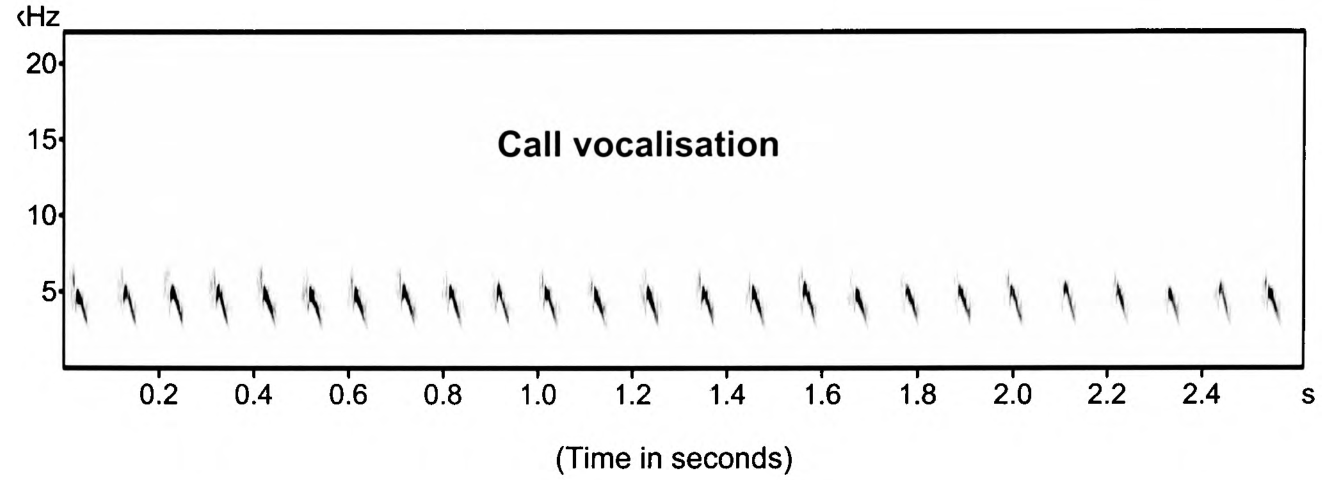


Figure 4.10a. Sample sonogram depicting a series of call notes of the Green-throated Sunbird *Chalcomitra rubescens crossensis* (**4.37**).

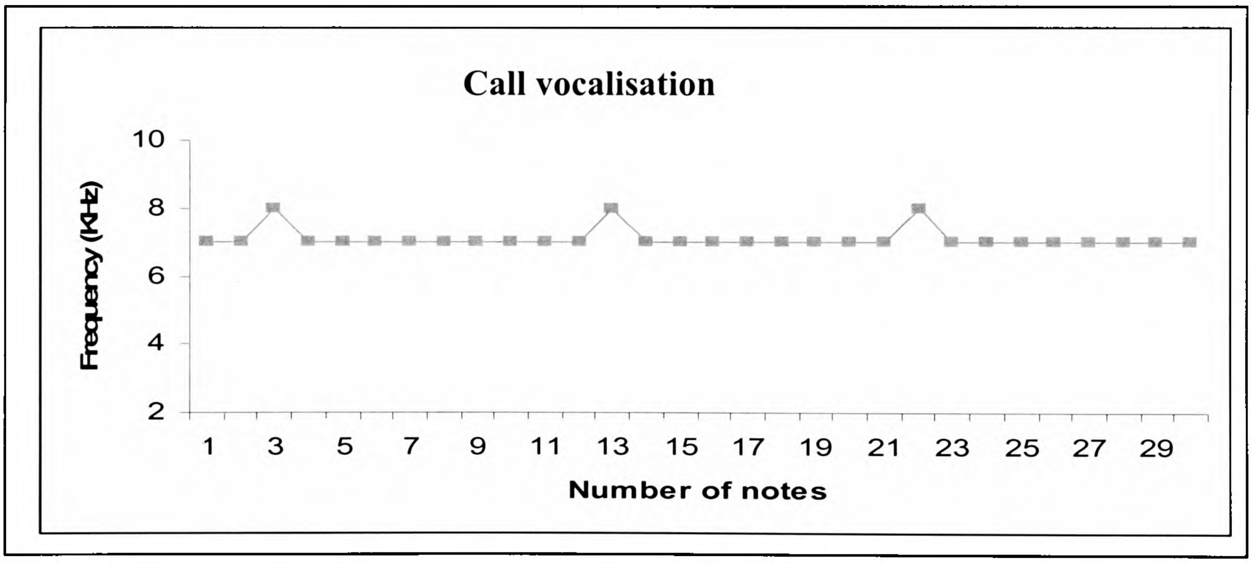


Figure 4.10b. Graph showing the rhythm of frequency of call notes of Green-throated Sunbird *Chalcomitra rubescens crossensis.*

Figures 4.10a and b show that calls are the simplest stereotypic song units of the same elements, rapidly repeated mostly on one frequency, the (7 kHz) frequency.

Also presented below (Figures 4.11a and b) is an example of the groupings for simple songs of the Nectariniidae.

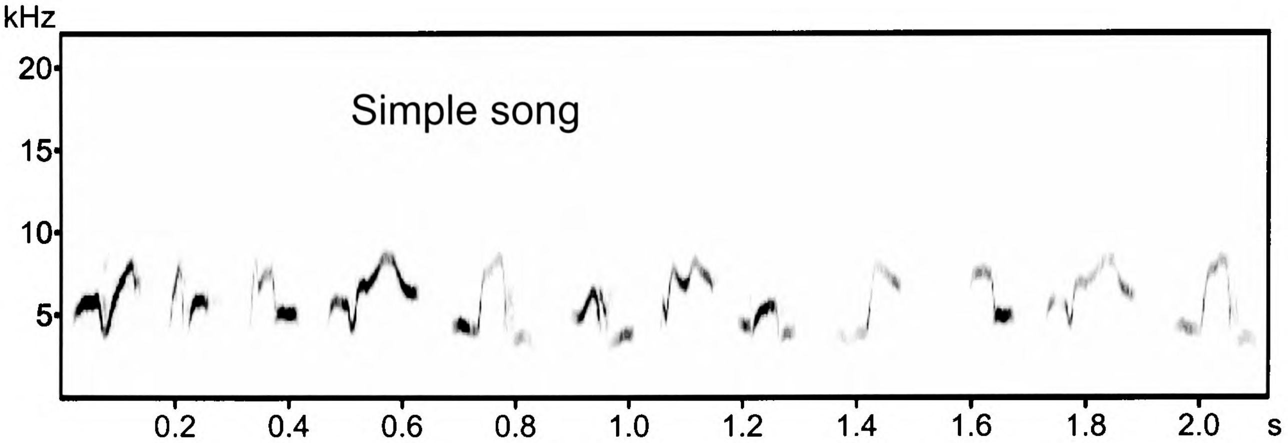


Figure 4.11a. Sonogram of simple song of Humblot's Sunbird *Cinnyris humbloti humbloti* (**5.29**).

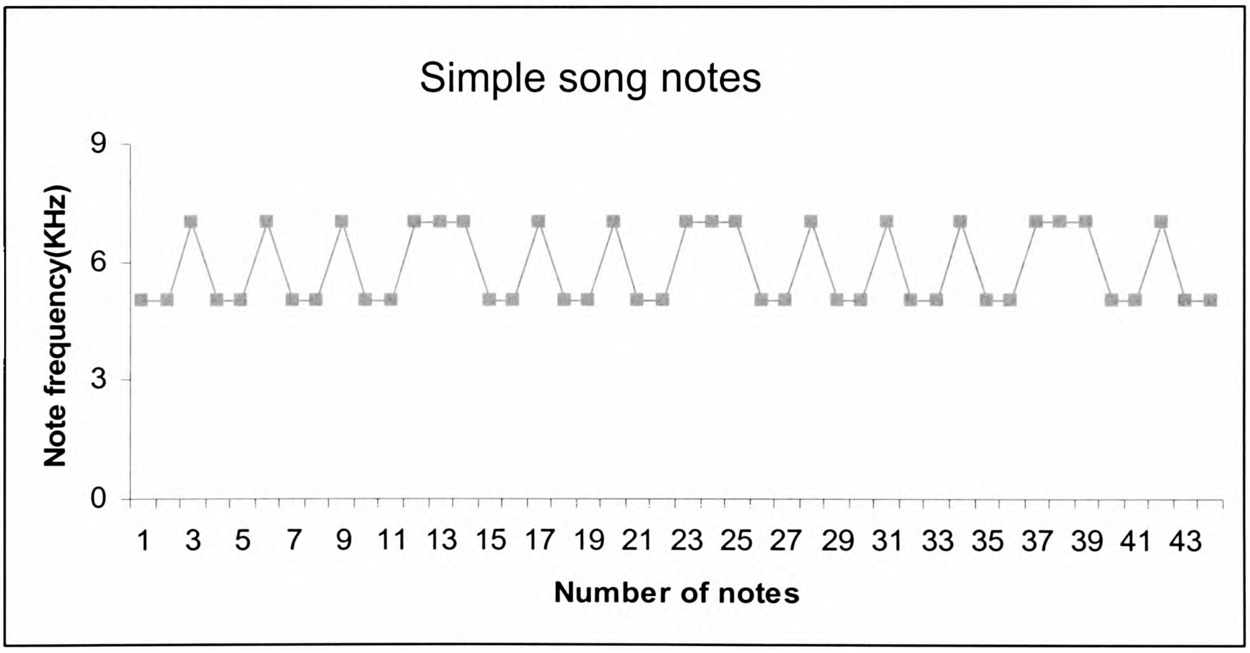


Figure 4.11b. The rhythm of simple song notes of the Humblot's Sunbird *Cinnyris humbloti humbloti.*

Figures 4.11a and b. show simple song with long pure tones of acoustic units within an evenly narrow band with two (5-7 kHz) frequency ranges with some harmonics.

The complex song category has been represented in Figures 4.12a and b.

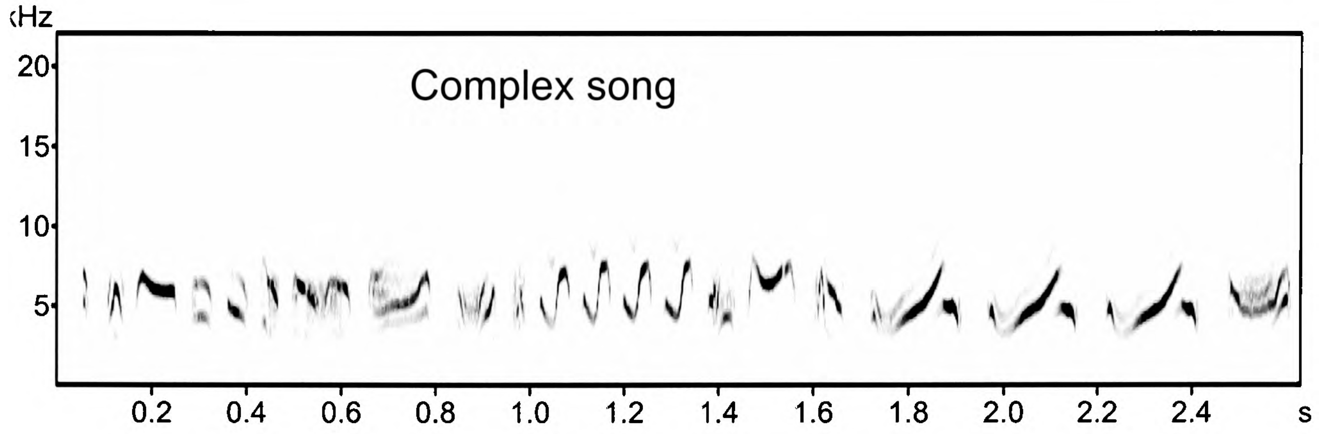


Figure 4.12a. Sonogram of the Pygmy Sunbird *Anthodiaeta platura* (**4.207**) showing a complex song.

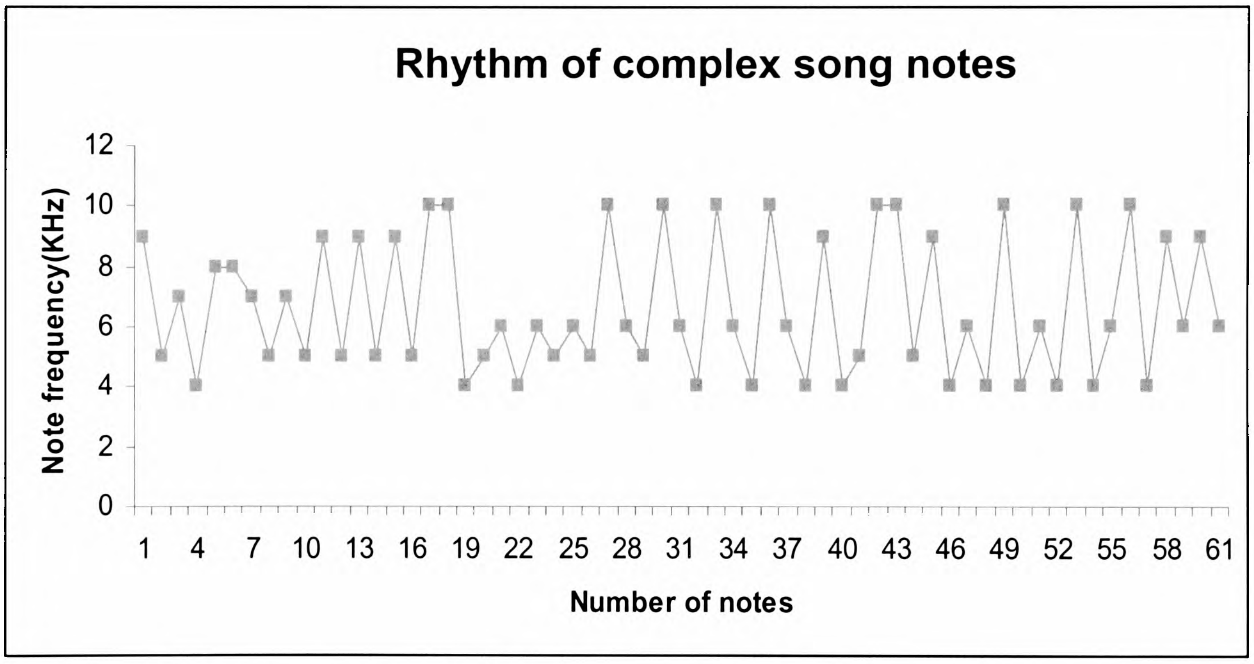


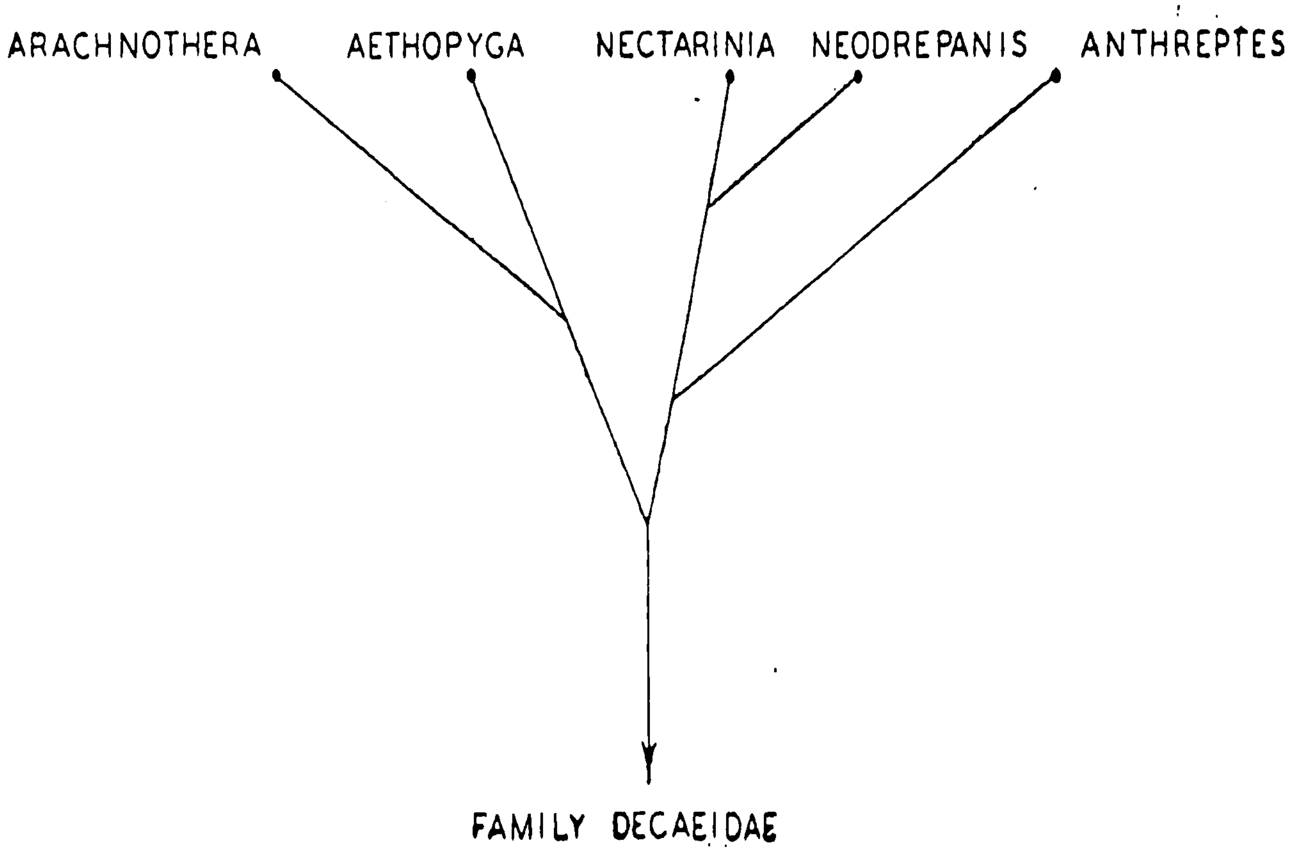
Figure 4.12b. Variation of frequency rhythm of the Pygmy Sunbird *Anthodiaeta platura.*

Figures 4.12a and b depict the considerable variation of the syllables of a complex song with a wide range of differing note frequencies (4-10 kHz) and amplitude.

4.3.3. Evolution and song complexity

A summary of the sequence of the level of song complexity (negentropy) correlates with the evolutionary lineage (as described by Delacour, 1944 in Figure 4.13a and b) of the Nectariniidae at genus level as shown in Figure 4.14.

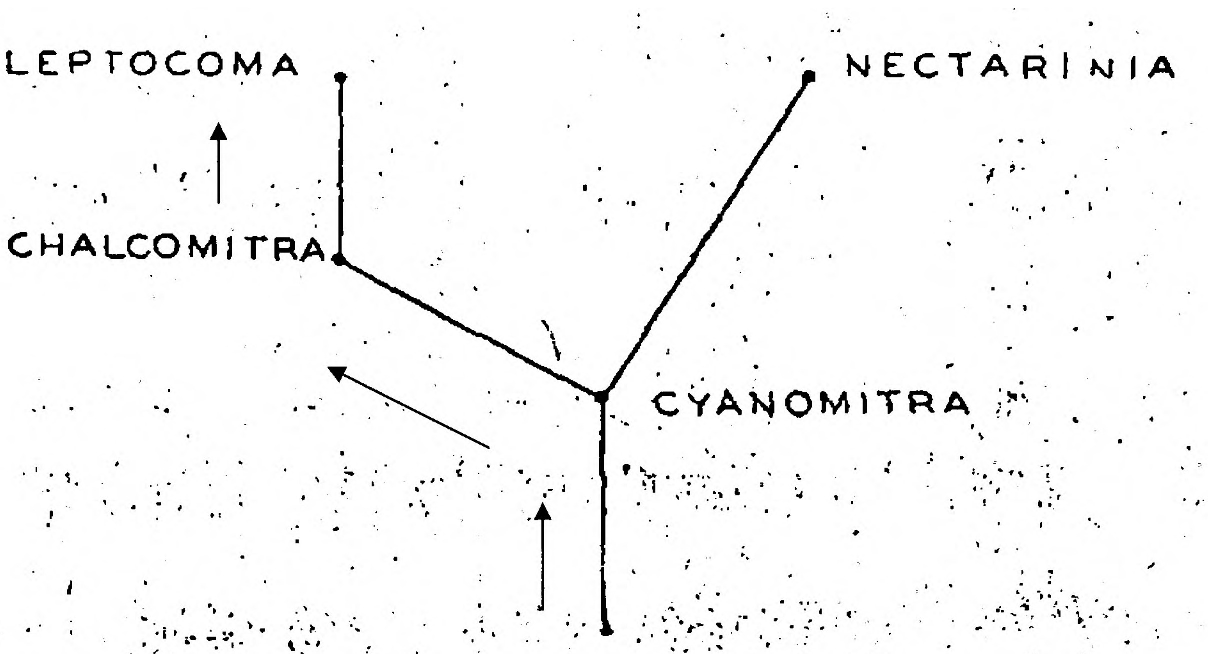
Delacour's (1944) evolutionary cladogram



TEXT-FIG. 8. Genera of the Family Nectariniidae.

Figure 4.13a. A sketched cladogram of the evolutionary lineage of the Nectarinidae (Delacour, 1944).

Note that the genus *Neodrepanis* used in this cladogram is under the family Philepittidae and include two species of "Sunbirds" (The Common Sunbirds *Neodrepanis corucans* and the Yellow-bellied Sunbird *Neodrepanis hypoxanthus*), now known as Sunbird–Asities and which were formerly known as false Sunbirds (Prum, 1993).



TEXT-FIG. 10. Subgenera of *Nectarinia.*

Figure 4.13b. A sketched cladogram of the subgenera of *Nectarinia* of the Nectariniidae (Delacour, 1944).

The second of Delacour's 1944 cladogram sketches (Figure 4.13b) proposed another evolutionary lineage of the Nectariniidae which appears to indicate that the genus *Leptocoma* composed of 5 sunbird species exclusively of the Asian or oriental region may have evolved from the genus *Chalcomitra* with 7 species, all of which occur only in Africa. This provides some support to Irwin's 1999 claim that sunbirds originate from Africa.

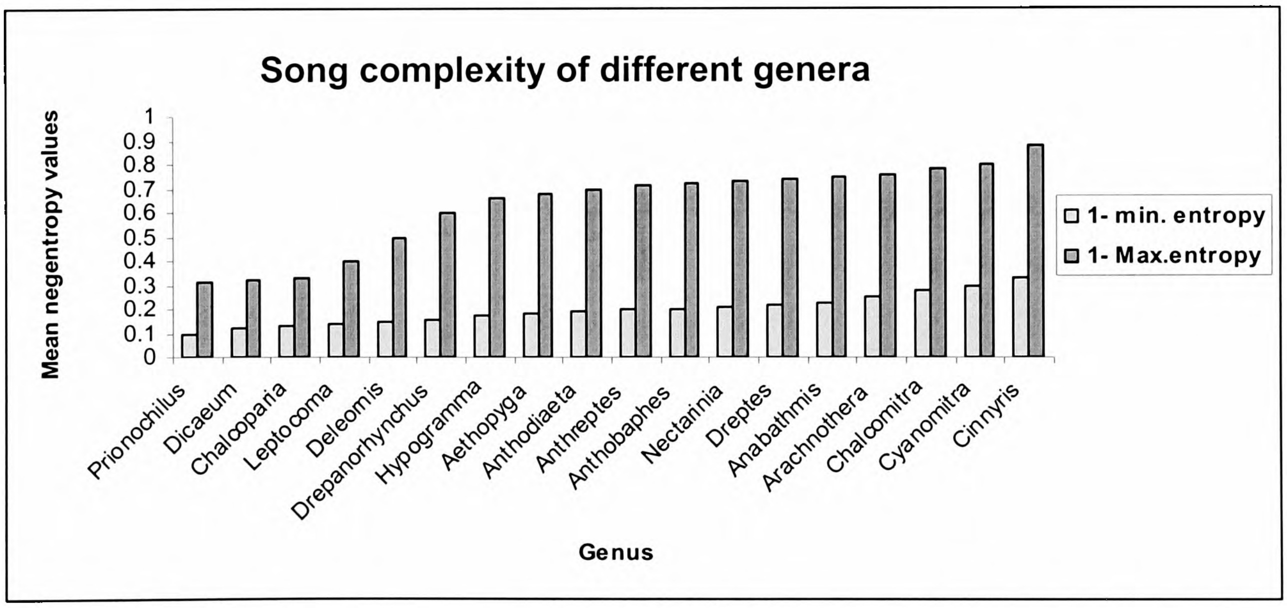


Figure 4.14. Mean negentropy values of different genera of the Nectariniidae. Note that *Prionochilus* and *Dicaeum* have the lowest negentropy or song complexity and that *Cyanomitra* and *Cinnyris* have the highest negentropy or the more complex songs.

4.3.4. Phylogenetic analysis

This section details the grouping technique used for the data derived from the acoustic analysis into the appropriate filing system required for the construction of trees by the PAUP* software and the three main methods (Neighbour-joining, Maximum parsimony and Bayesian) adopted by this study.

The computed variances of each of the 10 to 20 characters of each taxon were grouped by means of error bars following the preliminary grouping of the data by the similarity of mean and standard deviation values from the statistical analysis of the vocalisations of the taxa. The final outcomes of the grouping from the error bars were then put into a chosen file format (see table 4.1 for sample species) for use in the construction of phylogenetic trees (see Figure 4.2 for the entropy characters as such grouping is an essential pre-requisite for the PAUP* software). The grouping system was therefore designed to conform with the tree building program of PAUP* 4.0 (Swofford 1998) which uses ClustalX (Files created to display trees in such a way that facilitates recognising regions of high similarity of data inputs) to build trees.

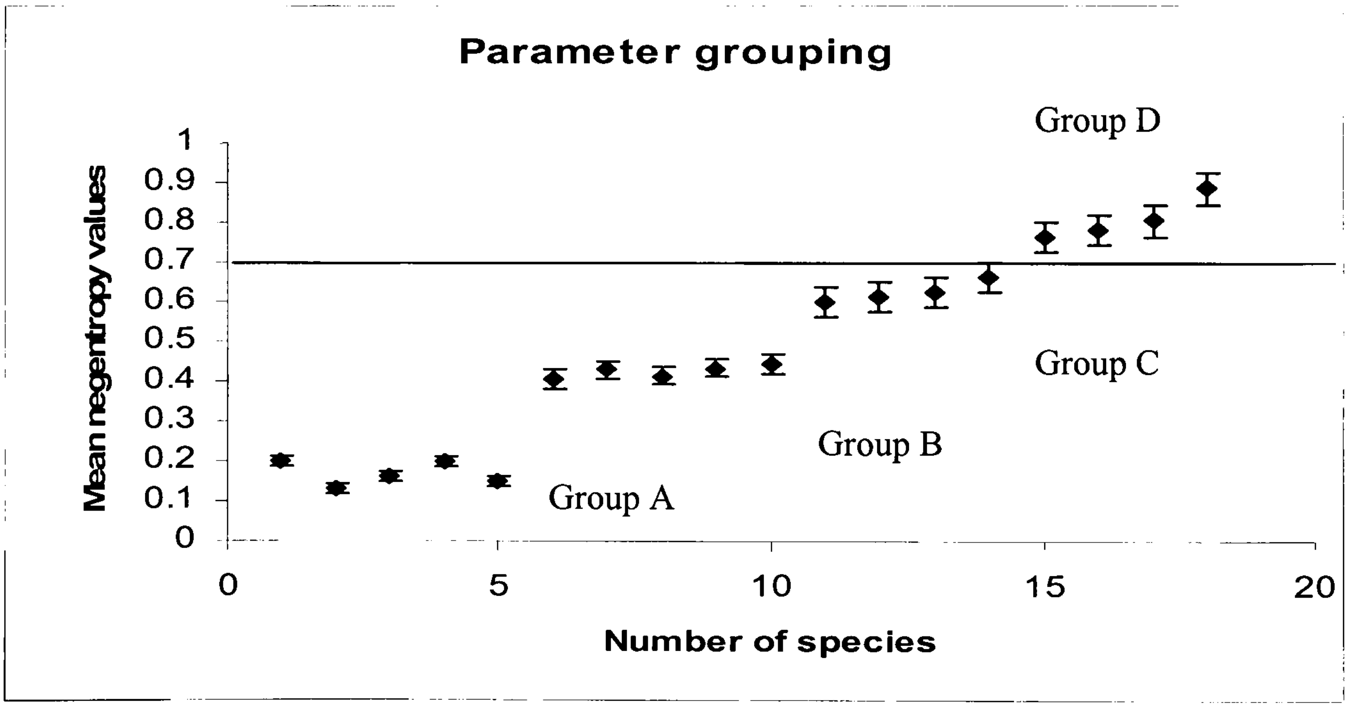


Figure 4.15. Species parameter grouping showing the criteria that were adopted in grouping the mean and standard deviation values of all the parameters derived from the various song types of the recorded species as required by PAUP format for the construction of the phylogenies.

As shown Figure 4.15, groups A, B and C with mean negentropy values of less than 0.66 and not above 0.7 represent simple songs whereas Group D with mean negentropy values of greater that 0.7 represent complex songs. Similar groupings were completed for the data of the other characters for the input file for the construction of the phylogenetic trees.

4.4. RESULTS OF PHYLOGENETIC ANALYSIS

This section presents the results of the phylogenies of the Nectariniidae. The first part represents the phylogeny of the flowerpeckers derived from a combination of calls and simple songs, followed by a tree for the spiderhunters derived from complex songs. The second part describes the three sunbird trees; one for calls only of sunbird species, one for simple songs only of sunbird species and finally the tree for sunbirds with complex songs. The third part is a copy of a comparative DNA phylogenetic tree for the Nectariniidae.

4.4.1. The phylogeny of flowerpeckers

Sonograms of 38 species of flowerpeckers (table 4.5) were analysed using the 10 characters recorded visually from the sonograms and those derived directly from the sonograms (see appendix 2) to construct two phylogenetic trees with essentially the same topography. The results from these trees indicate potential relationships between sister taxa of flowerpeckers that share a common ancestor with each other. These trees do not also explicitly show ancestor-descendant relationships. Whereas the Neighbour-joining tree (Figure 4.16 is an unrooted tree) displays only the relationships among taxa and clades, the Maximum parsimony tree is rooted and therefore displays the outgroup and ingroups of the taxa. The trees have shown a multifurcating scenario or polytomy of the clade *Prionochilus* and further suggest this genus as the outgroup and that it is basal to the flowerpeckers. This is confirmed by the bootstrap (90.5%) confidence level in Figure 4.17 of the Neighbour-joining tree with 5000 replicates.

The trees also unanimously provide evidence of monophyly and close sister relations within *D. t. xanthopygium, D. t. trigonostigma* and *D. t. cinereigulare*, all subspecies of the Orange-bellied Flowerpecker *Dicaeum trigonostigma*, which received (54.4%) bootstrap support (see figure 4.16).

UNROOTED PHYLOGENETIC TREE FOR FLOWERPECKERS

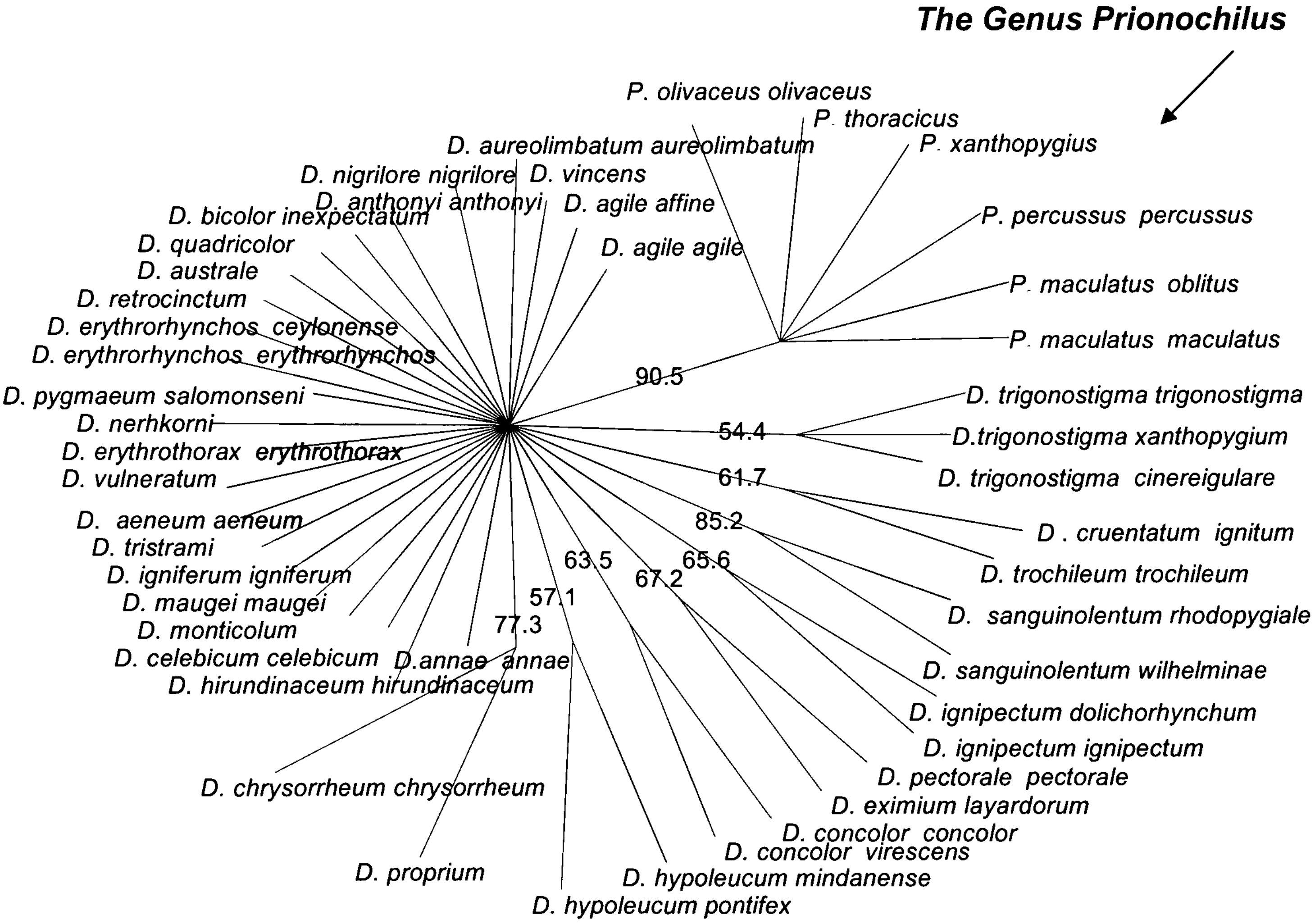


Figure 4.16. An unrooted neighbour-joining phylogenetic song tree of Flowerpeckers of the two genera *Prionochilus* (P.) and *Dicaeum* (D.) based on recordings of 36 species with 50% consensus of 5000 replicates. Values on the tree are bootstrap percentage support for species relationships.

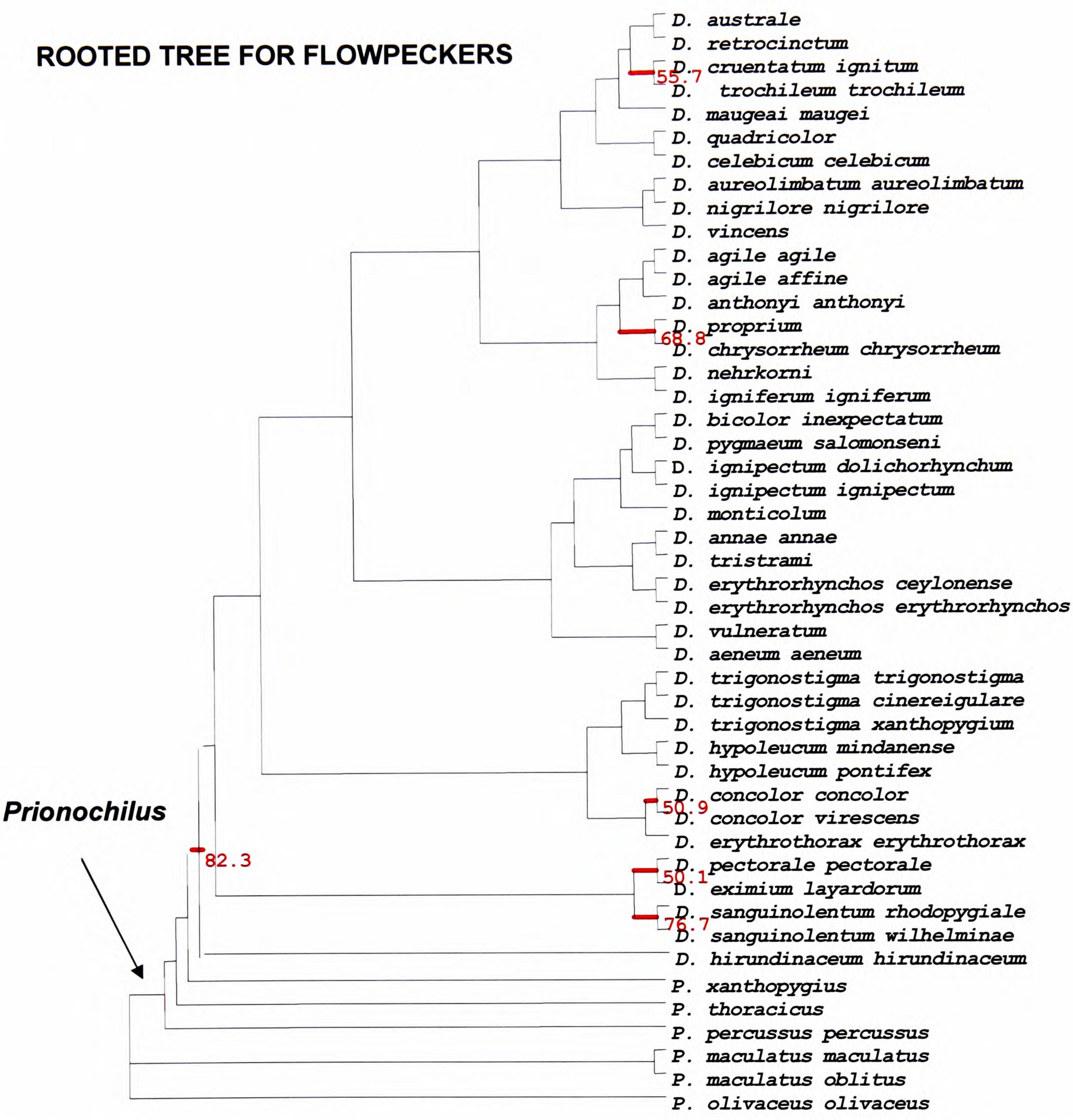


Figure 4.17. Maximum parsimony song tree of Flowerpeckers, calculated with heuristic searching. The bootstrap percentages from 5000 replications for those nodes where the value was greater than 50% are shown in red.

The trees further suggest a number of bifurcating lineages with high bootstrap support. An interesting example is the strong bifurcation of the Whiskered Flowerpecker *Dicaeum proprium* and the subspecies of the Yellow-vented

Flowerpecker *D. c. chrysorrheum* as close relatives as supported by the (77.3%) bootstrap value. The subspecies of the Blood-breasted Flowerpecker *Dicaeum sanguinolentum (D. s. trochileum* and *D. s. wilhelminae*) also received bootstrap support (85.2%) while the Fire-breasted Flowerpecker *Dicaeum ignipectum* received a 65.6% value for the bifurcation of its two subspecies (*D. i. ignipectum* and *D. i. dolichorhynchum,* Figure 4.16). However, the subspecies of the Thick-billed Flowerpecker *Dicaeum agile* (*D. a. agile* and *D. a. affine*) appear to have a weak subspecies relationship both with maximum parsimony and with Neighbour-joining tree construction, with a branching order that seems to suggest that they both relate equally in a clade of other species with less than 50% bootstrap support.

The Neighbour-joining tree also presents the rest of the large clade of species constituting about 70% of the genus *Dicaeum* as homologous taxa. However, the individualistic branching radiations, and unique directional pathways of each taxon with less than 50% bootstrap support of closest sister lineages is concordant with the biogeographical variations and polymorphological characterisations of the species and their subspecies within the Dicaeinii (Mann and Cheke, 2008a).

Table 4.5. The species of Flowerpeckers for which recordings have been obtained and reference codes to the list of recordings and sonograms in Appendices 1 and 2.

Ref. no.	Scientific Name	Common name
2.1	*Prionochilus olivaceus*	Olive-backed Flowerpecker
2.2	*Prionochilus olivaceus*	Olive-backed Flowerpecker
2.3	*Prionochilus maculatus*	Yellow-breasted Flowerpecker
2.4	*Prionochilus maculatus*	Yellow-breasted Flowerpecker
2.5	*Prionochilus percussus*	Crimson-breasted Flowerpecker
2.6	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker
2.7	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker
2.8	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker
2.9	*Prionochilus thoracicus*	Scarlet-breasted Flowerpecker
2.10	*Dicaeum agile*	Thick-billed Flowerpecker
2.11	*Dicaeum agile*	Thick-billed Flowerpecker
2.12	*Dicaeum agile*	Thick-billed Flowerpecker
2.13	*Dicaeum proprium*	Whiskered Flowerpecker
2.14	*Dicaeum proprium*	Whiskered Flowerpecker
2.15	*Dicaeum proprium*	Whiskered Flowerpecker
2.16	*Dicaeum nigrilore*	Olive-capped Flowerpecker
2.17	*Dicaeum nigrilore*	Olive-capped Flowerpecker
2.18	*Dicaeum quadricolor*	Cebu Flowerpecker
2.19	*Dicaeum quadricolor*	Cebu Flowerpecker
2.20	*Dicaeum australe*	Red-striped Flowerpecker
2.21	*Dicaeum australe*	Red-striped Flowerpecker
2.22	*Dicaeum australe*	Red-striped Flowerpecker
2.23	*Dicaeum australe*	Red-striped Flowerpecker
2.24	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker
2.25	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker
2.26	*Dicaeum trigonostigma*	Orange-billed Flowerpecker
2.27	*Dicaeum trigonostigma*	Orange-billed Flowerpecker
2.28	*Dicaeum trigonostigma*	Orange-billed Flowerpecker
2.29	*Dicaeum trigonostigma*	Orange-billed Flowerpecker
2.30	*Dicaeum hypoleucum*	Buzzing Flowerpecker
2.31	*Dicaeum hypoleucum*	Buzzing Flowerpecker
2.32	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker
2.33	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker
2.34	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker

2.35	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker
2.36	*Dicaeum concolor*	Plain Flowerpecker
2.37	*Dicaeum concolor*	Plain Flowerpecker
2.38	*Dicaeum concolor*	Plain Flowerpecker
2.39	*Dicaeum bicolor*	Bicolored Flowerpecker
2.40	*Dicaeum ignipectus*	Fire-breasted Flowerpecker
2.41	*Dicaeum pygmaeum*	Pygmy Flowerpecker
2.42	*Dicaeum eximium*	Red-banded Flowerpecker
2.43	*Dicaeum vincens*	White-throated Flowerpecker
2.44	*Dicaeum aeruginosum*	Striped Flowerpecker
2.45	*Dicaeum celebicum*	Grey-sided Flowerpecker
2.46	*Dicaeum celebicum*	Grey-sided Flowerpecker
2.47	*Dicaeum celebicum*	Grey-sided Flowerpecker
2.48	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker
2.49	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker
2.50	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker
2.51	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker
2.52	*Dicaeum igniferum*	Black-fronted Flowerpecker
2.53	*Dicaeum maugei*	Red-chested Flowerpecker
2.54	*Dicaeum nehrkorni*	Crimson-crowned Flowerpecker
2.55	*Dicaeum pectorale*	Olive-crowned Flowerpecker
2.56	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker
2.57	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker
2.58	*Dicaeum vulneratum*	Ashy Flowerpecker
2.59	*Dicaeum ignipectus*	Fire-breasted Flowerpecker
2.60	*Dicaeum ignipectus*	Fire-breasted Flowerpecker
2.61	*Dicaeum ignipectus*	Fire-breasted Flowerpecker
2.62	*Dicaeum ignipectus*	Fire-breasted Flowerpecker
2.63	*Dicaeum igniferum*	Black-fronted Flowerpecker
2.64	*Dicaeum igniferum*	Black-fronted Flowerpecker
2.65	*Dicaeum annae*	Golden-rumped Flowerpecker
2.66	*Dicaeum chrysorrheum*	Yellow-vented Flowerpecker
2.67	*Dicaeum anthonyi*	Flame-crowned Flowerpecker
2.68	*Dicaeum aeneum*	Midget Flowerpecker
2.69	*Dicaeum tristrami*	Mottled Flowerpecker
2.70	*Dicaeum hirundinacem*	Mistletoebird
2.71	*Dicaeum monticolum*	Black-sided Flowerpecker

4.4.2 The phylogeny of sunbirds and spiderhunters

The phylogenetic constructions of the trees of the sunbirds and spiderhunters were derived from the spectrographic analyses of the sonograms of 258 taxa of sunbirds and spiderhunters (Table 4.6).

Five phylogenetic trees were constructed, one for spiderhunters (a Neighbour-joining tree for complex songs) and four for sunbirds (3 Neighbour-joining trees, one for trills, one for whistles and one for complex songs; and a Bayesian tree for complex songs). The constructions of the sunbird trees were preceded by the categorisation of their vocalisations into calls, simple and complex songs. Though the topologies of the trees are essentially the same, the Neighbour-joining trees are unrooted and appear to present a clearer picture of distant relationships among taxa. Whereas the rooted Bayesian tree provided a more reliable base for predicting the origin of the sunbirds, the Neighbour-joining (NJ) trees were constructed with bootstraps from 2000 replicates and the Bayesian tree was constructed with an Ngen (number of generations for which the analysis was run) setting of 4 million tree generations and as many as 37,500 sample replications for the bootstrap values. The approach seeks the single most likely tree by re-scaling the likelihoods of the tree data to true probabilities and searches for the best set of trees by calculating the posterior probabilities of all the trees and selects the probability that it is the best of the equally likely trees. PAUP version 4.10 software was used for the construction of the phylogenies (Figures 4.18 and 4.19 for NJ trees and 4.20 and 4.21 for MP trees).

4.4.3 Spiderhunters

All the species of the genus *Arachnothera* appear as a monophyletic clade in the Radial Neighbour-joining tree constructed from mainly complex songs of 13 species and including 8 subspecies (Figure 4.18). Whereas all species radiated from the central point, there was further out-branching of nodes indicating some outstanding closeness among some species and the subspecies of others. The Grey-breasted Spiderhunter *Arachnothera modesta* (represented by *A. m. modesta*) and the Streaky-breasted Spiderhunter *Arachnothera affinis* (represented by *A. a. everetti*) emerged as being closely related with 59.6% bootstrap level support. Further significant (92.3% and 68.2%) bootstrap results were scored for the closeness of the three subspecies of the Little Spiderhunter *Arachnothera longirostra, A. l. prillwitzi, A. l. longirostra* and *A. l. buettikoferi.*

Unrooted song tree for complex songs of Spiderhunters (*Arachnothera*)

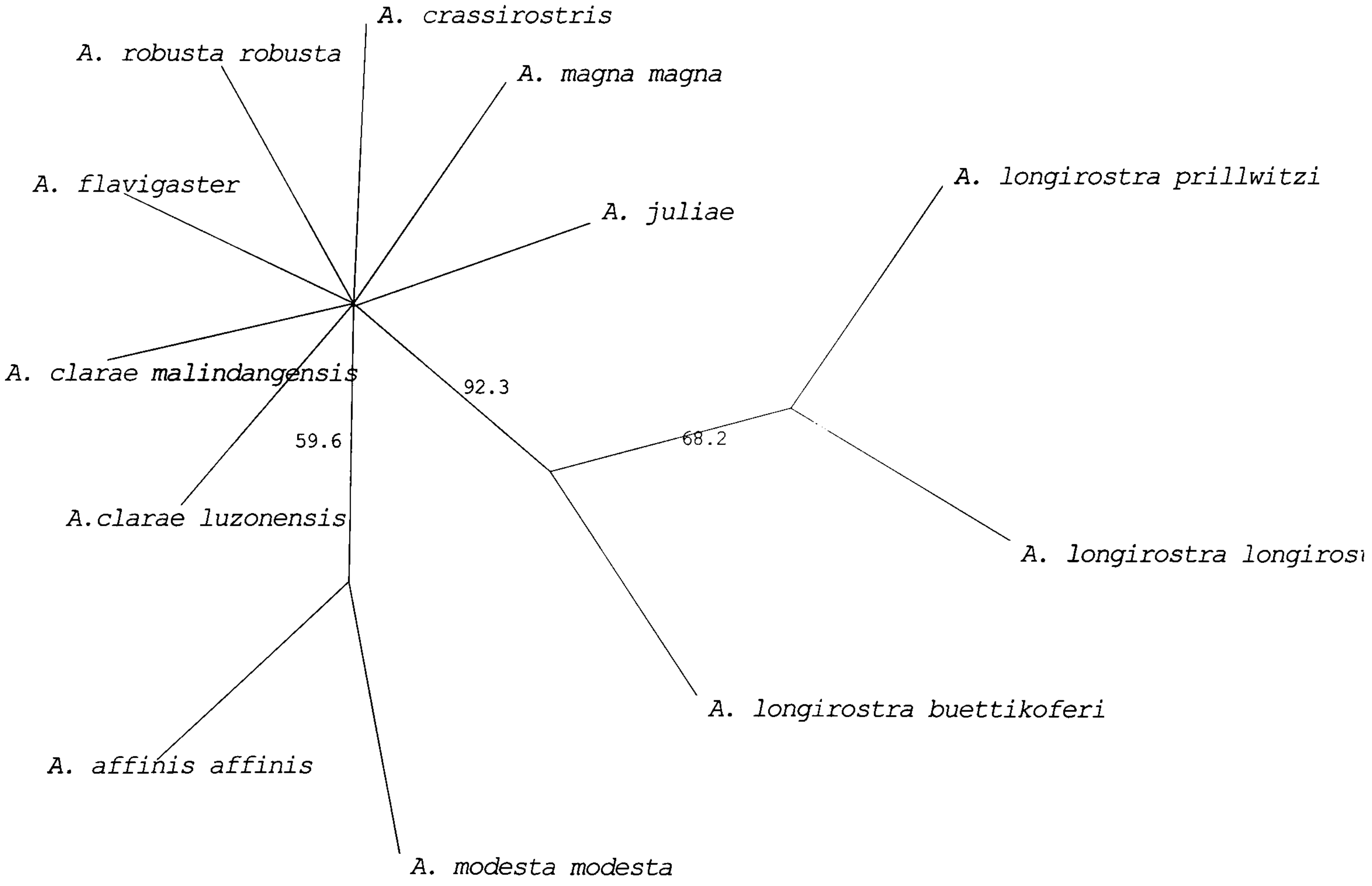


Figure 4.18. The phylogeny and close relationships among spiderhunters derived from their complex songs in a Neighbour-joining tree with 1000 bootstrap repeats.
**A* = *Arachnothera.*

Table 4.6. List of recorded spiderhunters and reference codes as on sonograms (Appendix 3) and list of recordings.

Ref.no.	**Scientific name**	**Common name**
3.117	*Arachnothera longirostra*	Little Spiderhunter
3.118	*Arachnothera longirostra*	Little Spiderhunter
3.119	*Arachnothera longirostra*	Little Spiderhunter
3.120	*Arachnothera longirostra*	Little Spiderhunter
3.121	*Arachnothera longirostra*	Little Spiderhunter
3.122	*Arachnothera longirostra*	Little Spiderhunter
3.123	*Arachnothera longirostra*	Little Spiderhunter
3.124	*Arachnothera longirostra*	Little Spiderhunter
3.125	*Arachnothera robusta*	Long-billed Spiderhunter
3.126	*Arachnothera robusta*	Long-billed Spiderhunter
3.127	*Arachnothera robusta*	Long-billed Spiderhunter
3.128	*Arachnothera flavigaster*	Spectacled Spiderhunter
3.129	*Arachnothera flavigaster*	Spectacled Spiderhunter
3.130	*Arachnothera clarae*	Naked-faced spiderhunter
3.131	*Arachnothera clarae*	Naked-faced spiderhunter
3.132	*Arachnothera clarae*	Naked-faced spiderhunter
3.133	*Arachnothera affinis*	Streaky-breasted Spiderhunter
3.134	*Arachnothera affinis*	Streaky-breasted Spiderhunter
3.135	*Arachnothera affinis*	Streaky-breasted Spiderhunter
3.136	*Arachnothera magna*	Streaked Spiderhunter
3.137	*Arachnothera magna*	Streaked Spiderhunter
3.138	*Arachnothera magna*	Streaked Spiderhunter
3.139	*Arachnothera modesta*	Grey-breasted Spiderhunter
3.140	*Arachnothera crassirostris*	Thick-billed Spiderhunter
3.141	*Arachnothera juliae*	Whitehead's Spiderhunter

4.4.4 Sunbird song trees

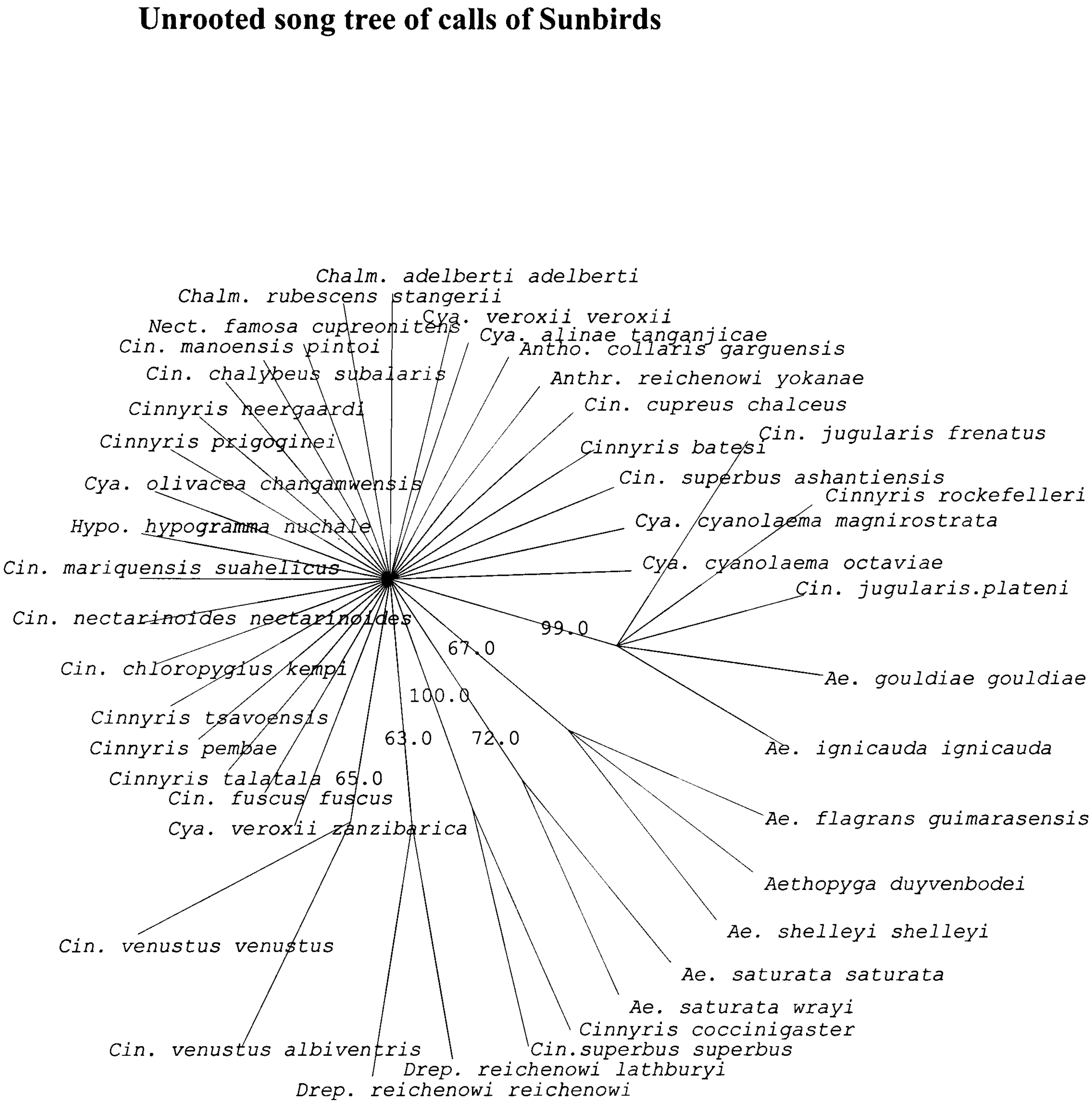


Figure 4.19. The topology of a Neighbour-joining tree with 2000 replicate bootstraps of Sunbird taxa with call vocalisations e.g. Splendid Sunbird *Cinnyris coccinigaster* (**4.120**) and the subspecies (*C. s. superbus*) of the Superb Sunbird *Cinnyris superbus* **(4.131)**. For explanation of abbreviations see tables 4.7 and 4.8.

Table 4.7. Summary of abbreviations of genera on figure 4.19.

Ref.no.	**Generic name**	**Abbreviation**
1	*Hypogramma*	*Hypo.*
2	*Cinnyris*	*Cin.*
3	*Aethopyga*	*Ae.*
4	*Anthreptes*	*Anthr.*
5	*Cyanomitra*	*Cya.*
6	*Chalcomitra*	*Chalm.*
7	*Nectarinia*	*Nec.*
8	*Drepanorhynchus*	*Drep.*

Figure 4.19 suggests close lineages of the three subspecies of the Olive-backed Sunbird *Cinnyris jugularis* (*C. j. frenatus, C. j. infrenatus* and *C. j. plateni*) and strangely with one of the subspecies of the Gould's Sunbird *Aethopyga gouldiae* (*A. g. gouldiae*), Rockefeller's Sunbird *C. rockefelleri,* as well as one subspecies of the Fire-tailed Sunbird *Aethopyga ignicuada* (*A. i. ignicuada*) supported by 99% bootstrap.

The Splendid Sunbird *Cinnyris coccinigaster* and the subspecies *C. s. superbus* of the Superb Sunbird *Cinnyris superbus* are monophyletic with a high bootstrap support of 100%, showing them as the closest relatives amongst the call songsters as shown on the NJ tree. Another significant grouping is the multifurcating of the subspecies of the Flaming Sunbird *Aethopyga flagrans* (*A. f. guimarasensis*), the Elegant Sunbird *Aethopyga duyvenbodei* and the subspecies of the Lovely Sunbird *Aethopyga shelleyi* (*A. s. shelleyi*) supported by a bootstrap of 67%. Also, the two subspecies (*A. s. saturata* and *A. s. wrayi)* of the Black-throated Sunbird *Aethopyga saturata* scored 72% support for their close sister relatedness. The *D. r. lathburyi* and *D. r. reichenowi* subspecies of the Golden-winged Sunbird *Drepanorhynchus reichenowi* scored 63% to confirm their close lineage status. The results further found the two subspecies of the Variable Sunbird *Cinnyris venutus* (*C. v. venustus* and *C. v. albiventris*) as a sister subclade with 65% bootstrap value.

The rest of the species have clustered linearly with multifurcating branches, which is a further indication of the phylogenetic affinity of the relatively closely related taxa with no bootstrap values assigned to the group, and which further suggests that no significance is attached to the particular positioning of the individual species and or subspecies of the various genera.

Table. 4.8 list of Sunbirds with calls vocalisations with reference codes to appendices 1, 3 and 4.

Ref. no.	Scientific name	Common name
3.226	*Hypogramma hypogrammicum nuchale*	Purple-naped Sunbird
3.43	*Cinnyris jugularis frenatus*	Olive-backed Sunbird
3.47	*Cinnyris jugularis plateni*	Olive-backed Sunbird
3.72	*Aethopyga flagrans guimarasensis*	Flaming Sunbird
3.80	*Aethopyga duyvenbodei*	Elegant Sunbird
3.83	*Aethopyga shelleyi shelleyi*	Lovely Sunbird
3.88	*Aethopyga gouldiae gouldiae*	Gould's Sunbird
3.100	*Aethopyga saturata saturata*	Black-throated Sunbird
3.101	*Aethopyga saturata wrayi*	Black-throated Sunbird
3.98	*Aethopyga ignicauda ignicauda*	Fire-tailed Sunbird
4.19	*Antheptes reichenowi yokanae*	Plain-backed Sunbird
4.196	*Anthodiaeta collaris garguensis*	Collared Sunbird
4.167	*Cyanomitra cyanolaema magnirostrata*	Blue-throated brown Sunbird
4.170	*Cyanomitra cyanolaema octaviae*	Blue-throated brown Sunbird
4.164	*Cyanomitra alinae tanganjicae*	Blue-headed Sunbird
4.172	*Cyanomitra olivacea changamwensis*	Oilve Sunbird
4.184	*Cyanomitra veroxii veroxii*	Mouse-collared Sunbird
4.185	*Cyanomitra veroxii zanzibarica*	Mouse-collared Sunbird
4.24	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird
4.26	*Chalcomitra rubescens stangerii*	Green-throated Sunbird
4.210	*Nectarinia famosa cupreonitens*	Malachite Sunbird
4.224	*Drepanorhynchus reichenowi lathburyi*	Golden-winged Sunbird
4.225	*Drepanorhynchus reichenowi reichenowi*	Golden-winged Sunbird
4.60	*Cinnyris chloropygius kempi*	Olive-bellied Sunbird
4.67	*Cinnyris manoensis pintoi*	Miombo Double-Collared Sunbird
4.57	*Cinnyris chalybeus subalaris*	Southern Double-collared Sunbird
4.75	*Cinnyris neergaardi*	Neergaard's Sunbird
4.76	*Cinnyris prigoginei*	Prigogine's Double-collared Sunbird

4.82	*Cinnyrids rockefelleri*	Rockefeller's Sunbird
4.101	*Cinnyris mariquensis suahelicus*	Mariqua Sunbird
4.105	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird
4.92	*Cinnyris tsavoensis*	Tsavo Purple-banded Sunbird
4.116	*Cinnyris pembae*	Pemba Sunbird
4.120	*Cinnyris coccinigaster*	Splendid Sunbird
4.130	*Cinnyris superbus ashantiensis*	Superb Sunbird
4.131	*Cinnyris superbus superbus*	Superb Sunbird
4.138	*Cinnyris talatala*	White-breasted Sunbird
4.144	*Cinnyris venustus albiventris*	Variable Sunbird
4.145	*Cinnyris venustus venustus*	Variable Sunbird
4.133	*Cinnyris fuscus fuscus*	Dusky Sunbird
4.153	*Cinnyris batesi*	Bate's Sunbird
4.161	*Cinnyris cupreus chalceus*	Copper Sunbird

Unrooted song tree of simple songs of Sunbirds

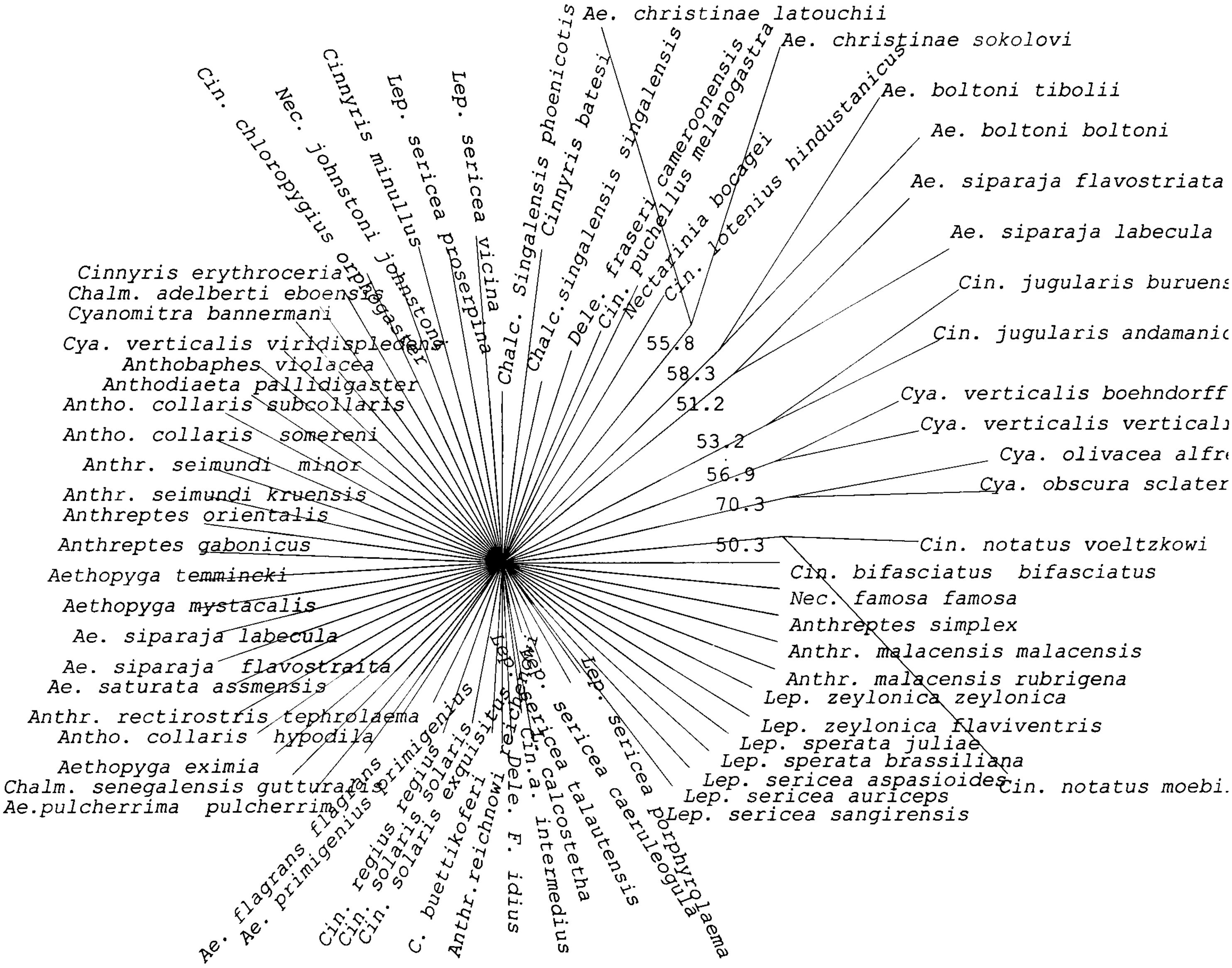


Figure 4.20. A phylogenetic Neighbour-joining tree with 2000 replicate bootstraps of Sunbirds with simple songs e.g. Olive-backed Sunbird *Cinnyris jugularis* (*C. j. andamanicus* (**3.46**) and *C. j. buruensis*, (**3.42**) and the Green-headed Sunbird *Cyanomitra verticalis* (*C. v. boehndorffi* (**4.187**) and *C. v. verticalis* (**4.188**).

For explanation of abbreviations see tables 4.9 and 4.10.

Table 4.9. Abbreviations for genera used in Figure 4.20.

Ref no.	Generic name	Abbreviation
1	*Chalcoparia*	*Chalp.*
2	*Anthreptes*	*Anthr.*
3	*Leptocoma*	*Lep.*
4	*Cinnyris*	*Cin.*
5	*Aethopyga*	*Ae.*
6	*Deleornis*	*Dele.*
7	*Anthodiaeta*	*Antho.*
8	*Cyanomitra*	*Cya.*
9	*Chalcomitra*	*Chalm.*
10	*Nectarinia*	*Nec.*

The phylogenetic tree of the sunbirds with simple songs indicates a high cluster of species in various monophyletic groupings. The Neighbour-joining tree has placed one out of the three subspecies of the Eastern Olive Sunbird *Cyanomitra olivacea alfredi* as a sister taxon to *C. obscura sclateri*, one of the four subspecies of Western Olive Sunbird *Cyanomitra obscura* analysed. This sister clade received 70.3% bootstrap support. Figure 4.20 also presents a number of diverged lineages with average bootstrap support for some sister clades. The subspecies (*A. c. latouchii* and *A .c. sokolovi*) of the Fork-tailed Sunbird *Aethopyga christinae* scored a 55.8%, while the two subspecies of the Apo Sunbird *Aethopyga boltoni* (*A. b. tibolii* and *A. b. boltoni*) received 58.3%. The Crimson Sunbird *Aethopyga siparaja* also scored a 51.2% for the closeness of the two subspecies (*A. s. flavostriata* and *A. s. labecula*). The apparent monophyletic clade of the subspecies of the Olive-backed Sunbird *Cinnyris jugularis* (*C. j. andamanicus* and *C. j. buruensis*) and the Green-headed Sunbird *Cyanomitra verticalis* (*C. v. boehndorffi* and *C. v. verticalis*) received 53.2% and 56.9% respectively. The tree has also derived another grouping of two subspecies (*C. s. apolis* and *C. n. moebii*) as close relatives with 50.3% bootstrap. These subspecies originate from the two separate species the Souimanga Sunbird *Cinnyris souimanga* and the Madagascar Sunbird *Cinnyris notatus*.

Table 4.10. List of recordings for species with simple song vocalisations and reference codes to appendices 1, 3 and 4.

Ref code	Scientific name	Common name
4.8	*Chalcoparia singalensis phoenicotis*	Ruby-cheeked Sunbird
4.9	*Chalcoparia singalensis singalensis*	Ruby-cheeked Sunbird
3.227	*Anthreptes simplex*	Plain Sunbird
3.1	*Anthreptes malacensis malacensis*	Plain-throated Sunbird
3.3	*Anthreptes malacensis rubrigena*	Plain-throated Sunbird
3.10	*Leptocoma zeylonica zeylonica*	Purple-rumped Sunbird
3.14	*Leptocoma zeylonica flaviventris*	Purple-rumped Sunbird
3.24	*Leptocoma sperata juliae*	Purple-throated Sunbird
3.25	*Leptocoma sperata brassiliana*	Purple-throated Sunbird
3.26	*Leptocoma sericea aspasioides*	Black Sunbird
3.27	*Leptocoma sericea auriceps*	Black Sunbird
3.28	*Leptocoma sericea sangirensis*	Black Sunbird
3.29	*Leptocoma sericea caeruleogula*	Black Sunbird
3.30	*Leptocoma sericea talautensis*	Black Sunbird
3.31	*Leptocoma sericea proserpina*	Black Sunbird
3.32	*Leptocoma sericea vicina*	Black Sunbird
3.33	*Leptocoma calcostetha*	Copper-throated Sunbird
4.71	*Cinnyris minullus*	Tiny Sunbird
4.83	*Cinnyris pulchellus melanogastra*	Beautiful Sunbird
4.88	*Cinnyris erythroceria*	Red-chested Sunbird
4.91	*Cinnyris bifasciatus bifasciatus*	Purple-banded Sunbird
4.154	*Cinnyris batesi*	Bate's Sunbird
3.59	*Cinnyris asiaticus intermedius*	Purple Sunbird
3.46	*Cinnyris jugularis andamanicus*	Olive-backed Sunbird
3.48	*Cinnyris jugularis buruensis*	Olive-backed Sunbird
3.54	*Cinnyris buettikoferi*	Apricot-breasted Sunbird
3.55	*Cinnyris solaris exquisitus*	Flame-breasted Sunbird
3.56	*Cinnyris solaris solaris*	Flame-breasted Sunbird
4.16	*Cinnyris notatus moebii*	Madagascar Sunbird
4.20	*Cinnyris notatus voeltzkowi*	Madagascar Sunbird
3.39	*Cinnyris lotenius hindustanicus*	Long-billed Sunbird
3.67	*Aethopyga primigenius primigenius*	Grey-hooded Sunbird
3.69	*Aethopyga boltoni boltoni*	Apo Sunbird
3.70	*Aethopyga boltoni tibolii*	Apo Sunbird

3.72	*Aethopyga flagrans flagrans*	Flaming Sunbird
3.74	*Aethopyga pulcherrima pulcherrima*	Metallic-winged Sunbird
3.96	*Aethopyga eximia*	White-flanked Sunbird
3.98	*Aethopyga christinae latouchii*	Fork-tailed Sunbird
3.97	*Aethopyga christinae sokolovi*	Fork-tailed Sunbird
3.100	*Aethopyga saturata assamensis*	Black-throated Sunbird
3.108	*Aethopyga siparaja flavostriata*	Crimson Sunbird
3.109	*Aethopyga siparaja labecula*	Crimson Sunbird
3.110	*Aethopyga mystacalis*	Javan Sunbird
3.112	*Aethopyga temmincki*	Temminck's Sunbird
4.191	*Deleornis fraseri idius*	Scarlet-tufted Sunbird
4.19	*Anthreptes reichenowi reichenowi*	Plain-backed Sunbird
4.10	*Anthreptes gabonicus*	Mouse-brown Sunbird
4.14	*Anthreptes orientalis*	Kenya Violet-backed Sunbird
4.21	*Anthreptes seimundi kruensis*	Little-green Sunbird
4.22	*Anthreptes seimundi minor*	Little-green Sunbird
4.15	*Anthreptes rectirostris tephrolaema*	Green Sunbird
4.199	*Anthodiaeta collaris hypodila*	Collared Sunbird
4.200	*Anthodiaeta collaris somereni*	Collared Sunbird
4.202	*Anthodiaeta collaris subcollaris*	Collared Sunbird
4.203	*Anthodiaeta pallidigaster*	Amani Sunbird
4.6	*Anthobaphees violacea*	Orange-breasted Sunbird
4.187	*Cyanomitra verticalis boehndorffi*	Green-headed Sunbird
4.188	*Cyanomitra verticalis verticalis*	Green-headed Sunbird
4.189	*Cyanomitra verticalis viridispledens*	Green-headed Sunbird
4.166	*Cyanomitra bannermani*	Bannerman's Sunbird
4.179	*Cyanomitra olivacea alfredi*	Eastern Olive Sunbird
4.172	*Cyanomitra obscura scateri*	Western Olive Sunbird
4.24	*Chalcomitra adelberti eboensis*	Buff-throated Sunbird
4.46	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird
4.219	*Nectarinia bocagei*	Bocage's Sunbird
4.210	*Nectarinia famosa famosa*	Malachite Sunbird
4.214	*Nectarinia johnstoni johnstoni*	Red-tufted Sunbird
3.62	*Cinnyris chloropygius orphogaster*	Olive-bellied Sunbird

Unrooted song tree for complex songs (SUNBIRDS)

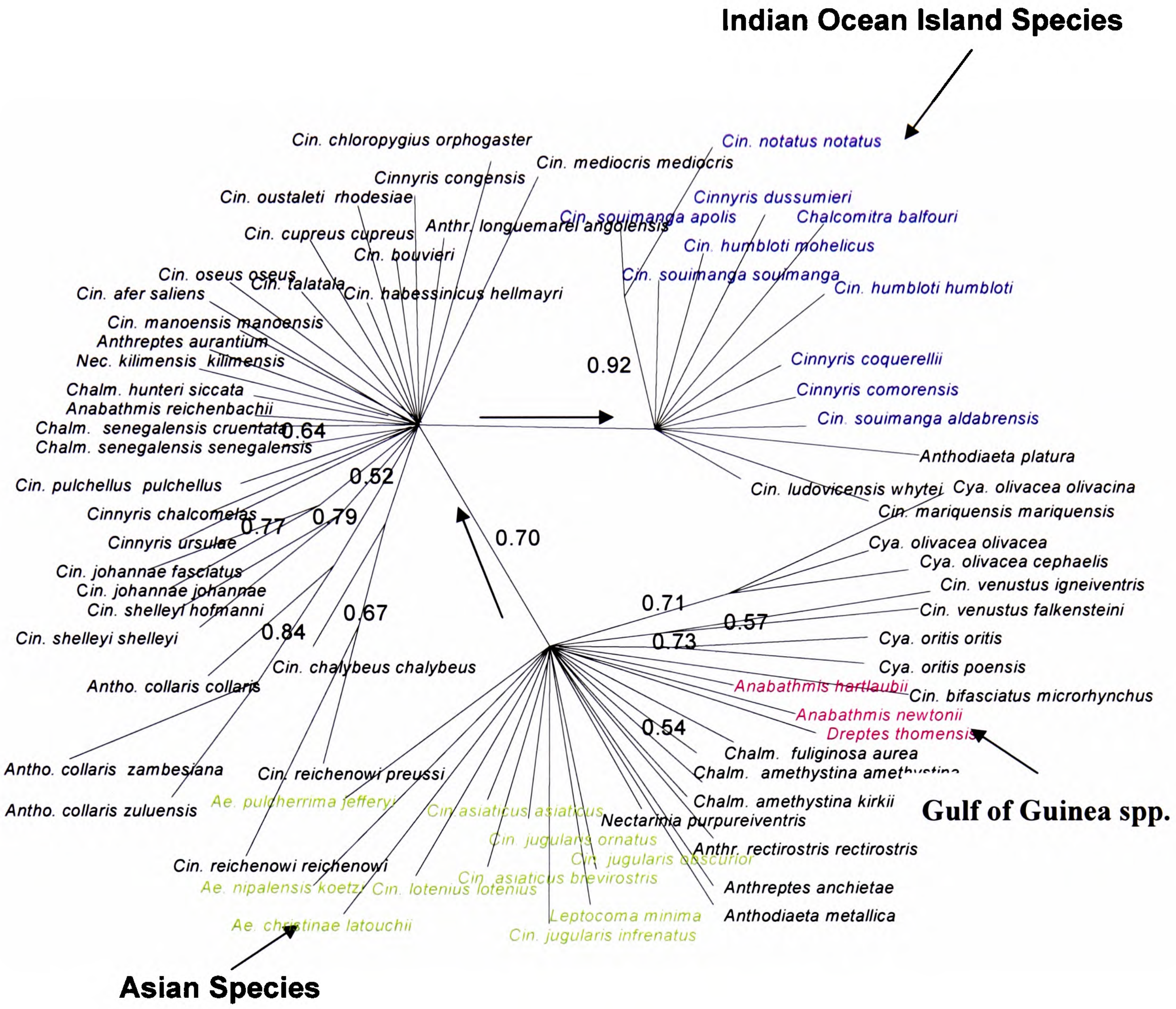


Figure 4.21. A Bayesian phylogenetic tree with Ngen 4million and 37,500 sample bootstrap of complex songs of sunbirds. For explanation of abbreviations see tables 4.11 and 4.12. Numbers refer to bootstrap values.

Table 4.11. Abbreviations for Sunbird species with complex vocalisations.

Ref.no.	Generic name	Abbreviation
1	*Leptocoma*	*Lep.*
2	*Cinnyris*	*Cin.*
3	*Aethopyga*	*Ae.*
4	*Anthreptes*	*Anthr.*
5	*Anthodiaeta*	*Antho.*
6	*Anabathmis*	*Anab.*
7	*Dreptes*	*Drept.*
8	*Cyanomitra*	*Cya.*
9	*Chalcomitra*	*Chalm.*
10	*Nectarinia*	*Nec.*

Of all the songs analysed of Asian sunbirds and including subspecies, only 10 (13.2%) were complex songs whereas 52 (72.2%) of the African sunbirds and subspecies included complex types. For the Indian Ocean Island species and including subspecies 11 recordings were analysed and 10 (90.9%) were of complex songs. This trend has been further replicated by the Bayesian song tree (Figure 4.21).

Figure 4.22 revealed three main monophyletic clades of sunbirds with multifurcating branching supported by their bootstrap values. The first distinct clade represents an ingroup of African sunbirds composed mainly of species with very complex songs and supported by 70% bootstrap confidence. Within the clade are species exhibiting close sister relationships and these include the two subspecies of the Scarlet-chested Sunbird *Chalcomitra senegalensis* (*C. s. cruentata* and *C. s. senegalensis*) supported by 64% bootstrap. The subspecies of the Johanna's Sunbird *Cinnyris johannae* (*C. j. fasciatus* and *C. j. johannae*) and Shelley's Sunbird *Cinnyris shelleyi* (*C. s. hofmanni* and *C. s. shelleyi*) received 77% and 79% bootstrap support, respectively. The clades further suggest a close sister relationship of the subspecies of the Collared Sunbird *Anthodiaeta collaris* (*A. c. collaris, A. c. zambesiana* and *A. c. zuluensis*) with 84% support, and one of the subspecies of the Southern Double-collared *Cinnyris chalybeus* (*C. c. chalybeus*) and two subspecies of the Northern Double-collared Sunbird *Cinnyris reichenowi* (*C .r. preussi* and

C. r. reichenowi) also receiving 67% bootstrap level support.

The second clade of ingroup species with multifurcating radians is composed mainly of the Indian Ocean Island species supported by a 92% bootstrap value. These include the Madagascar Sunbird *Cinnyris notatus* (*C. n. notatus*), Souimanga Sunbird *Cinnyris souimanga* (*C. s. souimanga* and *C. s. aldabrensis*), the Humblot's Sunbird *Cinnyris humbloti* (*C. h. humbloti*), Anjouan Sunbird *Cinnyris comorensis*, Mayotte Sunbird *Cinnyris conquerellii*, the Seychelles Sunbird *Cinnyris dussumieri* and some African species with very complex songs: the Pygmy Sunbird *Anthodiaeta platura* and the Mariqua Sunbird *Cinnyris mariquensis* (*C. m. mariquensis*) and a subspecies of Montane Double-collared Sunbird *Cinnyris ludovicensis* (*C. l. whytei*).

The third clade and outgroup is composed of a mix of species from Africa and Asia. The Asian sunbirds constituted the least of about 13.8% of the complex songs and are represented at the base of the tree with the very basic repertoire size of all the species with complex songs supported by 70% bootstrap confidence.

Also within the clade are species depicting the status of close sister relatedness. The two subspecies of the Amethyst Sunbird *Chalcomitra amethystina* (*C. a. amethystina* and *C .a. kirkii*) and the subspecies of the Cameroon Sunbird *Cyanomitra oritis* (*C. o. oritis* and *C. o. poensis*) scored 54% and 73% closeness reliability support respectively. The Variable Sunbird *Cinnyris venustus* had two of its subspecies (*C. v. igneiventris* and *C. v. falkensteini*) supported by a 57% bootstrap value.

There was also a further multifurcating radiation of the subspecies of the Eastern Olive Sunbird *Cyanomitra olivacea* (*C. o. olivacina* and *C. o. olivacea*) and one of the subspecies of the Western Olive Sunbird *Cyanomitra obscura* (*C. o. cephaelis*) as closest sister species with 71% bootstrap support.

The results from the phylogenetic song trees, the rooted Neighbour-joining tree and the Bayesian tree, illustrate the descendant relationships within sunbirds (Figure 4.22) and the relationships among flowerpeckers, spiderhunters and sunbirds (Figure 4.23). The Neighbour-joining tree (Figure 4.22) is rooted and displays the outgroup state representing the Asian sunbirds at the base of the tree as the primitive group among sunbirds. The position of the group is supported by a 70% bootstrap value and includes, for example, the Metallic-winged Sunbird *Aethopyga pulcherrima*, Green-tailed Sunbird *Aethopyga nipalensis koetzi* etc.

The ingroup states, representing the derived group, comprises the mainland African group of sunbirds and include among others the Mariqua Sunbird *Cinnyris mariquensis*, Pygmy Sunbird *Anthodiaeta platura* etc. The Gulf of Guinea group of species with a 71% bootstrap support includes the Sao Tome Sunbird *Dreptes thomensis*, Newton's Sunbird *Anabathmis newtoni* etc. The Indian Ocean group of sunbirds supported by 92% bootstrap, includes Souimanga Sunbird *Cinnyris souimanga souimanga*, Anjouan Sunbird *Cinnyris comorensis* etc.

Rooted Song tree for complex songs (SUNBIRDS)

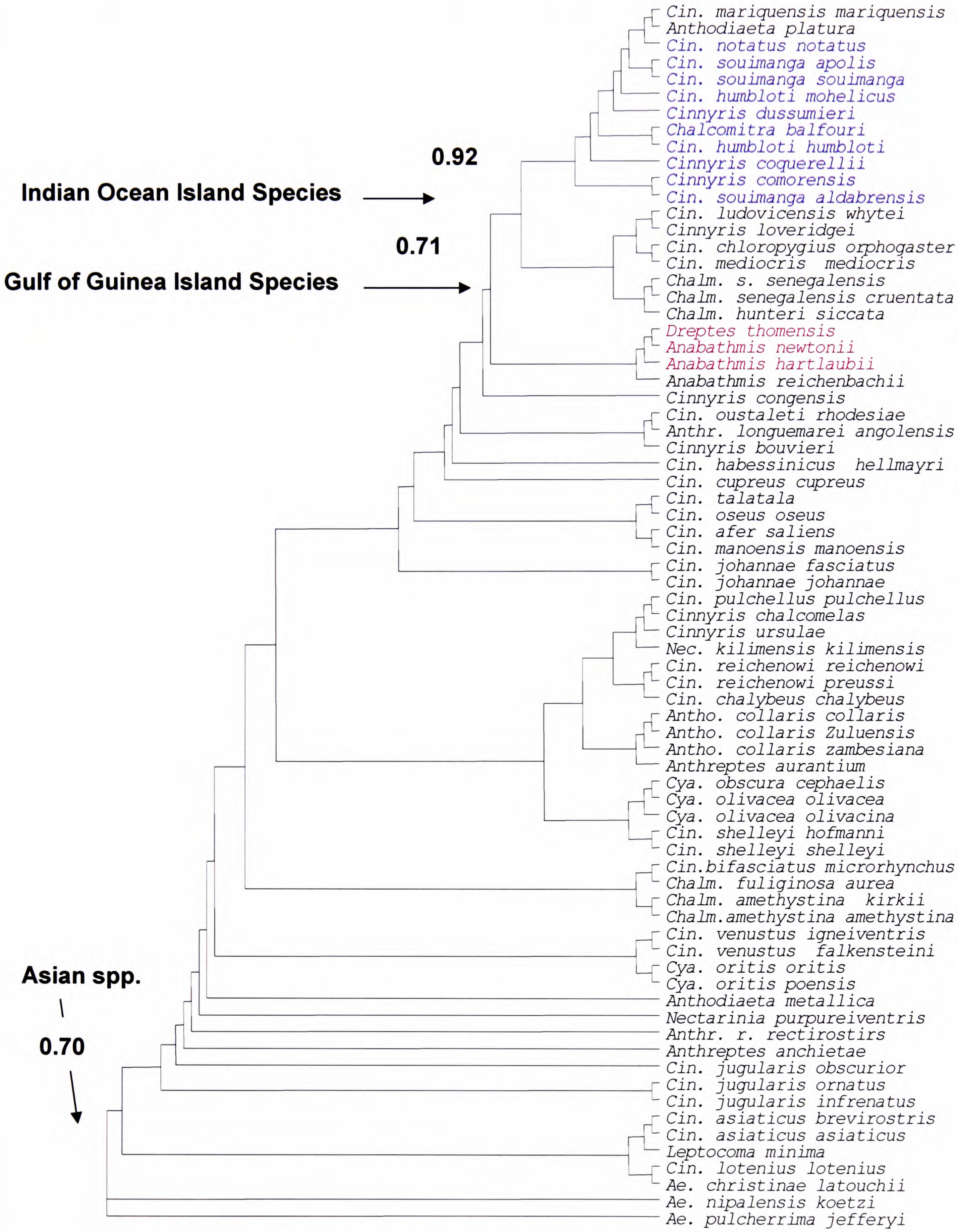


Figure 4.22. A rooted Neighbour joining phylogenetic song tree from 5 million generations and bootstraps for complex songs of sunbirds.

Rooted song tree for flowerpeckers, spiderhunters and sunbirds.

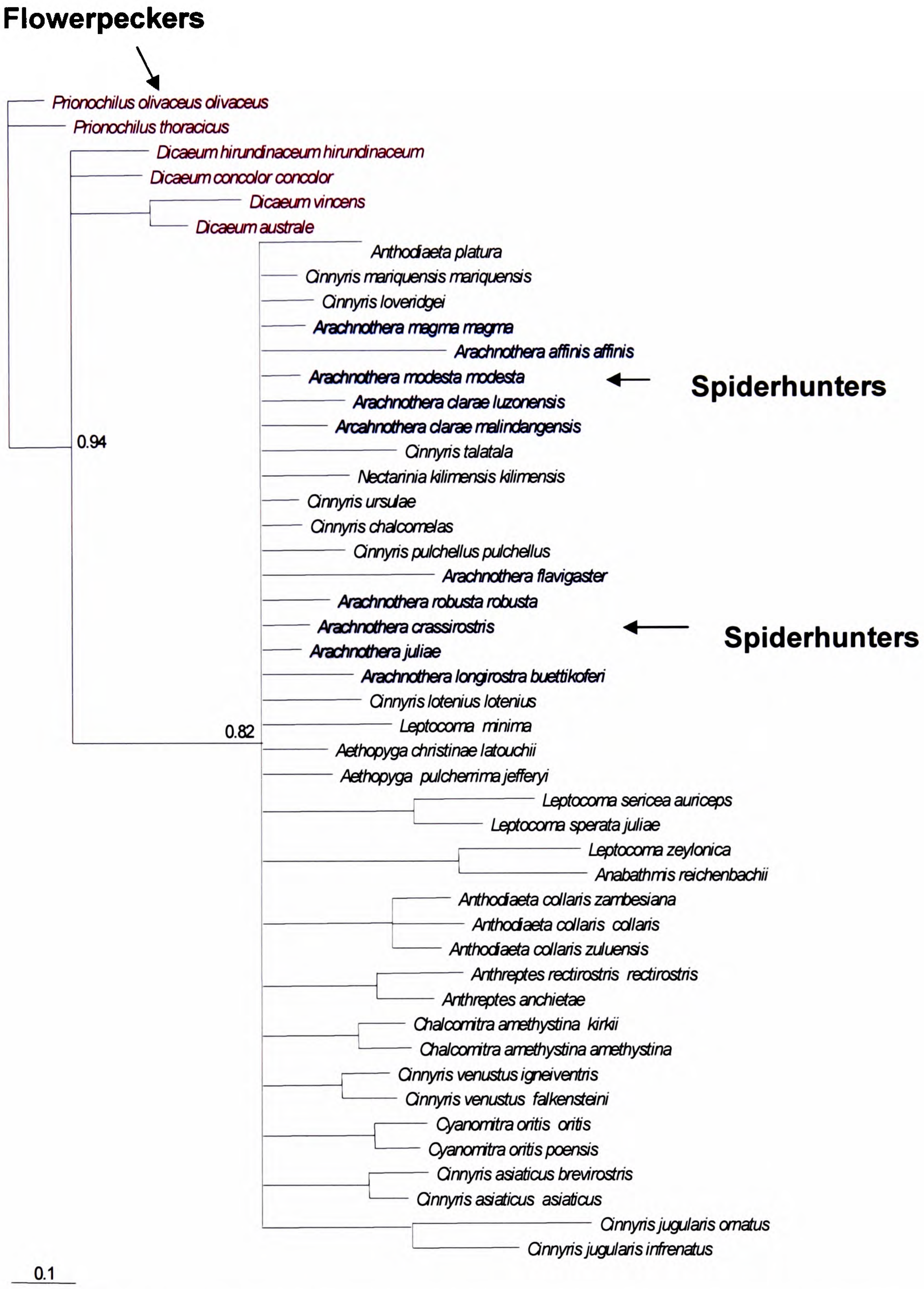


Figure 4.23. A Bayesian phylogenetic song tree derived from one million generations resulting from 2000 trees credited by bootstrap values in support of the three groupings (flowerpeckers, spiderhunters and sunbirds). Song tree from randomly selected songs used to derive the relationships between flowerpeckers, sunbirds and spiderhunters.

The tree (Figure 4.23) provides evidence of monophyletic and close relations between the sunbirds and the spiderhunters, separated from both each other (mostly) and from the flowerpeckers. The latter comprise an outgroup with *Prionochilus* (94% bootstrap) basal to *Dicaeum*. However, the flowerpeckers have also been confirmed as closely related to sunbirds and spiderhunters and this is supported by an 82% bootstrap confidence.

Table 4.12. Reference coding for sunbirds with complex songs.

Ref.code.	**Scientific name**	**Common name**
3.22	*Leptocoma minima*	Crimson-backed Sunbird
3.64	*Cinnyris asiaticus asiaticus*	Purple Sunbird
3.59	*Cinnyris asiaticus brevirostris*	Purple Sunbird
3.45	*Cinnyris jugularis ornatus*	Olive-backed Sunbird
3.52	*Cinnyris jugularis obscurior*	Olive-backed Sunbird
3.49	*Cinnyris jugularis infrenatus*	Olive-backed Sunbird
5.21	*Cinnyris souimanga aldabrensis*	Souimanga Sunbird
5.23	*Cinnyris souimanga apolis*	Souimanga Sunbird
5.25	*Cinnyris souimanga souimanga*	Souimanga Sunbird
5.28	*Cinnyris humbloti mohelicus*	Humblot's Sunbird
5.29	*Cinnyris humbloti humbloti*	Humblot's Sunbird
3.39	*Cinnyris lotenius lotenius*	Long-billed Sunbird
3.76	*Aethopyga pulcherrima jefferyi*	Metallic-winged Sunbird
3.93	*Aethopyga nipalensis koetzi*	Green-tailed Sunbird
3.98	*Aethopyga christinae latouchii*	Fork-tailed Sunbird
4.8	*Anthreptes anchietae*	Anchieta's Sunbird
4.13	*Anthreptes longuemarei angolensis*	Western Violet-backed Sunbird
4.20	*Anthreptes aurantium*	Violet-tailed Sunbird
4.18	*Anthreptes rectirostris rectirostris*	Green Sunbird
4.194	*Anthodiaeta collaris collaris*	Collared Sunbird
4.198	*Anthodiaeta collaris zambesiana*	Collared Sunbird
4.197	*Anthodiaeta collaris zuluensis*	Collared Sunbird
4.08	*Anthodiaeta metallica*	Nile Valley Sunbird
4.207	*Anthodiaeta platura*	Pygmy Sunbird
4.5	*Anabathmis reichenbachii*	Reichenbach's Sunbird
4.3	*Anabathmis hartlaubii*	Principe Sunbird
4.1	*Anabathmis newtonii*	Newton's Sunbird

4.11	*Dreptes thomensis*	Sao Tome Sunbird
4.180	*Cyanomitra oritis oritis*	Cameroon Sunbird
4.183	*Cyanomitra oritis poensis*	Cameroon Sunbird
4.174	*Cyanomitra olivacea changamwensis*	Eastern Olive Sunbird
4.178	*Cyanomitra olivacea olivacina*	Eastern Olive Sunbird
4.173	*Cyanomitra obscura cephaelis*	Western Olive Sunbird
4.35	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird
4.28	*Chalcomitra amethystina amethystina*	Amethyst Sunbird
4.31	*Chalcomitra amethystina kirkii*	Amethyst Sunbird
4.48	*Chalcomitra senegalensis cruentata*	Scarlet-chested Sunbird
4.46	*Chalcomitra senegalensis senegalensis*	Scarlet-chested Sunbird
4.39	*Chalcomitra hunteri siccata*	Hunter's Sunbird
4.50	*Chalcomitra balfouri*	Socotra Sunbird
4.220	*Nectarinia purpureiventris*	Purple-breasted Sunbird
4.216	*Nectarinia kilimensis arturi*	Bronze Sunbird
4.218	*Nectarinia kilimensis kilimensis*	Bronze Sunbird
4.59	*Cinnyris chloropygius orphogaster*	Olive-bellied Sunbird
4.67	*Cinnyris manoensis manoensis*	Miombo Double-collared Sunbird
4.58	*Cinnyris chalybeus chalybeus*	Southern Double-collared Sunbird
4.56	*Cinnyris ludovicensis whytei*	Montane Double-collared Sunbird
4.77	*Cinnyris reichenowi preussi*	Northern Double-collared Sunbird
4.80	*Cinnyris reichenowi reichenowi*	Northern Double-collared Sunbird
4.51	*Cinnyris afer saliens*	Greater Double-collared Sunbird
4.53	*Cinnyris mediocris mediocris*	Eastern Double-collared Sunbird
4.64	*Cinnyris loveridgei*	Loveridge's Sunbird
4.86	*Cinnyris pulchellus pulchellus*	Beautiful Sunbird
4.101	*Cinnyris mariquensis mariquensis*	Mariqua Sunbird
4.119	*Cinnyris shelleyi hofmanni*	Shelley's Sunbird
4.118	*Cinnyris shelleyi shelleyi*	Shelley's Sunbird
4.87	*Cinnyris congensis*	Congo Sunbird
4.91	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird
4.113	*Cinnyris chalcomelas*	Kenya Violet-breasted Sunbird
4.115	*Cinnyris bouvieri*	Orange-tufted Sunbird
4.112	*Cinnyris oseus oseus*	Palestine Sunbird
4.100	*Cinnyris habessinicus hellmayri*	Shining Sunbird
4.125	*Cinnyris johannae fasciatus*	Johanna's Sunbird
4.127	*Cinnyris johannae johannae*	Johanna's Sunbird
4.136	*Cinnyris oustaleti rhodesiae*	Oustalet's Sunbird
4.138	*Cinnyris talatala*	White-breasted Sunbird

4.145	*Cinnyris venustus falkensteini*	Variable Sunbird
4.151	*Cinnyris venustus venustus*	Variable Sunbird
4.159	*Cinnyris ursulae*	Ursula's Sunbird
4.162	*Cinnyris cupreus cupreus*	Copper Sunbird
5.17	*Cinnyris notatus notatus*	Madagascar Sunbird
5.13	*Cinnyris dussumieri*	Seychelles Sunbird

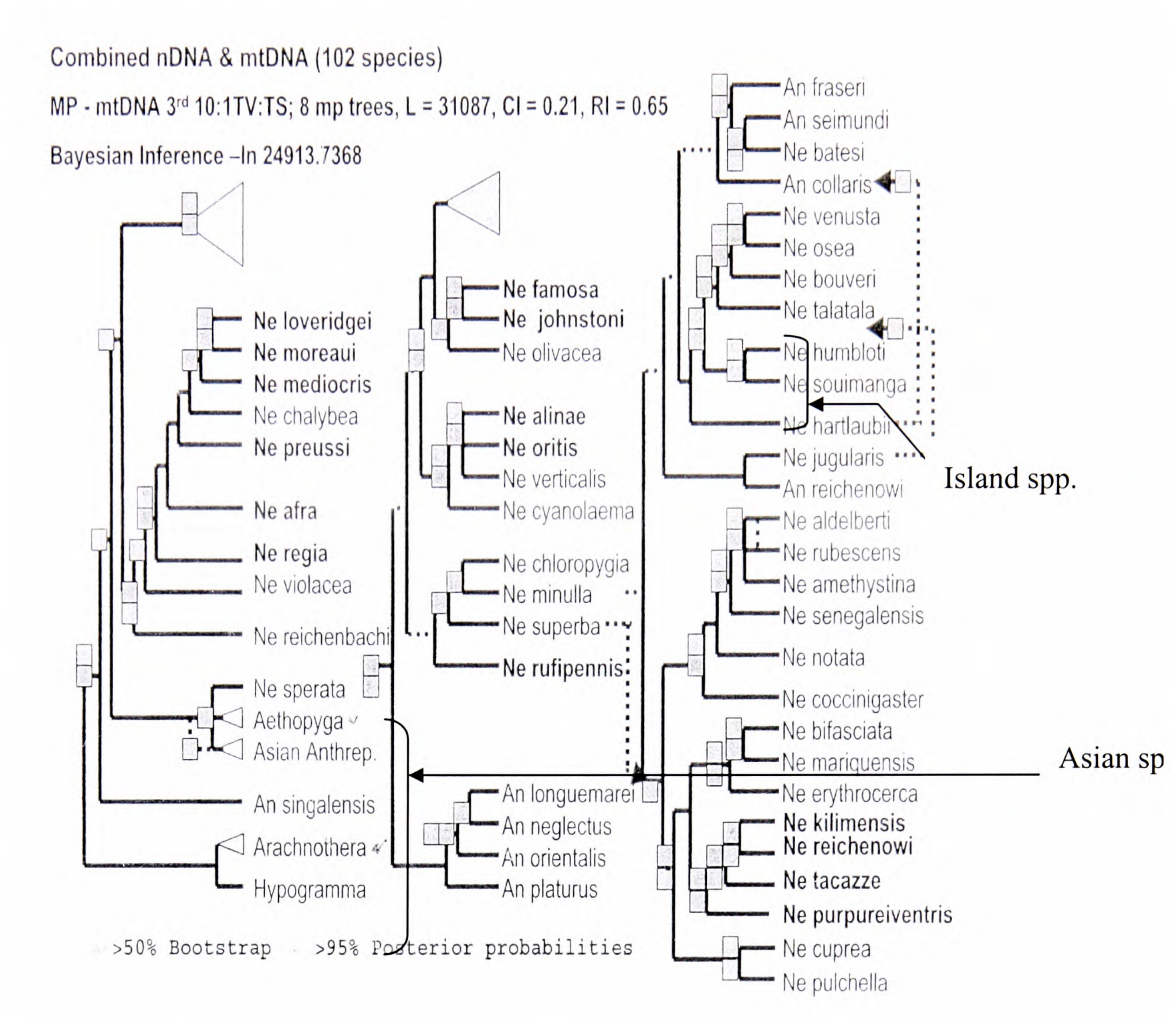


Figure 4.24. A sample DNA phylogenetic tree for sunbirds and spiderhunters (Bowie 2003). Note that Bowie used an old classification system, treating many species now included within *Cinnyris* as *Nectarinia*.

The Bayesian tree of Bowie (2003, Figure 4.24) comprising 102 species of the Nectariniidae indicates clearly that the 6 taxa (*Nectarinia sperata*, *Aethopyga spp.*, Asian *Anthreptes*, *Anthreptes singalensis*, *Aracthnothera* and *Hypogramma*) comprise the outgroup or basal clade of the taxa. The island species (listed here as *Nectarinia humbloti, Nectarinia souimanga, Nectarinia jugularis* and *Nectarinia notata*, equivalent to the biogeographic classification used in the rest of this thesis) are among the derived or ingroup African species.

4.5. DISCUSSION

The discussion in this chapter is divided into three main parts. The first part discusses the approaches used in song characterisation and the subsequent results of the acoustic analysis. The second part introduces the concept of evolution and tree topology, presenting an overview of the basics and understanding of phylogeny. The final section discusses the phylogenies of the Nectariniidae derived from their vocalisations and a summary of findings.

4.5.1. Vocalisation

Most authors have attempted to quantify and draw a distinction between songs and calls of birds. However, the approaches adopted vary considerably with some authorities adopting the voice and visual interpretation approach (Lohr *et al.*, 2003) or length of song (e.g. Ehrlich *et al.*, 1998) while others consider longer songs as more complex than calls. Others such as Howell (1994) based their distinction on the functional approach and their analysis on the content of the messages carried by the vocalisations as for example alarm, alert and feeding calls or territorial songs. For others, it is the way and manner that songs are constructed, arranged and structured. The latter technique also bases its song selection criteria on (a) whether the notes were simple and single repetitive notes or a mix of complicated syllabic notes and phrases or (b) whether the vocalisations were diverse, beautiful, melodious, musical or attractive (Rasmussen and Anderton, 2005; Mindlin and Laje, 2006).

The study applied the mixed methods approach, which is a combination of the visual inspection and scoring of species vocalisations from sonographic printouts and the automated derivation of quantitative values from spectrographs. The study derived two thresholds of (entropy 0.3 and 0.34) from the both the visual and the automated derivation techniques and used these to objectively separate calls from songs and simple songs from complex songs.

In addition, the results of this study have further provided insights based on the high number of species and magnitude of song characters analysed

(17,854) and the variances that exist in the entire Nectariniidae at the genus level (see Chapter 3, Table 3.1 and 3.2). The variations between calls, simple and complex songs in terms of the difference in note types and note frequency fluctuations were minimal within the taxa.

A conservative view of the sonograms (see Appendices 2, 3, 4 and 5) and the results section of this chapter indicate a general monophyletic acoustic structure for the entire Nectariniidae. However, even within species there is an appreciable degree of acoustic variation of the elements and structure of the song types, and among allopatric groupings. Some authors (Thorpe, 1958; Slater *et al.,* 1981) have argued that although the structural variation of song types between conspecifics might be difficult to interpret, the meaning of the signal could still be significantly conveyed to the intended receivers and could maintain the purpose and function of the vocalisation. The evidence of allopatric variation within sunbird species (Asian, African and Island) is suggestive of the influence that ecological differences can impose on the song structure and divergence of the vocal characters of songbirds (Irwin, 2000). The overall lower intraspecific variation compared with song types of generic groups confirms the importance of analysing song variation at both levels (Leitao *et al.*, 2004).

In general, the vocalisations within the flowerpeckers show less variation among taxa and comprise the most basic, simple and mostly stereotypic calls and simple songs. This poses some implications for interpreting the vocalisations of the flowerpeckers; firstly, most flowerpeckers are known to dwell at the top of the canopy of the forest and this could expose the signal transmission of most members of the group to the attenuation effect (Waser and Waser, 1977) and could account for the simplistic nature of their utterances. The second is an indication that the songs of the genus may have survived unchanged for a long period. It is, however, unclear whether this phenomenon is a result of geographical or cultural isolation that may have led to minimal introduction of different song types by immigrant or neighbouring species (Petrinovich, 1981).

Calls are often regarded as single song repertoires in the primitive state and constitute a rapid repetition of the units of the same elements of a song (Price and Lanyon, 2002), while simple songs consist of longer pure notes or acoustic units that often appear horizontal on sonograms with a more or less stable pitch. Simple songs are usually associated with a vibration frequency that is an integral multiple of the fundamental frequency of a tone and of smaller amplitude to the fundamental frequency (harmonics) (Rasmussen and Anderton, 2005).

The *Prionochilus* species displayed the most repetitive and stereotypic song types. Thus, the *"tri'ti'ti'ti"* calls of the Olive-backed Flowerpecker *Prionochilus olivaceus* are deemed to be the most primitive vocalisation within the Flowerpeckers, consistent with the view based on morphotaxonomy that the *Prionochilus* flowerpeckers are the most basal members of the group (Cheke and Mann, 2001). The 24 *Dicaeum* species exhibit a bit more variation in their song types than the *Prionochilus* species and show marked differences in their vocalisations (see Figure 4.16).

However, sunbirds and spiderhunters appear to display a higher variation of song attributes than the flowerpeckers uttering a combination of calls, simple and complex songs and including very large repertoires in most species. The elaborate songs of some sunbirds include a mix of stereotyped and complex syllables. Taxa in some generic groupings, for example the Cameroon Sunbird *Cyanomitra oritis oritis* and the Green-throated Sunbird *Chalcomitra rubescens crossensis*, utter a combination of calls and complex syllables in their song repertoires (Appendix 4). This is perhaps consistent with the view held by Cheke and Mann (2001) that the song types of members of *Chalcomitra* spp. and *Cyanomitra* spp. are fairly similar. The *Cinnyris* spp. exhibit much more elaborate song types with some taxa such as the Olive-bellied Sunbird *Cinnyris chloropygius orphogaster*, the Greater Double-collared Sunbird *Cinnyris afer saliens*, the White-breasted Sunbird *Cinnyris talatala* etc. capable of incorporating trills, whistles and very complex syllables in their song repertoires.

The wide song variation within sunbirds and spiderhunters raises the question of whether or not the vocalisations of many more species than the few documented cases could have been influenced by song 'dialects' (Baptista and King, 1980; Grimes, 1974), as a result of songs learned from conspecifics (Catchpole and Slater, 1995), or the lack of preference for their fathers' dialects (McGregor *et al.,* 1988, 2000), or cultural influence from immigrants (Chilton, 2003).

4.5.2. Phylogeny

4.5.2.1 Description of evolutionary pathway and tree topology

A species tree is a phylogenetic tree representing the evolutionary pathway of a group of species, aimed at reconstructing the history of successive divergences between the considered sequences and their common ancestor.

Every organism, both extant and extinct, has a common origin with another species somewhere in the past, from which has evolved the plethora of species found today. Closely related species share a more recent common ancestor than distantly related species (Li and Graur, 1991).

The phylogenetic tree is a graph composed of nodes and branches in which the branching event corresponds to the splitting (speciation) of an ancestral species into descendent, or daughter, species. The nodes represent taxonomic units, while the branches connecting them reflect their relationships in terms of descent and ancestry (Addoquaye, 2003).

A phylogenetic tree is characterized by its topology (form) and its length (length and number of branches) (Li and Graur, 1991). The topology is the pattern of branches found in the tree. The branching pattern (often called branching order) shows the genealogy of the organisms or shows which species share common ancestry with others. The branch length is commonly used to indicate some form of evolutionary distance represented by that branch. The actual, still existing, taxonomic units are often called operational taxonomic units (OTUs); a generic term that can represent many types of comparable taxa, for example, a family of organisms, individuals of a single species, a set of related genes or even gene regions. Any one of these categories can be represented by nodes on the tips of the branches, called external nodes (Weiller, 1998). The other nodes are called internal nodes. Internal nodes may be called hypothetical taxonomic units (HTU) to emphasise that they are the hypothetical progenitors of OTUs (Weiller, 1998).

Phylogenetic trees can be either rooted or unrooted. A tree where a special node indicating the common ancestor to all OTUs is present is called a rooted tree. An unrooted tree leaves the position of the common ancestor unspecified (Addoquaye 2003).

Sunbirds' ecological distribution patterns in the two isolated continental blocks (Africa and Asia) and islands, may have been associated with the faunistic exchanges across forested corridors during the Neocene colliding of Africa and Asia 19 million years ago (Thomas, 1985; Cox and Moore, 1993). This collision was followed by the rise of mountains in Arabia, Turkey and the Middle East, together with increased aridity in this area and the opening of the Red Sea that led to the isolation of the African and Indo-Australasian forests and their associated fauna (Juste *et al.*, 1999).

4.5.2.2. Phylogenies of study taxa

The phylogenetic song trees of the Nectariniidae were derived from the vocalisations of species capable of uttering calls and simple songs (see Figures 4.19 and 4.20) and those with large repertoires or complex syllables (Figures 4.21 and 4.22), respectively, and the trees comprising solely sunbirds were derived from species capable of complex songs. These phylogenies are consistent with the view held by many authors that many of the stereotypic displays of many birds contain evolutionarily conservative traits (McKinney, 1965; Price and Lanyon, 2002). Such conclusions have been reached from interpretations of phylogenies derived from morphology and molecular data (Irwin, 1996; Slikas, 1998; Johnson *et al.*, 2000) and elements contained in the vocalisations of song birds (Miller, 1996; Slabbekoorn *et al.*, 1999).

It has also been acknowledged that closely related species would have common genetic material through descent from common ancestors and that individuals that share a similar genetic composition may display similar phenotypes (Price and Lanyon, 2002). This conforms with the assertion of this study that the vocalisations of the Nectariniidae are monophyletic in character.

As indicated in the results, the monophyletic representation of the Splendid Sunbird *Cinnyris coccinigaster* and a subspecies (*C. s. superbus*) of the Superb Sunbird *Cinnyris superbus*, with a high bootstrap support of 100% as the closest relatives of the call songsters (Figure 4.19), accords with their being sister taxa on morphological grounds and supports the use of vocalisations as taxonomically meaningful signals. Their closeness is expected as both species occupy extensive ranges of habitats (from forest to woodlands and sometimes in cultivations or plantations) and within the same geographical range i.e. West and Central Africa (Cheke and Mann, 2001).

Similarly, the analyses of vocalisations has placed one out of the three subspecies of the Eastern Olive Sunbird *Cyanomitra olivacea* (*C. o. alfredi*) as a sister taxon to *C. obscura sclateri*, of the four subspecies of Western Olive Sunbird *Cyanomitra obscura* analysed (Figure 4.20). This sister clade received 70.3% bootstrap support. Perhaps this result could add a new dimension to the debate as to whether or not the taxonomic assignment of the two species should remain separated as individual species (Fry, 2000; Cheke and Mann, 2001) or invalidate the split owing to insufficient genetic variation (Bowie *et al.*, 2004).

Also, the analyses link one of the subspecies of the Southern Double-collared *Cinnyris chalybeus* (*C .c. chalybeus*) and two subspecies of the Northern Double-collared Sunbird *Cinnyris reichenowi* (*C .r. preussi* and *C .r. reichenowi*) together (Figure 4.21), a result receiving 67% bootstrap level support. It is strange that the subspecies of the Southern Double-collared (*C. c. chalybeus*), a species restricted to Southern Africa should appear to have a close relationship with the subspecies of the Northern Doubled-collared

Sunbird *C. r. reichenowi* (*C. r. preussi*) another species found mainly in East and Central Africa (Cheke and Mann, 2001). However, this may be less surprising given the recent discovery of an undescribed subspecies of *C. chalybeus* in Tanzania (R. Bowie, J. Fjeldsa, P. Leonard, R. Sternjstedt, unpublished; pers. comm. via R. A. Cheke).

The phylogenetic trees (Figures 4.21 and 4.22) present data to assess hypotheses on the lineage origin of sunbirds and the probable colonisation channels between the two main continents of Africa and Asia and the intermediate islands in the Indian Ocean and those in the Gulf of Guinea. The trees firstly present sunbirds as generally monophyletic taxa with multifurcating branching with varying degrees of bootstrap support. The clade representing the African sunbirds capable of complex song indicates a mix of groupings but showing clearly in the rooted tree (Figure 4.22) that the African group of sunbirds are a derived, or ingroup, of species with 70% bootstrap confidence. Within the clade are species exhibiting close sister relationships and examples include the Collared Sunbird *Anthodiaeta collaris*, (*A. c. collaris*, *A. c. zambesiana* and *A. c. zuluensis*) with 84% support and one of the subspecies of the Southern Double-collared *Cinnyris chalybeus*, (*C. c. chalybeus*) and two subspecies of the Northern Double-collared Sunbird *Cinnyris reichenowi* (*C. r. preussi* and *C. r. reichenowi*) also receiving 67% bootstrap level support, as discussed above.

Another suggested derived or ingroup clade is the Gulf of Guinea group of species (Figure 4.22), including the Sao Tome Sunbird *Dreptes thomensis*, Newton's Sunbird *Anabathmis newtonii* and the Principe Sunbird *Anabathmis hartlaubii* supported with 71% bootstrap and, more interestingly, including Reichenbach's Sunbird *Anabathmis reichenbachii*, a species common in Cameroon and known to occur along the coastal fringes of West and Central Africa including the coasts opposite the Gulf of Guinea islands (Cheke and Mann 2001). The Gulf of Guinea islands comprise oceanic islands of Principe, Sao Tome, Annobon and Bioko, the latter known to have formed a land bridge linking it to the "ecological island" of Mt Cameroon on the mainland. All of these islands form part of the line of volcanoes with an impressive level of endemism (Jones, 1994, Cheke and Mann, 2001; Melo, 2004, Jones and Tye, 2006). This clade raises the possibility that the lineage for the sunbirds of the Gulf of Guinea islands derives from Reichenbach's Sunbird *Anabathmis reichenbachii* colonising from the African continent.

The third clade comprising of Indian Ocean island species (Figures 4. 21 and 4.22) can be hypothesised as the most recently derived or ingroup of Sunbirds that include the Madagascar Sunbird *Cinnyris notatus* (*C. n. notatus*), Souimanga Sunbird *Cinnyris souimanga* (*C. s. souimanga* and *C. s. aldabrensis*), the Humblot's Sunbird *Cinnyris humbloti* (*C. h. humbloti*), Anjouan Sunbird *Cinnyris comorensis*, Mayotte Sunbird *Cinnyris coquerellii*, the Seychelles Sunbird *Cinnyris dussumieri* and the Socotra Sunbird *Chalcomitra balfouri* with multifurcating radians and supported by 92% bootstrap value. The islands in the western part of the Indian Ocean where the above sunbirds occur include Madagascar, the Comoros, and the granitic Seychelles. The close sister relations of the island species is consistent with generally uniform morphological characters and the high level of endemism (over 90%) of species analysed within the group (Cheke and Mann, 2001). These species are also mainly forest dwellers and the song complexities could have been further shaped by the uniform environmental factors. In addition, the Socotra Sunbird *Chalcomitra balfouri* (see above) should be placed within *Cinnyris* and not *Chalcomitra*.

Although the colonisation history of the Indian Ocean Sunbirds could not be inferred from precise dating, it is thought to have preceded the era of the existence of the sea mount stepping stones about 2.7 million years ago and dating back to the origin of the Comoros archipelago (Bremer, 1992; Warren *et al.*, 2003). This is consistent with the position in this study that the Indian Ocean Island species may represent the most recent sunbird clade. An alternative channel of the colonisation of the sunbirds onto the African continent could be held on the basis that the Souimanga Sunbird *Cinnyris souimanga* is probably the most derived of the Indian Ocean island species and may have colonised Madagascar from Anjouan Island (Warren *et al.*, 2003) and so sunbirds could then have invaded the African continent from

Madagascar. Thus, sunbirds may have originated on the Indian subcontinent, reached Indian Ocean islands including Madagascar and then penetrated into Africa. Even if this were the case, it is possible that some oceanic island species were later derived from secondary invasions from Africa.

The fourth clade (Figure 4.22) suggests that the Asian group of sunbirds are the hypothetical outgroup or the most primitive clade of the sunbird lineage with 70% bootstrap support. The Asian sunbirds as shown on the rooted Neighbour-joining tree (Figure 4.22) emerged as the basal clade of the African, Gulf of Guinea and the Indian Ocean Island clades. This result provides significant evidence to infer that the lineage origin of sunbirds may have evolved from the Asian clade and from which the Indian Ocean islands, the Gulf of Guinea islands and mainland African sunbirds may have descended. Although these results corroborate the DNA phylogenetic-based hypothesis (Bowie, 2003) that sunbirds are of Asian origin, it is contrary to the proposition by Irwin (1999) supported by Fry *et al.* (2000) that sunbirds are of African origin on the basis of their bill structure. The agreement between the phylogenetic outcome of this study and that of the DNA study indicates the high potential of applying acoustically derived phylogenies of avian vocalisations in resolving the affinities and lineage origin of distantly related taxa.

The trend of vocal phylogenies also conforms to the evolutionary ladder of the genera on the basis of their song complexity (negentropy). The primitive group of *Prionochilus*, *Dicaeum* and *Chalcoparia* utter simple songs with the lowest negentropy values of 0.1-0.3, whereas the proposed advanced group of the genera, *Cyanomitra* and *Cinnyris*, sang the most complex songs with the highest negentropy values of 0.7-0.9 (see Figure 4.15). The findings also appear consistent with the evolutionary sequence of the Nectariniidae proposed by Delacour (1944) (see Figures 4.14a and b) and the arrangement of Cheke and Mann (2001).

The relationships within the Nectariniidae (flowerpeckers, sunbirds and spiderhunters) implied from the phylogenetic analyses of their vocalisations are intriguing. The phylogenetic Bayesian tree (Figure 4.23) postulates two clades; the first of which is the basal clade of the tree representing the flowerpeckers, with 94% bootstrap support (for the second see below), which lends further support to the view held by Cheke and Mann (2001) that the flowerpeckers constitute the most primitive group of the Nectariniidae.

The second clade is a mix of sunbirds and spiderhunters that received 84% bootstrap support. The monophyletic outlook from the vocal phylogeny of this group fails to distinguish between sunbirds and spiderhunters, which is consistent with the taxonomic grouping sunbirds and spiderhunters in the tribe Nectariniini, but was expected to separate on the basis of the influence of their body size and beak morphology (Farquhar *et al.*, 1996; Cheke and Mann, 2001).

4.6 SUMMARY

Analytical and sonographic representation of the vocalisations showed that in spite of the generally unformed acoustic structure of the vocalisations of all members of the Nectariniidae, there was significant variation of acoustic elements of the song types, to allow worthwhile analyses. However, much of the uniformity of acoustic variables was common among intraspecific recordings. This is congruent with the generally similar morphological characters but varied plumage and behavioural attributes within the taxa.

The vocalisations within the flowerpeckers were found to be simple, mostly single repetitive notes, calls and simple songs. However, sunbirds and spiderhunters appeared to be more varied in attributes and uttered a combination of trills, whistles and complex songs and many species possessed very large repertoires of phrases. Examples include the Cameroon Sunbird *Cyanomitra oritis oritis* and the Green-throated Sunbird *Chalcomitra rubescens*.

The phylogenies have affirmed the affinities of the flowerpeckers, spiderhunters and sunbirds. The phylogenetic analysis and song tree (see Figure 4.22) provides strong evidence that the lineage origin of sunbirds may have been Asia, from where they reached the Indian Ocean islands and subsequently invaded the African mainland and then invaded the Gulf of Guinea islands.

CHAPTER 5

THE MORPHOTAXONOMIC CHARACTERISTICS OF THE NECTARINIIDAE

5.1 INTRODUCTION

Most morphological characters possess traits that are conserved or have diverged during speciation (Lanyon, 1992; Mayr *et al*., 2003) and some have contributed to the derivation of comparative phylogenies together with vocal and molecular data (Mayr *et al*., 2003). They have primarily been used for resolving relationships within and differences between genera and between sibling and cryptic species but not always successfully (Martens *et al.,* 2004).

The primary aim of this chapter is to present the output of the analysis of data sourced from secondary materials on some key morphological and behavioural characters that can be assessed in terms of their relevance to aspects of bird vocalisation, affinity and origin. It was originally envisaged that these data would be used to construct phylogenetic trees to compare with those described in chapter 4. However, the lack of variation in the morphological and nest architecture data meant that no useful signals could have emerged from the construction of any comparative phylogenetic tree.

The chapter is in two parts, part one provides details of the approach used for collating and analysing the data and the results. The second part presents a discussion of the results and a short summary of the findings.

5.2 DETAILED METHODS

The morphotaxonomic characters analysed in this study comprise the data detailed in Cheke and Mann (2001). For each species, five main morphological characters were considered: (1) plumage sex similarities; (2) non-breeding plumage; (3) pectoral tuft; (4) beak morphology (bill length); (5) body size; together with (6) the varying habitat types in which taxa of the Nectariniidae are found; and (7) nest architecture and structure. Character states of the plumage differences were scored on the presence or absence of a particular plumage character at both species and subspecies levels. For example, species that do not moult directly into a distinct non-breeding plumage were scored 0 while those that do moult into a non-breeding (eclipse) plumage after the breeding season were scored 1. Multistate characters or characters for which more than two categories of differences were found, as in the case of plumage colouration, the scores ranged from 1, for species in which males are brighter or with glossy colouration, to 1, 1 for species with similar plumage in both sexes and 0, assigned to species in which females were found drably coloured (as clearly stated in Cheke and Mann 2001). The pectoral tuft was also scored on the basis of the multistage attribute, for which 0 was assigned to species without pectoral tuft, 1 for species in which pectoral tufts occurred in males only and 1,1 for species in which the feature occurred in both sexes (See table 5.1 for examples and appendix 6 for all species scores).

Similarly, the habitat types and nest architecture and structure were scored on the bases of the particular preferences each species exhibited for a habitat or nest type (See sections under habitat and nest architecture).

The beak morphology (bill length) and body size were sourced from the mean scores of the measurements of the bill and wing lengths given by Cheke and Mann (2001). Their data were derived from a combination of published records, measurements that they took of museum specimens and their unpublished field data.

Table 5.1. Sample species character matrix with species morphotaxonomic characters. The table shows data for the three plumage characters (1) plumage sex similarity and plumage brightness; (2) for non-breeding plumage and (3) the occurrence of the pectoral tuft. For this table, 25 species were randomly selected as a sample from the full list (Appendix 6).

	Character number		
Species name	**1**	**2**	**3**
Prionochilus maculatus	1,1	Unknown	0
Prionochilus percussus	0	Unknown	1
Dicaeum agile	1,1	Unknown	1
Dicaeum trigonostigma	1,1	Unknown	0
Dicaeum maugei	1	Unknown	1
Dicaeum cruentatum	1	1	1
Chalcoparia singalensis	1	1	0
Anabathmis newtoni	1,1	1	0
Dreptes thomensis	1,1	1	0
Cyanomitra olivacea	1	1	1,1
Cyanomitra obscura	1.1	1	1
Cyanomitra veroxii	1,1	1	1,1
Cinnyris oseus	1	0	0
Cinnyris venustus	1	0	1
Cinnyris cupreus	0	0	0
Cinnyris souimanga	1	0	1,1
Cinnyris notatus	1	0	0
Cinnyris humbloti	1	1	1
Cinnyris coquerelii	1	1	1
Arachnothera longirostra	1,1	1	1
Arachnothera robusta	1,1	1	1
Arachnothera affinis	1,1	1	0
Arachnothera magna	1,1	1	0

5.3 RESULTS ON PLUMAGE ANALYSIS

The morphotaxonomic results for the Nectariniidae indicate a mix of similarity and variation in colouration and behavioural attributes within and between species, genera and biogeographical clades (African, Asian and Indian Ocean). The overall percentage analysis was based on the total number of species under the various families and genera of the Nectariniidae.

5.3.1 Sex based plumage variation.

The sex similarity analyses showed that the two genera of flowerpeckers (*Prionochilus* and *Dicaeum*) were similar in this respect. The results indicate that 25% of flowerpeckers possess similar plumage in both males and females, examples being the Yellow-breasted Flowerpecker *Prionochilus maculatus* and the Yellow-vented Flowerpecker *Dicaeum chysorrheum.* Sexually dimorphic plumage was found in 27 (75%) species. Examples include the Crimson-breasted Flowerpecker *Prionochilus percussus* and the Grey-sided Flowerpecker *Dicaeum celebicum.*

The results for the sunbirds and spiderhunters were similar. The similarity score for these two major groups also show a small number, 14 (12.7%) of the species with similar plumage whereas 96 (87.3%) exhibit sexual plumage dimorphism.

5.3.2. Pectoral tufts

In the case of the flowerpeckers, males of 11 (25%) species are reported to possess pectoral tufts and only 5 (11.4%) appear to exhibit the character in both sexes. It is yet to be determined whether 28 (63.6%) flowerpecker species possess pectoral tufts or not (See Table 5.2).

Table 5.2: Frequencies of pectoral tufts in species of flowerpeckers.

Presence of Pectoral Tuft	Frequency	Percentage (%)
Male	11	25
Both sexes	5	11.4
None / unknown	28	63.6
Total	44	100.0

5.3.2.1 Sunbirds

The sunbirds seem to exhibit this kind of morphological ornament far more than the other members of the Nectariniidae and a total of 68 (56.7%) species of sunbirds have been reported to possess pectoral tufts. Out of the 61 species, 50.8% of males have been confirmed to possess them and seven species (5.8%) have pectoral tufts in both sexes. However, 21 species (17.5%) of sunbirds are known not to possess pectoral tufts. The remaining 31 species (25.8%) of the sunbirds are without records as to whether they possess the feature or not (Table 5.3).

Table 5.3: Frequencies of pectoral tufts in species of sunbirds.

Presence of Pectoral Tuft	**Frequency**	**Percentage (%)**
Male	61	50.8
Both sexes	7	5.8
None	21	17.5
Unknown	31	25.8
Total	120	100

5.3.2.2 Spiderhunters

Out of the ten species of spiderhunters only four species (40%) are reported to possess pectoral tufts and these occur only in males.

Table 5.4: Frequencies of pectoral tufts in species of spiderhunters.

Variable	**Frequency**	**Percentage (%)**
Male	4	40
Both sexes	0	0
None / unknown	6	60
Total	10	100.0

5.3.3 Non-breeding plumage

Flowerpeckers and spiderhunters appear not to engage in moulting into non-breeding plumages, but this impression may be due to the lack of adequate breeding information about these two groups. Even within the sunbirds, only 33 (27.5%) have been confirmed to engage in moulting into a non-breeding plumage as against 87 (72.5%) of species yet to be determined. The non-breeding plumage also occurs in only some subspecies but not in others of the same species as is the case in the Green-throated Sunbird *Chalcomitra rubescens* where it occurs only in *C. r. stangerii*, the subspecies found in Bioko, Equatorial Guinea (Cheke and Mann 2001).

5.4 RESULTS OF HABITAT ANALYSIS

5.4.1 Flowerpeckers

Flowerpeckers are mostly birds of forests with nearly 70% occupying closed habitats with only about 2.8% occurring in open habitats and found at sea-level. Also, about 25% of the species are partial to both closed and open habitats.

5.4.2 Spiderhunters

The spiderhunters are mainly understory forest dwelling birds (98%), with only a few species such as the Grey-breasted Spiderhunter *Arachnothera modesta* venturing into more open areas such as scrub, secondary growth areas, plantations and gardens. While others such as the Streaked Spiderhunter *Arachnothera magna* are exclusively forest dwellers with occasional strays into nearby forest villages (Cheke and Mann 2001).

5.4.3 Sunbirds

Fifty-one species (43%) of sunbirds are found in both closed and open habitats (See Figure 5.1).

Whereas 34 (28%) species of sunbirds, such as the Scarlet-tufted Sunbird *Deleornis fraseri*, are exclusively forest specialists a similar number 35 (29%) of species, such as the Western Violet-backed Sunbird *Anthreptes longuemarei*, are restricted to open habitats.

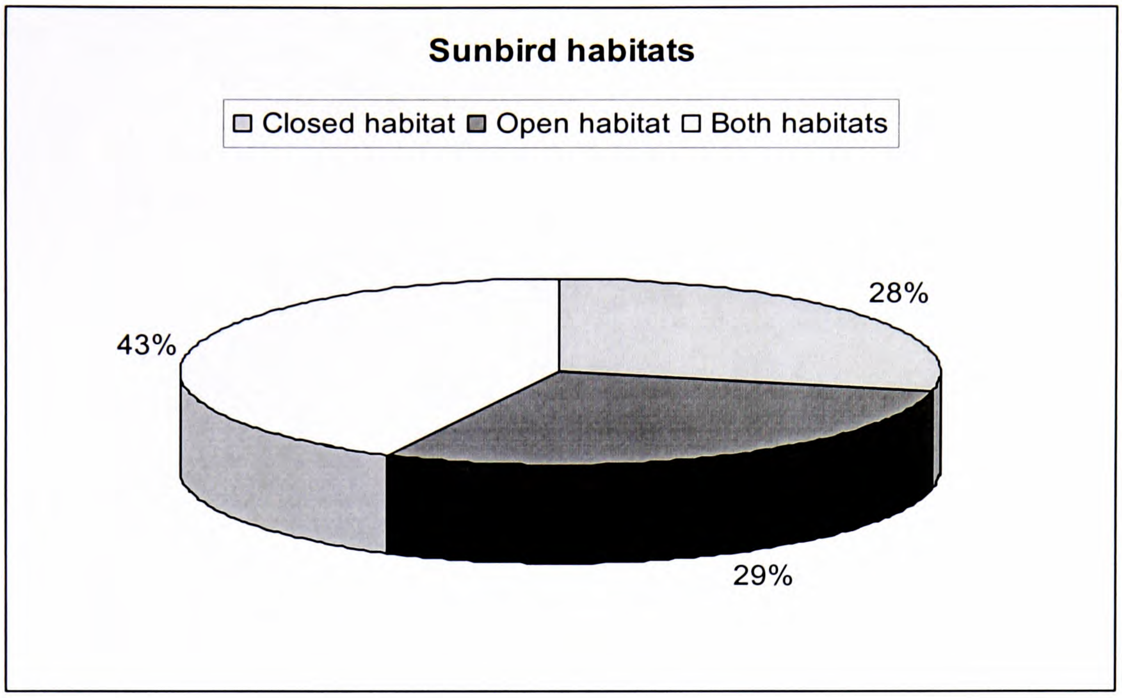


Figure 5.1: Pie chart of percentages of sunbird species using closed or open habitats or both habitats.

5.5 NEST STRUCTURE AND ARCHITECTURE

The construction and shapes of nests range from very simple structures to more elaborate and elegant shapes and structures, including unique features such as the beard and porch as extended attachments. Addition of a porch appears to be the most prominent feature that influences the nest building technique of most sunbirds. About 71 (60%) of the species construct their nest with a projecting porch fixed at the entrance of the nests as for example the Western Violet-backed Sunbird *Anthreptes longuemarei*. Only about 19 (15.8%) are known to include the beard in the construction of their nests. Examples include the Tacazze Sunbird *Nectarinia tacazze*. There are also 12 (10%) species that construct their nests with both features, the porch at the entrance of their nests and a beard below the nest, e.g. the Purple-breasted Sunbird *Nectarinia purpureiventris*.

A further 99 (82.5%) species of sunbirds characteristically suspend or hang their nests on trees or bushes e.g. the Eastern Olive Sunbird *Cyanomitra olivacea* and the Copper Sunbird *Cinnyris cupreus* (see figure 5.2).

Figure 5.2. A suspended nest of Copper Sunbird *Cinnyris cupreus* hanging on a thin branch of a tree. Note, also, the porch above the entrance hole. (Photograph: R. A. Cheke).

Twenty one species (17.5%) of sunbirds, including the Orange-breasted Sunbird *Anthobaphes violacea* and Pygmy Sunbird *Anthodiaeta platura* place their nests directly into the twigs of nest trees (see for example **C** in figure 2.9).

5.6 RESULTS ON BEAK MORPHOLOGY AND BODY SIZE

5.6.1 Bill length and body size.

Traditionally, measurements of bill size / length and structure have informed the understanding of the evolutionary divergence and the taxonomic classification of the Nectariniidae. Bill sizes, length and body sizes differ greatly among families and even within species of the same genus. This study has focused on the analyses of these features at the generic level in relation to vocal variation measured in terms of frequency and entropy / negentropy. Measurements of the mean bill lengths are shown in Figure 5.3.

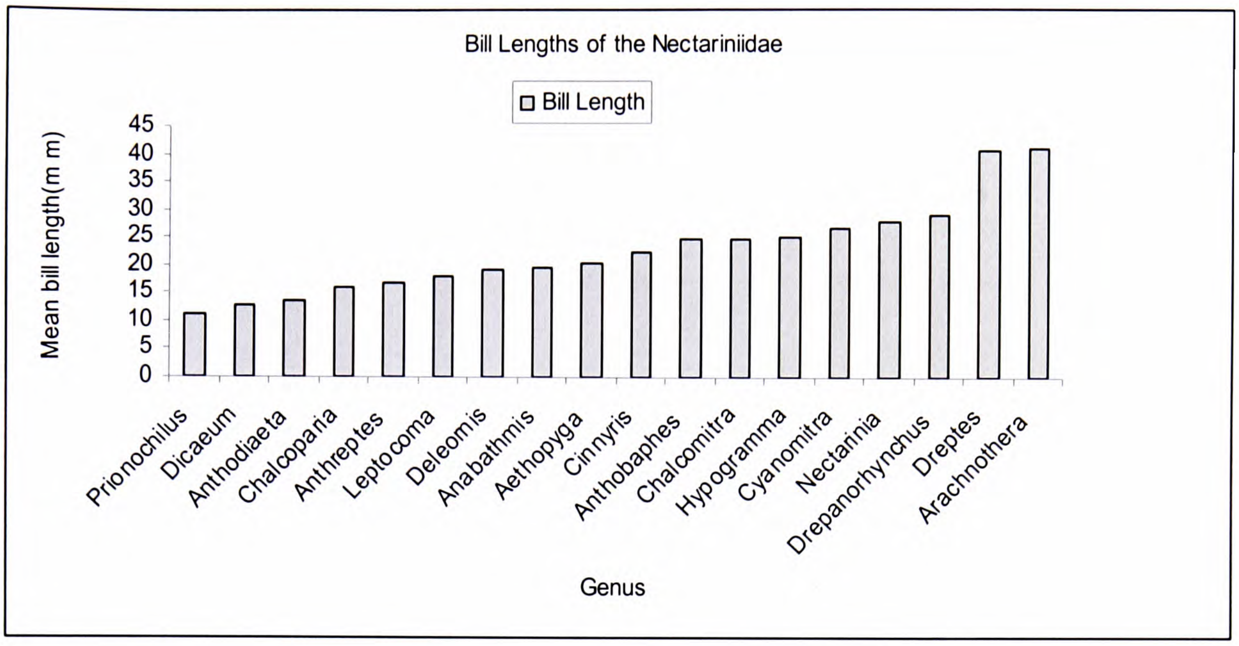


Figure 5.3 Mean bill length of different genera. Note that the flowerpeckers *Prionochilus* and *Dicaeum* have the shortest bills and that the spiderhunters (*Arachnothera* spp.) the longest.

The relation between bill length and song complexity (represented here as negentropy i.e. 1-entropy; Schrödinger, 1944) is shown in Figure 5.4 and supported by a significant correlation ($r_s = 0.61$, n =18, $P < 0.05$).

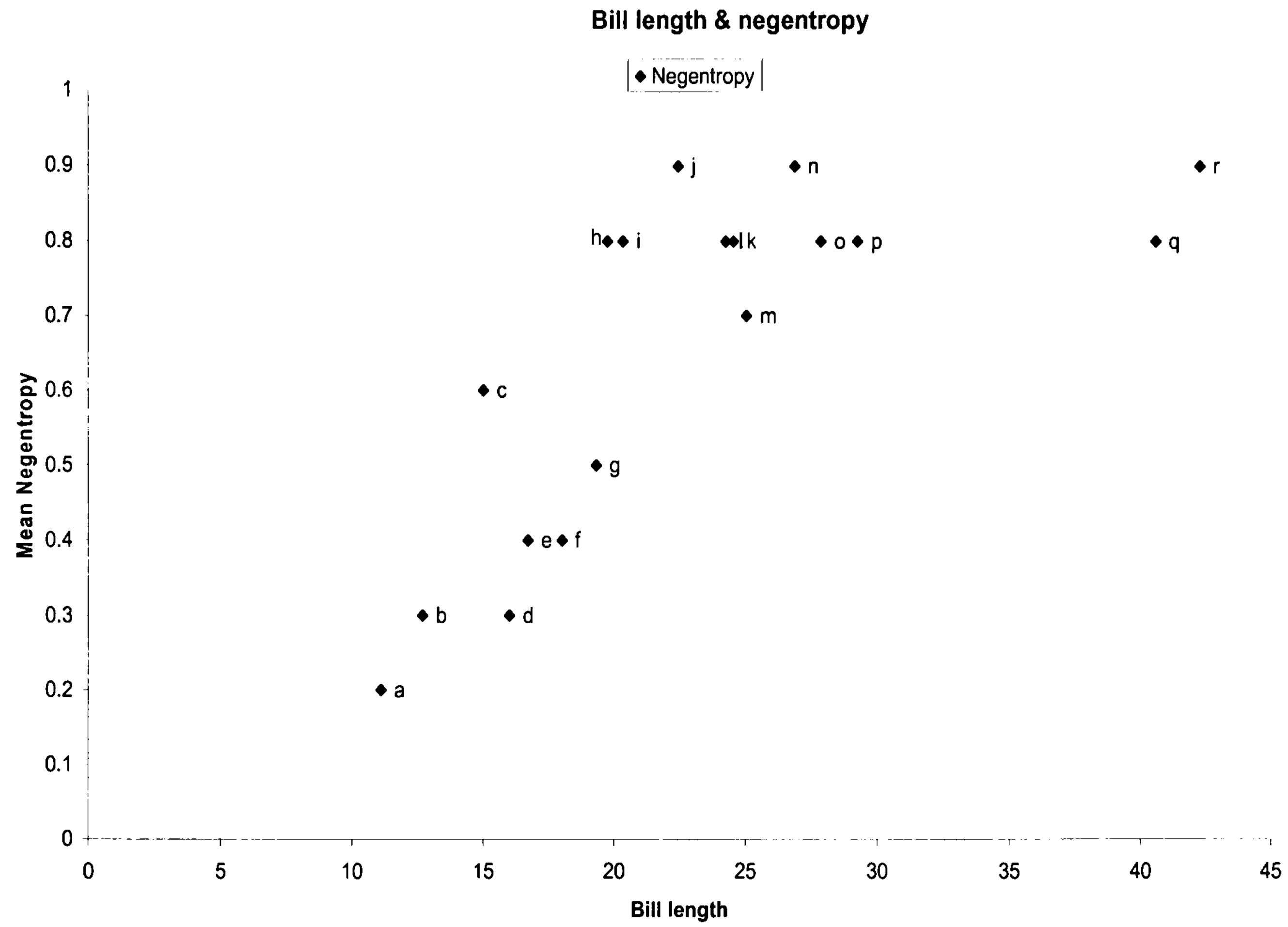


Figure 5.4. The relationship between bill length and the level of song complexity (negentropy) in songs of different genera of the Nectariniidae. (a) *Prionochilus*, showing shorter bill length and lowest negentropy; (b) *Dicaeum*; (c) *Anthodiaeta*; (d) *Chalcoparia*; (e) *Anthreptes*; (f) *Leptocoma*; (g) *Deleornis*; (h) *Anabathmis*; (i) *Aethopyga*; (k) *Anthobaphes*; (j) *Cinnyris*; (l) *Chalcomitra*; (m) *Hypogramma*; (n) *Cyanomitra*; (o) *Nectarinia*; (p) *Drepanorhynchus*; (q) *Dreptes*; (r) *Arachnothera,* showing the largest in terms of bill length.

Analysis of the relationship between bill length and vocal frequency (Figure 5.5) did not show a linear correlation but rather a grouping based on habitat types. Species in closed habitats grouped with vocalisations with lower frequencies than those in the open habitat group whose vocalisations had consistently higher frequencies (see Table 5.5 for habitat allocations). Interestingly, a genus classified as mostly in mixed habitats (*Dreptes*) appeared as intermediate in the analysis depicted in Fig. 5.5. When this is accounted for it is clear that the two habitat-based groupings are distinct clusters.

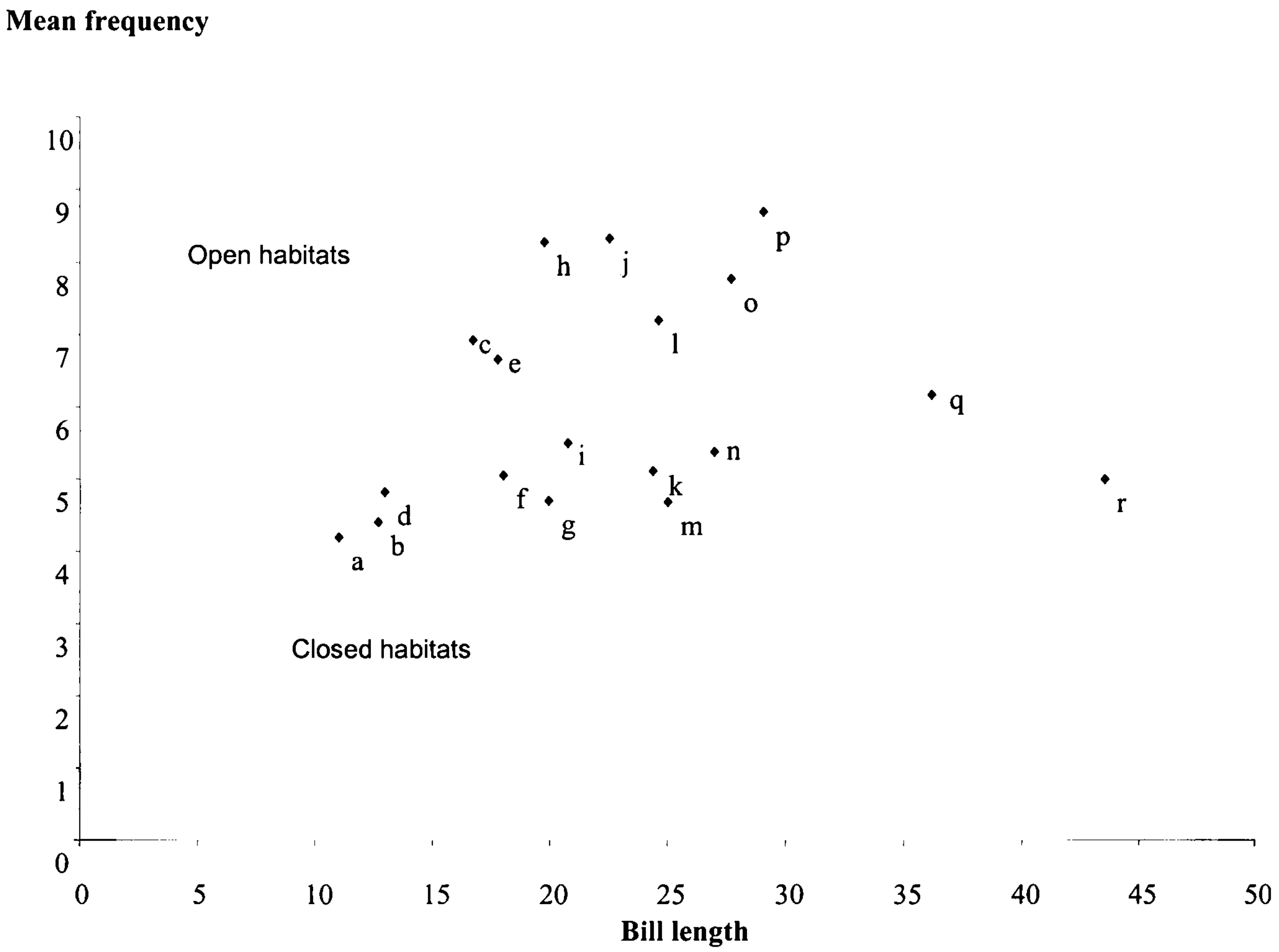


Figure 5.5. The relationship between bill length and mean frequency of songs. (a) *Prionochilus*; (b) *Dicaeum*; (c) *Anthodiaeta*; (d) *Chalcoparia*; (e) *Anthreptes*; (f) *Leptocoma*; (g) *Deleornis*; (h) *Anabathmis*; (i) *Aethopyga*; (j) *Cinnyris*; (k) *Anthobaphes*; (l) *Chalcomitra*; (m) *Hypogramma*; (n) *Cyanomitra*; (o) *Nectarinia*; (p) *Drepanorhynchus*; (q) *Dreptes*; (r) *Arachnothera.*

The body size (bill length / wing length) of the various genera is illustrated in Figure 5.6. Although body size seemed to vary considerably even between species of the same genera, the general representation of body size at the generic level appeared to conform to the taxonomic categorisation in that *Prionochilus* of the flowerpeckers are the smallest while the *Arachnothera* spiderhunters are the largest among the Nectariniidae.

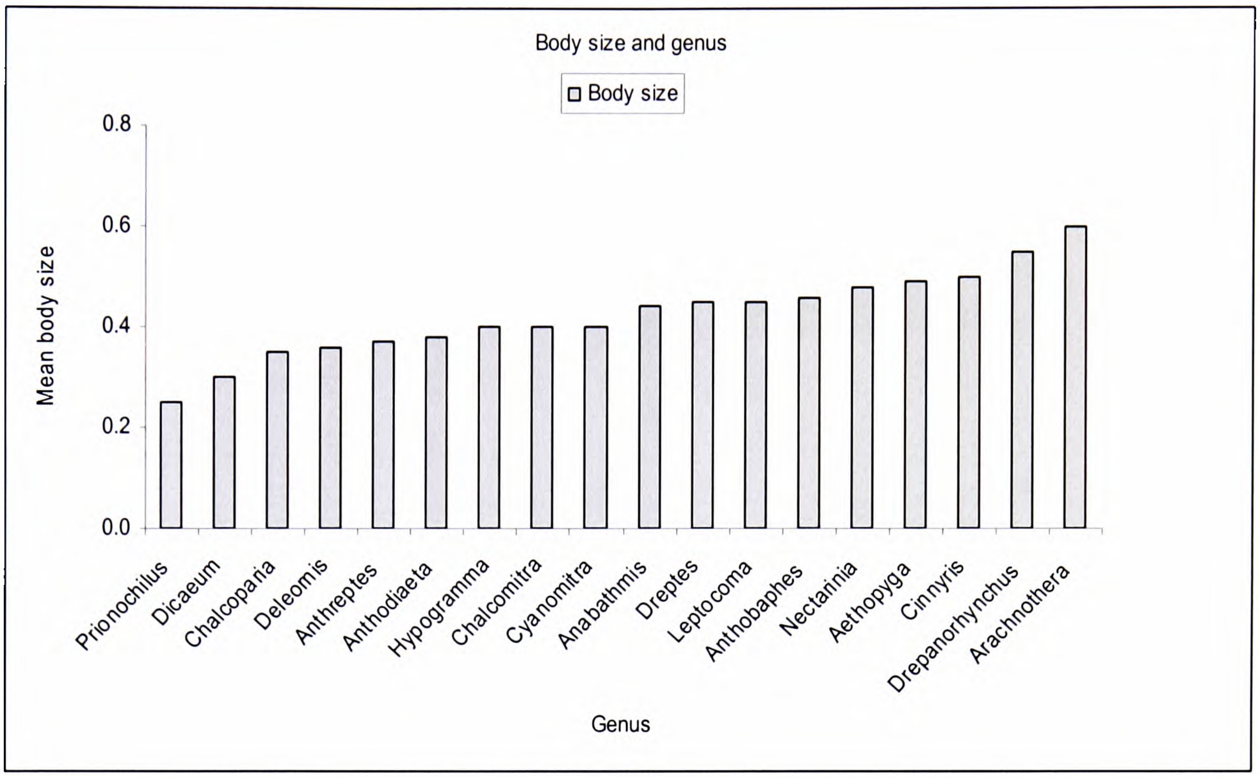


Figure 5.6. Mean body sizes (bill length / wing length) for different genera of the Nectariniidae.

Figure 5.7 shows that there is a positive relationship between song complexity and body sizes amongst the genera of the Nectariniidae ($r_s = 0.6$, $n = 18$, $P < 0.001$).

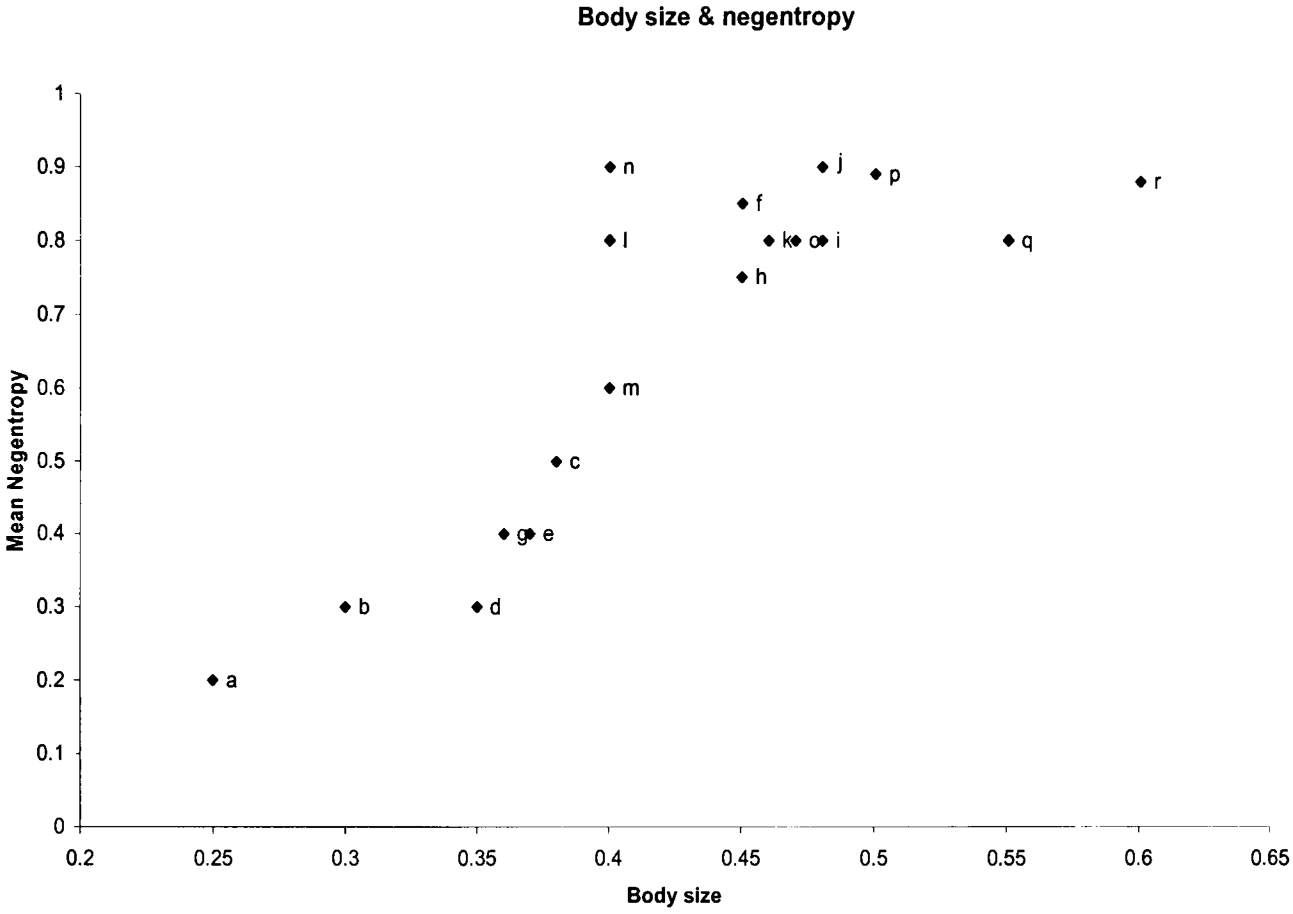


Figure 5.7 Mean negentropy values of songs of different genera according to average body sizes (mean bill length / mean wing length). (a) *Prionochilus*; (b) *Dicaeum*; (c) *Anthodiaeta*; (d) *Chalcoparia*; (e) *Anthreptes*; (f) *Leptocoma*; (g) *Deleornis*; (h) *Anabathmis*; (i) *Aethopyga*; (j) *Cinnyris*; (k) *Anthobaphes*; (l) *Chalcomitra*; (m) *Hypogramma*; (n) *Cyanomitra*; (o) *Nectarinia*; (p) *Drepanorhynchus*; (q) *Dreptes*; (r) *Arachnothera*.

The outcome of the analysis of body size and mean frequency of songs is presented in Figure 5.8. Body size seems not to show any clear linear relationship with vocal frequency but the data do cluster into two distinct groups according to habitats, with *Dreptes* (classified as mixed) intermediate. Thus, the results for body size correspond with those for bill length (Figure 5.5).

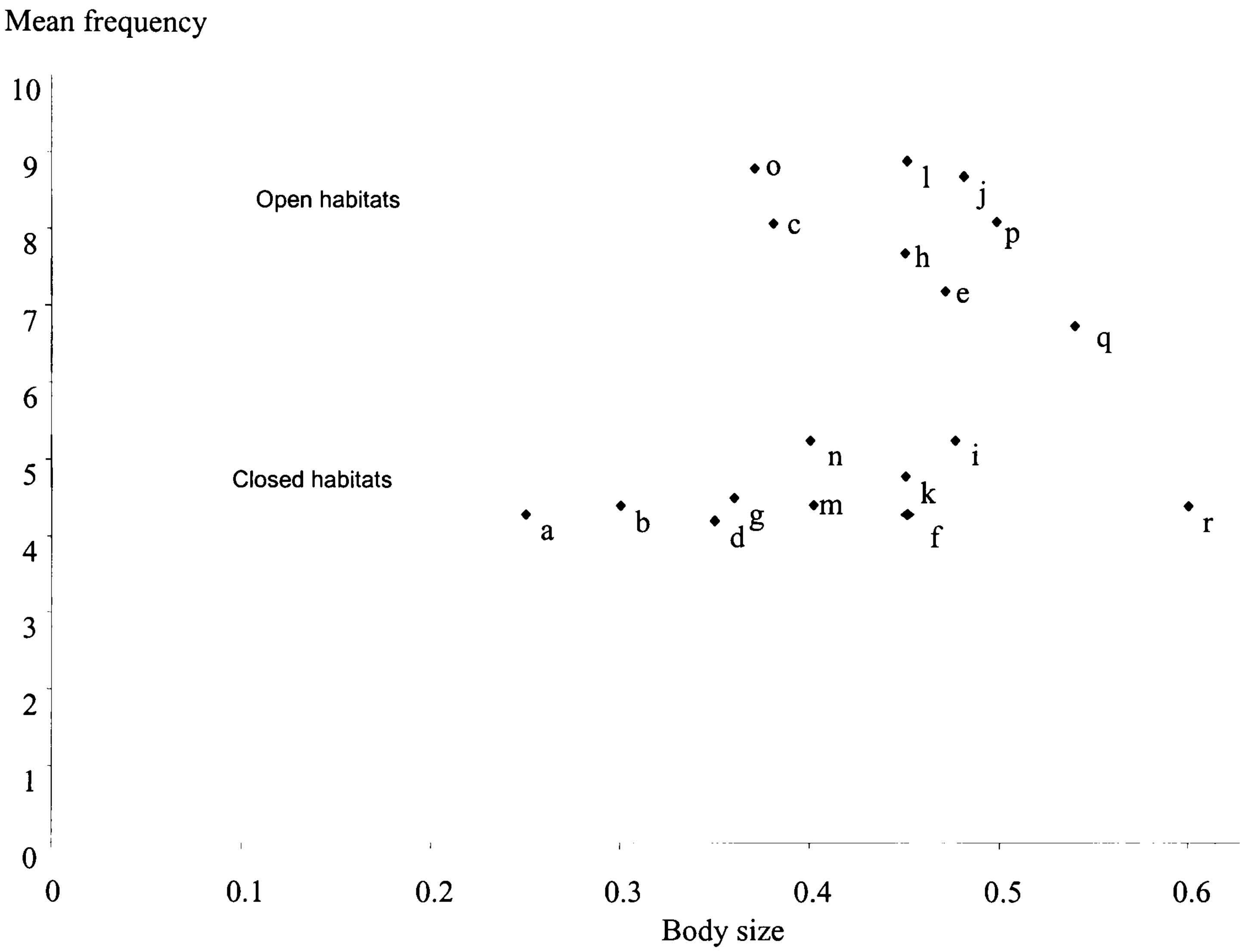


Figure 5.8 Mean frequency of song according to body size of different genera. (a) *Prionochilus*; (b) *Dicaeum*; (c) *Anthodiaeta;* (d) *Chalcoparia*; (e) *Anthreptes*; (f) *Leptocoma*; (g) *Deleornis*; (h) *Anabathmis*; (i) *Aethopyga*; (j) *Cinnyris*; (k) *Anthobaphes*; (l) *Chalcomitra*; (m) *Hypogramma*; (n) *Cyanomitra*; (o) *Nectarinia*; (p) *Drepanorhynchus*; (q) *Dreptes*; (r) *Arachnothera*.

The mean maximum song frequencies of the Nectariniidae at the generic level and the percentage habitat occupancy of the various genera are given in Table 5.5.

Table 5.5 Song frequency and percentage habitat occupancy at the generic level.

Vocal frequency and habitats				
Genus	**Frequency**	**Percentage habitat occupancy**		
	Mean of max-Frequency.	**Closed**	**Open**	**Mixed habitats**
Prionochilus	4.4	80%	0%	20%
Dicaeum	4.4	74%	6%	20%
Chalcoparia	4.2	100%	0%	0%
Deleornis	4.5	100%	0%	0%
Anthreptes	8.8	22%	42%	36%
Anthodiaeta	5.4	25%	50%	25%
Hypogramma	4.7	100%	0%	0%
Anabathmis	8.9	0%	66.7%	33.3%
Dreptes	7.2	0%	0%	100%
Anthobaphes	4.5	100%	0%	0%
Cyanomitra	4.8	25%	0%	75%
Chalcomitra	7.4	14%	58%	28%
Leptocoma	5.5	60%	20%	20%
Nectarinia	7.2	16%	68%	16%
Drepanorhynchus	8.7	0%	100%	0%
Cinnyris	8.7	22%	38%	40%
Aethopyga	5.2	47%	6%	47%
Arachnothera	4.4	70%	0%	30%

5.7 DISCUSSION

5.7.1 Plumage and behavioural correlates

The acquisition of breeding plumage is an adaptation by almost all male sunbirds to attract females and defend territories. However, the males of some species (27.5%) are capable of moulting into a non-breeding plumage or eclipse plumage, usually after the breeding season. At the start of the next breeding season, they moult out of it back into breeding plumage. The function of the non-breeding plumage is unclear. The non-breeding plumage moult is part of a cyclical process whereby birds routinely shed off old feathers and replace them by growing new ones (Rappole, 1983). However, it has been further argued that moulting into a non-breeding plumage is a mechanism adopted by birds to reduce body mass and found in individuals without the physiological condition to migrate (Carmem *et al.*, 2004).

The pectoral tuft is another sexually dichotomous attribute in birds (McGraw *et al.*, 2002) and in the cases of flowerpeckers, sunbirds and spiderhunters (Nectariniidae) it may occur only in males in some species and in both sexes in other species and is sometimes completely absent (Tables 5.2 and 5.3). Although pectoral tufts have been used as a morphological character for the taxonomic classification of some species, it is thought to have a sexual function and is specifically utilised by males during mating sessions (Cheke and Mann, 2001; Bowie *et al.*, 2004) but it is unknown if the pectoral tuft has any specific function within the females as well.

Evidence from studies on the Red-tufted Sunbird *Nectarinia johnstoni* has confirmed the use of the pectoral tuft by males for repelling intrusions by other males (Evans and Hatchwell, 1992a). It has also been confirmed that the pectoral tuft of most species is a territorial defence apparatus and usually displayed to varying degrees, depending on the size of the tuft (Evans 2003).

5.7.2 Habitat

Various studies have attempted to show the constraints that the physical structures of the environment can place on the song structure of birds (Marten and Marler, 1977; Willey and Richards, 1982; Mathevon *et al.*, 1996). The acoustic adaptation hypothesis (AAH) originates from attempts to draw find a correlation between bird song structure and habitat (Morton, 1975; Saunders and Slotow, 2004). The acoustic adaptation hypothesis predicts 'that signal portion intended to transmit information accurately over a distance on the order of territory diameters, should be in a form or structure that is minimally degraded on passage through native habitat' (Brown and Handford, 1996). This prediction implies that the composition of a species's song attributes would depend largely on the habitat in which it evolved. Some also categorised habitats into two: open habitats such as grasslands and closed habitats such as forest (Saunders and Slotow, 2004).

Habitat choice by the Nectariniidae is quite diverse and reflects the widespread and bio-geographically diverse nature of the taxa. Flowerpeckers and spiderhunters (both Asian restricted groups) are generally categorised as mainly forest dwelling species. The Flowerpeckers (70%) dwell mostly at the top canopy of forest, whereas the spiderhunters (98%) are thought to prefer mainly the understory portion of the forest (Cheke and Mann 2001). However, sunbirds (See Figure 5.1) appear to occupy more varying habitat types, ranging from closed forest to semi-desert habitats.

Proponents of the acoustic adaptation hypothesis strongly support the view that habitat structures can impose a degradation and attenuation effect on long distance acoustic signals of some bird species, particularly in forest habitats (Morton, 1986; Brown and Hanford, 1996; Fotheringham *et al.*, 1997; Saunders and Slotow, 2004), but others are of the view that the attenuation effect is greatest only when the source of signal is close to 1m to the ground or within the closed canopy of forest habitats (Morton, 1975; Marten *et al.*, 1977; Waser and Waser, 1977). Little is known of the correlation between habitat type and vocalisations of the Nectariniidae. However, this study has established at the generic level that there is a correlation between vocal frequency and bill length of the taxa in relation to habitat types (open or closed). Perhaps this could form the basis for which we could begin to understand the extent to which habitat structures have contributed to shaping the acoustic features of the taxa. However, the causal effect of this finding on the overall vocal phylogeny of the Nectariniidae provides a good support to the acoustic adaptation hypothesis (see Figures 5.5 and 5.8). Nevertheless, as the more highly evolved species tend to have longer bills there is evidence that, irrespective of habitat type, the songs of the more advanced genera are more complex, as discussed above.

5.7.3 Nest structure

Nests and nest architecture are neglected areas of bird study but nest structure and design constitute an integral part of the behavioural attributes of most avian species, resulting in a wide diversity of nest structures. These range from simple shallow scrapes used by species such as gulls, terns and vultures to elaborate, sophisticated and elevated nests with varied shapes and sizes constructed by species such as swallows (Hirundinidae), weaver finches (Ploceidae) and sunbirds (Nectariniidae) (Brieschke, 1992; Hansel, 2001; Dial, 2003). The evolution of nest building stems from three main reasons: (1) to attract a mate; (2) to provide a safe site for egg and young; (3) to provide shelter from adverse weather. It is, however, unclear why some species, notably Cuckoos *Cuculus* spp. and the Brown-headed Cowbird *Molothrus ater* do not build their own nests and tend to be brood parasites using other species' nests (Hoover, 2007). Some studies have revealed that nest construction involves so much expenditure of time and energy (Collias and Collias, 1984; Putnam, 1949) that many species have evolved several tactics to either avoid nest construction (Hoover, 2007) or adopt styles to considerably reduce costs by exploiting materials close to nest sites or the removal of materials from old nests (Skutch, 1976; Brieschke, 1992).

Nest architecture is one of the specialised behavioural functions exhibited by all species of the Nectariniidae, and for which some sunbirds are highly renowned for their distinctive "designs" of what is exceptionally known as 'sunbird-type oval' nests (Tarboton, 2001).

Nest placement has been reported to correlate with some avian behavioural features such as flight ability, predation and protection (Dial, 2003). The habit of some species such as the kinglets, vireos and orioles of suspending their nests on trees, cliffs and man-made structures may have evolved from the need for camouflage and to make their nests inaccessible to predators or to achieve suitable microclimatic conditions (Hartman and Oring, 2003; Leonard and Picman, 1987; Dial, 2003). Perhaps the most significant aspect of sunbird nesting is the style of nest placement. Most species (82.5%) place their nest above ground and usually attached at the roof to tree branches, bushes, telephone lines etc. Although it is unknown why most sunbirds choose to suspend their nests, it is clear, however, that nest placement could enhance egg security and successful breeding.

5.7.4 Beak morphology

The results of this study have shown that both bill length and body size correlate positively ($r_s = 0.61$, $n = 18$, $P < 0.05$ for the former; $r_s = 0.6$, $n = 18$, $P < 0.001$ for the latter) with song complexity (negentropy) within the genera of the Nectariniidae (see Figures 5.4 and 5.7). This finding is consistent with an earlier study conducted on different populations of the Reed Bunting, *Emberiza schoeniclus*, in which a positive correlation was found between the beak morphology and the number and diversity of syllable types of their vocalisation (Matessi *et al.*, 2000).

However, both bill length and body size failed to show any significant correlation or relationship with vocal frequencies (See Figures 5.5 and 5.8), except when classified according to habitats. The former results are inconsistent with the resonance hypothesis (intensification and prolongation of sound, especially of a vocal tone, produced by sympathetic vibration and which correlates directly to a vocal organ). Claims in support of the hypothesis have included a study of seven species of Darwin's finches *Camarhynchus* and *Geospiza* spp. Birds of one species *Geospiza fortis* have larger beaks and produce songs with lower trill rates and which required lower levels of vocal performance than the others (Podos, 2001). Also, another study on Darwin's finches revealed a positive correlation between body mass and acoustic features of their songs (Bowman, 1983). This could, perhaps, be attributed to syrinx size, which is also thought to correlate positively with body size (Cutler, 1970; Bowman, 1983).

Contrarily, these claims have been disputed by other studies that have revealed that out of the four species of the genus *Geospiza* examined so far only one species *Geospiza fortis* of Santa Cruz Island has had its song characters correlated with beak morphology (Ballentine *et al.,* 2004). Also comparative analyses of the songs and beak morphology of the African finch, *Pyrenestes ostrinus* (Slabbekoorn and Smith, 2000), the Swamp Sparrow, *Melospiza georgiana* (Ballentine *et al.*, 2004), or the Yellow Warbler, *Dendroica petechia* (Beebee, 2004a), all failed to establish any correlation between the acoustic features of these birds and their beaks or body size. In a further study on the Chough *Pyrrhocorax pyrrhocorax*, a negative relationship was established between body mass and frequency of their vocalisation (Laiolo *et al.*, 2001, 2004).

The inconsistencies among the results from the above studies on the resonance hypothesis call into question the relationship between beak morphology and the acoustic features of bird songs. However, this present study is the first to use entropy / negentropy values as a measure of the level of song complexity of vocalisations (negentropy) and has shown a clear effect of varying bill length and body size on vocal capabilities. The presumably most primitive genera with the shortest bills (the flowerpeckers) had simpler songs than the more highly evolved sunbirds and spiderhunters in which the most complex songs were uttered by species with the longest bills. This is consistent with a view that, in general, evolution of living systems leads to increasing order and complexity from more disordered, simpler, precursors.

In addition, birds inhabiting closed habitats for example the *Prionochilus* (80%) and *Dicaeum* (78%) species, had lower frequency vocalisations than those such as *Drepanorhynchus* found in (100%) open areas and *Cinnyris* often found in (38%) open and (40%) mixed habitats (see table 5.5). The Nectariniidae are a large group of birds with a variety of species specific vocal variation and inhabiting a number of different habitats ranging from semi-desert areas to primary forest. Even forest dwelling species are known to occupy different levels of the forest and this is typical of *Prionochilus*, *Dicaeum* and the *Arachnothera*. Sound transmission across forest habitat types is therefore expected to vary in relation to the different degrees of influence imposed on transmitted signals by the environment and this has been confirmed by studies conducted on several Eurasian species (Nikol'skii 1994, 1996). The expectation of a functional relationship between bill length and body size and frequency was not apparent but the clusters tended to group according to the closed and open and mixed habitat classifications.

This study has therefore provided modest support for the acoustic adaptation hypothesis (AAH) and results consistent with the suggestions by Morton (1975) and Marten *et al.* (1977) that structural differences in the habitat may influence signal transmission. The acoustic adaptation hypothesis according to Brown and Handford (1996), 'predicts that the signal portion intended to transmit information accurately over a distance on the order of territory diameters should be of a form that is minimally degraded on passage through native habitat'. AAH according to Blumstein and Turner (2005) and Saunders and Slotow (2004) predicted specifically that: (1) Birds in open habitats would produce higher maximum frequencies than birds in forest habitats and this is attributed to the reverberation effect on signal transmission; (2) Birds in the open would have greater bandwidth (maximum - minimum frequency) when measured at the level of the song and at the level of the element than birds in the forest; (3) Birds in the open would vocalize at faster rates when measured by examining element duration, the interval between elements, the number of elements produced per second, and the number of acoustically unique elements per song than birds in the forest; (4) Birds in the open would tend to sing trills while birds in the forest are more likely to sing whistles; (5) repeated units would be more common in birds that lived in open habitats compared to birds in the forest.

The first specific prediction (birds in open habitats would produce higher maximum frequencies than birds in forest habitations and this is attributed to the reverberation effect on signal transmission) is supported by the correlation between the vocal frequency and habitats of the Nectariniidae. This has also been supported by arguments that signals transmitted through a forest are more likely to be affected by reverberation off leaves and tree trunks than signals transmitted in the open (Richards and Wiley, 1980). On the other hand, signals transmitted across large open areas are subject to degradation by moving air of varying degrees of temperature and humidity and this tends to favour signals with high rates of repetition (Wiley and Richards, 1978; Richards and Wiley, 1980).

It has, however, been argued that the AAH has so far been supported by only large-scale studies focusing on the broad categories of the habitat classification system (closed and open). Blumstein and Turner (2005) further argued that most of the previous studies relating to habitat and avian vocalisations by authors such as Smith and Yu (1992), Date and Lemon (1993) and Slabbekoorn and Smith (2001) focused mostly on a restricted group of Neotropical birds.

Although the general applicability of the AAH is unknown, the probable reason for the conformity of the finding of the study to prediction (1) of the AHH could be attributed to natural selection favouring different song structures in closed and open or mixed habitats over bill length and body size within the genera of the Nectariniidae.

5.8 SUMMARY

Despite the marked sexual dimorphism in the plumage of the Nectariniidae, little of consequence was found to relate even some of their elaborate plumage features to their vocalisations. However, the results revealed a significant correlation between song complexity and bill length which was maintained when bill length was adjusted by dividing it by wing length, giving an index of body size. The results also revealed a relation between vocal frequency and habitat types. However, the results failed to establish any clear linear relationship between frequency and bill length or body size apart from habitat-related clustering.

Habitat selection, nest structure and nest placement were examined as examples of behavioural attributes of the Nectariniidae. The general semblance of these features amongst the various taxa reflects their closeness. The flowerpeckers (70%) and spiderhunters (98%) are mostly forest dwelling birds. However, sunbirds (see Figure 5.1) appear to occupy more varying habitat types, ranging from closed forest to semi-desert habitats. There is a strong relationship between suspected evolutionary development and bill length at the generic level, although the spiderhunters with the longest bills are anomalous. With the exception of the spiderhunters with cup-shaped types of nests, the nests of flowerpeckers and sunbirds are purse, oval or pear in shape sometimes with a porch over the nest entrance hole and or a beard, or both. Over 60% of sunbirds construct their nest with a porch affixed to the entrance, 82.5% suspend their nests on a tree or bush or on artificial objects.

CHAPTER 6

GENERAL DISCUSSION

The first part of this chapter presents a brief overview of avian phylogenies and the role of the biological species concept in species taxonomy and phylogeny. This is followed by a review of published studies on aspects of acoustic analysis and ecological implications of birdsongs, and reviews of previous studies on the vocal characteristics of the Nectariniidae. This section highlights the entropy concept as applied in this study. The second part provides a comparative discussion on the phylogenetic hypothesis tested, based on the vocal phylogeny findings. The third part examines the implications of this study for the conservation and management of the taxa and the overall limitations of the study.

Although phylogenies derived from vocal and morphological analyses are recent developments, many aspects of bird traits have been used to reconstruct the evolutionary histories of many species (Marler and Pickert, 1948; Kroodsma and Canady, 1985; Baptista, 1996) and some comparative studies involving avian taxa (Payne, 1986; Irwin, 1988; Van Buskirk, 1997; Podos, 1997, 2001) have included measurements of acoustic features of bird song to derive the phylogenies. These include phylogenetic studies of (a) the genus *Regulus* (Packert *et al.*, 2003); (b) Canarian Blue Tits *Parus teneriffae*, the common syntax of which differs from that of continental Blue Tits *P. caeruleus* and Azure Tits *P. cyanus* (Schottler 1995; Martens, 1996); (c) oropendolas in the genera *Psarocolius, Gymnostinops* and *Ocyalus* (Price and Lanyon, 2002); (d) the warblers *Dendroica petechia aestiva*, *Dendroica petechia eritachorides*, *Dendroica petechia petechia* (Boulet and Gibbs, 2006); (e) pipits in the genus *Anthus* (Voelker, 1999) and (f) white-eyes *Zosterops* spp. (Warren *et al.*, 2006).

Until recently, the classification and delineation of most avian species have been derived from the study of morphological features under the biological species concept paradigm. However, the emergence of molecular data has posed serious challenges to the biological species concept and has now heightened the debate on taxonomic revision and placement of some species and the evolutionary histories of avian taxa (Ryan *et al.*, 1998; Garcia-Moreno and Fjeldsa, 1999; Bowie *et al.*, 2004). Equally, recent advances in Fourier analysis and sonographic evidence of the composition and structure of vocal communication have projected vocal analyses to the forefront of the debate on bird taxonomy (Cramp *et al.*, 1983; Clancey, 1990; Bradbury and Vehrencamp, 1998; Alstrom and Ranft, 2003).

The vocalisations of several species of songbirds have been studied to date, and have comprised a wide range of aspects of bioacoustics, phylogeny, morphology, ecology and speciation. However, most of these studies have focused solely on species specific investigations or, occasionally, analyses at the generic level and this study is the first of which I am aware to cover a whole family (or two families if the Flowerpeckers are treated as a family (Dicaeidae) and not merely a tribe (Dicaeini)).

Case studies on bioacoustics and involving signal transmission and reception have been described (Lind *et al.,* 1996; McGregor and Peake, 2000; Pytte *et al.,* 2003; Peake, 2005). Others have delved into the linkages that exist between bird vocalisations and evolution (Helbig *et al.*, 1996; Martens *et al.,* 1999; Martens and Eck, 2000; Irwin, 2001; Irwin *et al.,* 2001), while others have published on various specific vocal characteristics of numerous birds including the Golden-spectacled Warbler *Seicercus burkii* complex (Alstrom and Olsson, 2000); Magpie-larks *Grallina cyanoleuca* (Hall and Magrath, 2000); Great Tits *Parus major* (Van Duyse *et al.*, 2002); Gambel's White-crowned Sparrows *Zonotrichia leucophrys gambelii* (Chilton *et al.*, 2002); doves in the genus *Streptopelia* (Gabriel *et al.*, 2003, De Kort and Ten Cate, 2004); Blue-throated Hummingbird *Lampornis clemenciae* (Pytte *et al.*, 2003); Western Greygone *Greygone fusca* (Baker *et al.,* 2003); White-Crowned Sparrows *Zonotrichia leucophrys oriantha* (Chilton, 2003) and *Z. leucophrys* (Rose *et al.,* 2004); Black-capped chickadees *Poecile atricapillus* (Gammon and Baker, 2004); Chaffinch *Fringilla coelebs* (Leitao and Riebel, 2004; Gorestskaia, 2006); Common Nightingales *Luscinia megarhynchos* (Brumm, 2004, Kiefer and Hultsch, 2006); Zebra finches *Taeniopygia guttata* (Cynx and Gell, 2004); Tropical Boubou, *Laniarius aethiopicus* (Grafe *et al.*, 2004); Black-browed Reed Warbler *Acrocephalus bistrigiceps* (Hamao and Eda-Fujiwara, 2004); Hawk-eagle, *Nisaetus cirrhatus* (Gjershaug, 2005); Eurasian Woodcock *Scolopax rusticola* (Mulhauser and Zimmermann, 2006); Greater Racket-tailed Drongo *Dicrurus paradiseus* (Goodale and Kotagama, 2006); Black Coucal *Centropus grillii* (Geberzahn, 2006); flycatchers in the genus *Empidonax* (Lein and Haines, 2006); Magpie-Robin *Copsychus saularis* (Bhatt and Sethi, 2006); Zebra finches *Taeniopygia guttata* (Brumm and Slater, 2006) and cuckoos *Cuculus spp*. (Slabbekoorn and Boer-Visser, 2006). General descriptions and the application of acoustic signals in conservation have also been examined (McGregor *et al.,* 1998, 2000; Langemann, 2006; Brumm, 2006).

Another area of songbirds' vocalisations that has attracted the attention of researchers is the role of morphological attributes in signal expression with particular reference to beak morphology and body size and size of the syrinx. Several recent studies on the construction of vocal syllables suggest that the evolution of beak form and function in birds may have a significant influence on song evolution (Cutler, 1970; Slabbekoorn and Smith, 2000; Podos and Nowicki, 2004a and b; Hendry *et al.*, 2006) and that body size may also provide a more direct insight into the influence of beak size on song production and evolution (Palacios and Tubaro, 2000). Selection on body size, for example, may be derived, as a secondary consequence of syrinx size that could influence the range of vocal frequencies of a bird's song (Ryan and Brenowitz, 1985).

Other studies have examined the role that ecological factors can exert on shaping signal elaboration (Catchpole, 1980, 1982; Endler, 1992; Price, 1993; Hill, 1994) and traits such as repertoire size and song complexity in avian taxa (Howard, 1974; Kroodsma, 1977; Vehrencamp, 1999). Also Robert *et al.* (2006) are among those who have attempted to integrate song analysis with plumage and molecular data in their study of the systematics of the quailfinches *Ortygospiza*. This study has extensively investigated vocal phylogeny of an entire family (Nectariniidae), mainly from acoustic measurements of their vocalisations and drawn attention to correlations between bill length and body size and song complexity.

A few researchers (Maclean, 1985; Grimes, 1974, 2007; Langrand, 1990; Brieschke, 1990, 1991; Rasmussen and Anderton, 2005) have previously attempted to investigate the vocalisations and acoustic structure of the Nectariniidae. But these studies have focused mostly on specific species of flowerpeckers and sunbirds and have relied solely on visual inspection of sonograms. Sonograms produced by these authors include those of the nominate subspecies of the Amethyst Sunbird *Chalcomitra amethystina amethystina* (Brieschke, 1990) and the Southern Double-collared Sunbird *Cinnyris chalybeus chalybeus*, a subspecies of the Greater Double-collared Sunbird *Cinnyris afer saliens* (Brieschke, 1991) and the differing dialects of the Splendid Sunbird *Cinnyris coccinigaster* (Grimes, 1974, 2007; Payne, 1978). Also, a sonographic analysis of the vocalisations of 17 species of Southern African Sunbirds (Maclean, 1985) presented sonograms of the Malachite Sunbird *Nectarinia famosa*, Bronze Sunbird *Nectarinia kilimensis*, Mariqua Sunbird *Cinnyris mariquensis*, Purple-banded Sunbird *Cinnyris bifasciatus*, Shelley's Sunbird *Cinnyris shelleyi*, Neergaard's Sunbird *Cinnyris neergaardi*, Greater Double-collared Sunbird *Cinnyris afer*, Variable Sunbird *Cinnyris venustus*, Oustalet's Sunbird *Cinnyris oustaleti*, Dusky Sunbird *Cinnyris fuscus*, Southern Double-collared Sunbird *Cinnyris chalybeus*, Olive-bellied Sunbird *Cinnyris chloropygius*, Scarlet-chested Sunbird *Chalcomitra senegalensis,* Amethyst (or Black) Sunbird *Chalcomitra amethystina amethystina*, Collared Sunbird *Anthodiaeta collaris*, Blue-throated Sunbird *Cyanomitra cyanolaema* and Violet-backed Sunbird *Anthreptes longuemarei.* The sonograms published in the above studies are similar to those of the same taxa analysed during this study. In some cases the same recordings may have been used.

This study provides the first comprehensive study of the vocalisations of the flowerpeckers, sunbirds and spiderhunters involving comparative, acoustic and statistical analyses and derivations of phylogenies based on them. This study is also one of the few studies that has applied a large number of vocal parameters (10-20 characters; chapter 3) to independently derive the phylogeny of an entire family (Nectariniidae) of birds. Some aspects of morphology and behavioural correlates have also been examined.

This study is also the first to adopt thresholds of entropy values derived directly from sonograms as criteria for the classification of bird songs through the frequency domain technique. Boltzmann (1974) presented a constant (1.380658 x 10-23 Joules/Kelvin) as the basis for measuring entropy values (ranging between 0-1). Since the concept of entropy postulates that a system will almost always be found to be moving towards the direction of maximum disorder, ordered systems are thought to produce entropy faster and at higher energy than a disordered system. And this provides the basis for the entropy values generated from calls (high entropy values) and songs (low entropy values) to be used as an objective classification (> 0.34) for separating calls from songs and (≥ 0.3 and ≤ 0.34) for distinguishing simple from complex songs.

This means that entropy values above a maximum of 0.34, relate to entropy levels characteristic of ordered states and characteristic of bird calls, as against the minimum value of less than or equal to 0.3 as low entropy levels of more ordered states corresponding to the nature of varying syllables embedded in a complex song. Simple songs have entropy values ranging between 0.3 and 0.34. See below for entropy and negentropy conversions:

(negentropy = 1-entropy).

Entropy	Negentropy	Song type
>0.34	<0.66	Calls
>0.3 & ≤ 0.34	≥0.66	Simple songs
<0.3	>0.7	Complex songs.

The idea of entropy was born from classical thermodynamics, as a quantitative entity and not a qualitative one. Perhaps the first major excursion of entropy into new domains comes at the hands of Shannon (1948), widely recognized as the father of modern communication and information theory. In *A Mathematical Theory of Communication*, Shannon proves that Boltzmann's (1974) concept of entropy is the only function which satisfies the requirements for a function to measure the uncertainty in a message and where a "message" is a string of binary bits or successive bits in a string as not random, and therefore not a subjective quantity but an objective quantity, measured in bits (binary digits). It is therefore under the above premise that this study adopted the entropy values derived from the vocal communication of bird songs as an objective measure of distinguishing calls from songs and simple songs from very complex songs. Complex songs with low entropy can transmit signals with more information (measured in bits) than calls.

Irwin (1999), supported by Fry *et al.* (2000), proposed that sunbirds are of African origin. Although Irwin (1999) did not derive any phylogeny in support of his postulation, while broadly following that of Delacour (1944) see (Figure 4.14a and b), he was motivated by several observations. The first was on the bill size / structure and the feeding adaptation of sunbirds. On the basis that the most primitive African Sunbirds have shorter bills than their Asian counterparts and would, perhaps, be mostly insectivorous rather than nectar feeders, he formed the view that the Afrotropical sunbirds are more likely to be the source of a major radiation from which the entire family may have arisen.

Strangely, the genus *Anthreptes* was classed as the most primitive and *Cinnyris* the most derived genera of the subfamily Nectariini based on bill size and length. However, the two genera share both the Afrotropical and the Oriental regions and even within *Anthreptes* such an inference presents some difficulty, given that some members of the genus such as *A. reichenowi* and *A. anchietae* possess rather long bills (Delacour, 1944; Cheke and Mann, 2001). Irwin (1999) further proposed that since two-thirds of sunbirds (16 genera) are of Afrotropical origin with only about a third (5 genera) from the oriental regions extending to Australia, it was most likely that sunbirds are of African origin.

Further arguments advanced in support of Irwin's (1999) position were on the basis of species endemism and the evolutionary histories of the two continents. Since two-thirds (8 genera) of sunbirds, including the largest genus *Cinnyris*, are endemic to the Afrotropics, as against only (4 genera) of endemic oriental sunbirds, and on the assumption that the African continent has had a much more primitive and long evolutionary history than the oriental region, he speculated that sunbirds were of African origin.

Prior to this study beak morphology has played a significant role in the taxonomic grouping and generic placement of most members of the Nectariniidae. The short, stout and straight bills of flowerpeckers, for example, has contributed greatly to the separation of the group into the tribe Dicaeini as the most basal of the Nectariniidae, which is consistent with acoustic categorisation of their vocalisation reported here. And on the same basis, the spiderhunters were separated into the genus *Arachnothera* by their larger body size and longer and more heavily built decurved bills as compared to sunbirds (Grzimek, 1973; Maclean, 1985; Cheke and Mann, 2001).

In his revision of the Nectariniidae, Delacour (1944) constructed an evolution ladder (cladogram) (Figures 4.13a and b) representing the evolutionary pathway of the family aimed at reconstructing the history of successive divergences within the family at the generic level. Among other characters such as tongue shape, bill size / length, tail length and other plumage features, Delacour's (1944) evolutionary sequence of the family was based primarily on the presence and or the absence of the bright metallic plumage found in most males or only by the similarity or slight differences in both sexes of some species. Delacour (1944) and others are of the view that dull colouration is a fundamental attribute of primitivism among bird species and that bright and or glossy colours are features that evolve over time and are a characteristic of a derived phenomenon. He argued that primitive species are mostly without metallic colours or appeared duller except in the cases of open and closed forest species. In his evolutionary cladogram, he placed the tribe Dicaeini as the basal clade of the Nectariniidae representing the group with few species exhibiting glossy plumage. The rest of the evolutionary sequence followed a lineage gradient with the *Anthreptes* radiating closely after the basal Dicaeini, followed by *Arachnothera* and *Aethopyga*. *Nectarinia* and other genera including *Cinnyris* were placed at the top of the cladogram and classed in a similar order as the most advanced members of the family representing the groups with the highest members displaying the brighter or glossy plumage.

Delacour's 1944 cladogram (Figure 4.13b) also appears to suggest that the genus *Leptocoma* which is exclusively from the oriental region with 6 species (Purple-rumped Sunbird *Leptocoma zeylonica*, Crimson-backed Sunbird *Leptocoma minima*, Purple-throated Sunbird *Leptocoma sperata*, Black Sunbird *Leptocoma sericea* and the Copper-throated Sunbird *Leptocoma calcostha*) may have had its root in Africa with the indication that the genus may have evolved from the genus *Chalcomitra* another exclusively African genus with 7 species (Buff-throated Sunbird *Chalcomitra adelberti*, Carmelite Sunbird *Chalcomitra fuliginosa*, Green-throated Sunbird *Chalcomitra rubescens*, Amethyst Sunbird *Chalcomitra amethystina*, Scarlet-chested Sunbird *Chalcomitra senegalensis*, Hunter's Sunbird *Chalcomitra hunteri* and including the Socotra Sunbird *Chalcomitra balfouri*). This provides further support to Irwin's 1999 claim that sunbirds originate from Africa but is based only on the above two genera out of the 11 genera currently proposed for sunbirds.

The sequence of song complexity (negentropy) and the phylogeny derived in this study at the generic level are consistent with the evolutionary lineage of the Nectariniidae proposed by Delacour (1944). *Prionochilus* and *Dicaeum* have the lowest negentropy (Figures 4.14 and 4.23) or song complexity, suggestive of their being the most primitive clade of the Nectariniidae while *Cyanomitra* and *Cinnyris* had the highest negentropy (or the more complex songs) and therefore representative of the advanced members of the family. This study is the first to use vocalisations to demonstrate a comprehensive evolutionary lineage of an entire avian family (Nectariniidae) and is partly supportive of a lineage constructed through morphology, although its main conclusions concur more with the DNA-based lineages.

Bowie (2003) conducted a combined nDNA and mtDNA analyses on 102 species of sunbirds (without considering flowerpeckers or spiderhunters) and derived a DNA phylogeny of the Nectariniidae (Figure 4.24 of Chapter 4). Bowie's phylogeny included a clade of 6 species or species groups (*Nectarinia sperata, Aethopyga,* Asian *Anthreptes, Anthreptes singalensis, Arachnothera* and *Hypogramma*) from the Asian continent and another of 4 Indian Ocean Islands species (*Nectarinia humbloti, Nectarinia souimanga, Nectarinia jugularis* and *Nectarinia notata*). He used an old classification. Hence all these species are treated as *Nectarinia* and *Cinnyris* as the most basal. Bowie's (2003) DNA phylogenetic tree therefore indicated clearly that the Asian clade of 6 species was basal to the African and the Indian Ocean species and therefore represents the primitive or outgroup of the taxa contrary to Irwin's claim that the sunbird lineage rather originates from Asia.

Evidence of strong congruence of vocal and DNA phylogenies has been shown before in species or groups including *Regulus* (Packert *et al.*, 2003), the various old world warblers such as *Phylloscopus trochiloides* (Irwin, 2001; Irwin *et al.*, 2001); the *P. collybita* complex (Helbig *et al.*, 1996), *P. bonelli* (Helbig *et al.*, 1995) and the Golden-spectacled Warbler *Seicercus burkii* complex (Martens *et al.*, 1999; Alstrom and Olsson, 2000; Martens and Eck, 2000).

The vocal phylogeny from this study involving 294 taxa (when subspecies are counted separately) has revealed that the 10 Asian sunbirds with complex songs include 72 taxa. The Olive-backed Sunbird (represented by *Cinnyris jugularis obscurior*, *Cinnyris jugularis ornatus* and *Cinnyris jugularis infrenatus*), Purple Sunbird (*Cinnyris asiaticus brevirostris*, *Cinnyris asiaticus asiaticus*), Long-billed Sunbird (*Cinnyris lotenius lotenius*), Crimson-backed Sunbird (*Leptocoma minima*), Fork-tailed Sunbird (*Aethopyga christinae latouchii*), Green-tailed Sunbird (*Aethopyga nipalensis koetzi*) and Metallic-winged Sunbird (*Aethopyga pulcherrima jefferyi*) emerged as the basal clade of the sunbird complex song tree (Figure 4.22, chapter 4) and therefore were confirmed as the most primitive clade of the Sunbird lineage.

The derived or ingroup clades of the African sunbirds include (a) the Indian Ocean sunbirds comprising the Madagascar Sunbird *Cinnyris notatus* (*C. n. notatus*), Souimanga Sunbird *Cinnyris souimanga* (*C. s. souimanga* and *C. s. aldabrensis*), Humblot's Sunbird *Cinnyris humbloti* (*C. h. humbloti*), Anjouan Sunbird *Cinnyris comorensis*, Mayotte Sunbird *Cinnyris coquerellii*, Seychelles Sunbird *Cinnyris dussumieri* and Socotra Sunbird *Chalcomitra balfouri* with multifurcating radians and supported by 92% bootstrap value and (b) the Gulf of Guinea species; Sao Tome Sunbird *Dreptes thomensis*, Newton's Sunbird *Anabathmis newtonii* and Principe Sunbird *Anabathmis hartlaubii* supported with 71% bootstrap and including Reichenbach's Sunbird *Anabathmis reichenbachi.* These separations and their positions on the tree suggested that the origin of sunbirds may have been Asia and that they reached Africa via the Indian Ocean islands and Madagascar. The Gulf of Guinea species lineage may have been defined along a colonisation route from the African continent and thus in support of Bowie's hypothesis.

Vocal phylogeny has also been used extensively to attest the affinities of other birds. Jordan and Lanyon (2002), Whitney and Pacheco (1994) among others, have used song characters to estimate the phylogenetic affinities of *Psarocolius*, *Gymnostinops* and *Ocyalus* of the Oropendola taxa and the genera *Gyalophylax* and *Megaxenops,* while Miller (1996) and Winkler and Short (1978) have used vocal characteristics to infer the relationships among plovers *Pluvialis* and some sandpipers *Calidris* and Pied Woodpeckers *Picoides* and *Dendrocopos*. The vocal phylogenies derived in this study (Figures 4.16 and 4.23; Chapter 4) further confirmed the affinities within the flowerpeckers and, as a separate clade distinct from spiderhunters and sunbirds. The flowerpecker genus *Prionochilus* (restricted to Asia) was affirmed as the most primitive and basal of the Nectariniidae. The sunbirds and spiderhunters appeared inseparable by vocal phylogeny and were contained in a single clade. Although the vocal phylogeny of this study failed to support the above separation, it supported the grouping of the two genera into the tribe Nectariniini, distinct from the Dicaeini.

The study revealed that there are varying degrees of acoustic variations among conspecifics, and among allopatric groupings and, as expected, are most uniform among intraspecific samples. Some songs appear to be very simple while others are very complex.

6.1. CONSTRAINTS OF THE RESEARCH

It is clear from the design of this study that good quality recordings of all the vocalisations of the Nectariniidae would have enhanced the strength of the overall conclusions. The collection and collation of pre-recorded vocal tracks of the taxa were not without several inherent problems and these included confusion with the names of some species when they were recorded and inadequate information on the locality in which some of the recordings were made. Information on habitat type and behavioural and functional attributes of the songster were often omitted from the supporting documentation.

Although filtering and editing mechanisms are built into the Avisoft software, the Frequency Domain transformation (FFT) filter technique and the edit menu are limited in their handling of background noise from water currents, wind blow, songs / calls of other animals and birds in the background, buzzing of insects across the microphone, humans' voices, booming of cars or aircraft etc. As a consequence, the quality of some sonograms and the exported statistical values of some parameters were sometimes impeded.

In addition, bird duetting and choir singing reported in some species and including the Amethyst Sunbird *Chalcomitra amethystina* (Brieschke 1990) are among the features that further complicated editing and compromised the quality of some sonogram output. The somewhat uniform morphological attributes of the Nectariniidae impeded attempts to derive comparative morpho-phylogenies for the taxa.

Dialectal variation has been reported in birds (Baker, 1982, 1983; Chilton, 1991; Lampe and Baker, 1994), but in only three species of sunbirds: Lesser Double-collared Sunbird *Cinnyris chalybeus,* Splendid Sunbird *C. coccinigaster* and Bronze Sunbird *Nectarinia kilimensis* (Brieschke, 1990; Grimes, 1974, 2007). The extent to which dialects could have masked or exaggerated differences detected in analyses of the vocalisations of the Nectariniidae and hence the phylogeny is unknown. The habitat signals attenuation effect (Marten and Marler, 1977; Martens, 1980; Endler, 1992; Forrest, 1994; Brown and Handford, 1996, 2000) may have contributed to modifying the vocalisations of the Nectariniidae analysed. Some apparent indication of habitat influences on the vocalisations has been shown by the clustering of the groupings of the family at generic level into open or closed habitat types by the analysis of the vocal frequency in relation to bill length and body size.

Although no particular study has been conducted on the Nectariniidae on the constraints that song learning (Chilton, 1991; Doupe and Kuhl, 1999; Brenowitz, 2002), mimicry (Lemaire, 1975; Dowsett-Lemaire, 1979) and song repertoire size (Anderson, 1994; Searcy and Yasukawa, 1996; Spencer *et al.*, 2003) might have, it is possible that these phenomena may have affected the results and hence the phylogenies derived in this study. It is, however, unlikely that the above limitations would have compromised the overall reliability of the outcome.

6.2. CONSERVATION IMPLICATIONS

The conservation of birds in the tropics has been hampered by a lack of comprehensive conservation policies and strategies for most species. The Nectariniidae have additionally suffered from a lack of awareness and insufficient scientific information at generic and species levels. Conservationists' attention to these taxa has mostly emanated from their concerns over species under specific types of threat.

Habitat loss and degradation based on human encroachment have resulted in some species or populations, particularly those restricted to forest or specific types of habitat, being threatened with extinction. However, recent developments in phylogeny are giving conservationists insights into the magnitude of the anthropogenic threat to biodiversity. In some cases, phylogeny is helping to delimit species diversity assessments and management (Vane-Wright *et al.*, 1991). In some cases, understanding the origins of species can assist in the conservation of biodiversity by contrasting current versus historical patterns, and the processes that have generated these patterns. Phylogeny further provides frameworks for detailed investigations of how anthropogenic processes (overexploitation and habitat loss) affect biodiversity (Fisher and Owens, 2004). Other phylogenetic inferences also enable conservationists to extrapolate the past and the future and predict what might happen to biodiversity under different possible scenarios (Rosenzweig, 2001).

Many other studies have implicated habitat loss or fragmentation and the occurrence of anthropogenic barriers to the transmission of song cultures and how it could lead to isolation (Laiolo and Tella, 2005) or species split through the dialectal effect (McGregor *et al.*, 1997; Vos and Chardon, 1998). However, few of these have attempted to highlight the overall communication system or song variation among species (Holland *et al.,* 1996), song sharing by neighbours and clues that bird song can give to imminent habitat loss or fragmentation and the need for conservation intervention (Laiolo and Tella, 2005).

The studies of acoustic signals of many animals have provided very useful insight to the understanding of the social life of most species and have contributed greatly to the conservation and management of many animal species and their habitats. The recognition of species specific acoustic signals has been used in the monitoring and management of marine and moist forest dependent animals. For example elephants and in particular the Indian elephant *Elephas maximus* have been monitored and censused from the infrasonic recordings of their vocalisations (Kumar, 2002).

Recent evidence further indicates that some morphologically similar animals can easily be identified by their vocalisations. Individually distinctive acoustic features have been demonstrated in many animals, examples of which include Chimpanzees *Pan* spp. (Marler and Hobbet, 1975); Stumptail Macaques *Macaca arctoides* (Lillehei and Snowdon, 1978); Japanese Macaque *Macaca fuscata* (Riede 1997); African Wild Dog *Lycon pictus*

(Hartwig, 2005); Wild dogs (McGregor *et al.*, 2000; Terry *et al.*, 2001); Wolves *Canis lupus* (Tooze *et al.*, 1990), Arctic foxes *Alopex lagopus* (Frommolt *et al.*, 2003), Asiatic wild dog *Cuon alpinus* (Durbin, 1998), and Swift foxes *Vulpes velox* (Darden *et al.*, 2003).

The role of acoustic features in discriminating vocalisations has also been studied in a number of bird species (Falls, 1982) including Zebra finches, *Taeniopygia guttata* (Okanoya and Dooling, 1991); Canaries *Serinus canaria* (Dooling *et al.*, 1992); Great Tits *Parus major* (Weary, 1990); Brown-headed Cowbirds *Molothrus ater* (Sinnott, 1980) and used in the application of bioacoustic techniques for conservation (McGregor and Kump, 2006; Fox *et al.*, 2006). Individual recognition by acoustic signals, a non-invasive identification method has also been tested on a number of bird species. For example the Eurasian Cuckoo *Cuculus canorus* and the Indian Cuckoo *Cuculus micropterus* are morphologically very similar but the songs of the two species are quite different and have been separated based on the elements of their song phrases and amplitude (Kumar, 2002).

It would be possible to apply the acoustic signal technique for the identification of members of the Nectariniidae with similar morphology or those that are inaccessible and difficult to observe, as in the case of the top canopy forest-dwelling flowerpeckers or those species of sunbirds inhabiting closed and impenetrable habitats, whose accessibility and identification is problematic in the field (Cheke and Mann 2001).

Advocates of this technique are of the view that it is non-stressful (Villiers *et al.*, 1995) and non-injurious (Creel and Creel, 2002; Hartwig, 2005) to animals as compared to radio-tagging that may inflict excessive stress and injury on tagged species.

The relation between morphological characters and the vocalisation of sunbirds highlights the role of vocal communication in sexual selection and competition and for determining the outcome of agonistic contests (Anderson, 1994) and male to male interactions among songbirds.

It is imperative that the emerging techniques in vocal analyses and acoustic signals be incorporated into conservation strategies for the effective conservation and monitoring of bird species and populations together with their roles in taxonomic placing and phylogenies.

CHAPTER 7

7.1. SYNOPSIS OF FINDINGS

Although detailed aspects of the findings of this study have already been described in the preceding six chapters, the purpose of this chapter is to highlight the key findings and noteworthy discoveries in relation to secondary sources. The hypotheses relating to the lineage origin of Sunbirds and affinities of Flowerpeckers, Spiderhunters and Sunbirds within the family Nectariniidae have been tested based on their vocalisations. The morphotaxonomic and habitat analyses and any correlations with the vocalisations were conducted to seek behavioural and conservation implications for the taxa. Data from a total of 294 taxa including 158 species, 136 subspecies and involving 17,854 notes/elements were analysed. Of these taxa, 36 were Flowerpeckers, 18 were Spiderhunters and 240 were Sunbirds.

7.2. VOCALISATIONS

Analytical and sonographic representation of the vocalisations showed that in spite of the generally unformed acoustic structure of the vocalisations of all members of the Nectariniidae, there was significant variation amongst acoustic elements of the song types, to allow worthwhile analyses. However, much of the uniformity of acoustic variables was common among intraspecific recordings. This is congruent with the generally similar morphological characters but varied plumage and behavioural attributes within the taxa.

The vocalisations within the Flowerpeckers were found to be simple, mostly single repetitive call notes and very simple songs. However, Sunbirds and Spiderhunters appeared more varied in attributes and uttered a combination of call notes (mostly trills), simple songs (mostly whistles) and phrases, as well as complex songs, and many species possessed very large repertoires of phrases. Examples include the Cameroon Sunbird *Cyanomitra oritis oritis* and the Green-throated Sunbird *Chalcomitra rubescens crossensis.*

7.3. PHYLOGENY

Important findings based on the vocal phylogenies of the Nectariniidae were the strong affinities and close sister relationships between genera, species and subspecies, of the same species and among those with the same habitat type or overlapping geographical range. Examples include the strong relatedness of the Splendid Sunbird *Cinnyris coccinigaster* and the subspecies *C. s. superbus* of the Superb Sunbird *Cinnyris superbus* with a high bootstrap support of 100% as very simple songsters (Figure 4.17) which is outstanding and accords with their being sister taxa on morphological grounds. Another example was that one of the phylogenetic trees (Figure 4.18) further uncovered a subspecies of the Eastern Olive Sunbird *Cyanomitra olivacea* (*C. o. alfredi*) as sister taxon to *C. obscura sclateri*, a subspecies belonging to the Western Olive Sunbird *Cyanomitra obscura*. This close sister clade received 70.3% bootstrap support and adds the vocal dimension to the morphological and DNA debate on the validity of the split of the Olive Sunbird and furthers the role that avian vocalisations can play in the determination of species affinities.

Perhaps the most important finding of the study (See Figures 4.19 and 4.20) was the postulation from the vocal phylogeny of the lineage origin of Sunbirds suggesting the probable colonisation of Sunbirds on the main continent of Africa was from the Asian subcontinent and probably rooted through the Indian Ocean islands and Madagascar. The study further contended that a clade of Gulf of Guinea Island Sunbirds provides the possibility of another lineage of sunbirds derived from the African continent.

The generic relationship of the Dicaeini (Flowerpeckers) and Nectarinii (Sunbirds and Spiderhunters) was further tested using vocalisations from randomly selected species of each of the above groups. The resulting phylogenies on the Bayesian tree (Figure 4.21) also indicated that the Flowerpeckers are a clearly distinct group, with the genus *Prionochilus* confirmed as basal with 94% bootstrap support.

The Sunbirds and Spiderhunters appeared inseparable by vocal phylogeny and remained in a single clade with 84% bootstrap support. The vocalisations of the family also demonstrated a concrete evolutionary lineage within the family (Nectariniidae) at the generic level consistent with an earlier linage constructed through morphological reviews.

7.4. MORPHOLOGY AND BEHAVIOURAL CORRELATES

Although the Nectariniidae may present a rather unique small bodied and a generally monophyletic group on their morphological outlook, there is significant sexual dimorphism in the plumage of the taxa. Peculiar and sometimes elaborate plumage features were tested to assess the correlation with their vocalisations, but with no important result.

7.5. HABITAT AND NEST STRUCTURE

Habitat selection, nest structure and nest placement were examined as examples of behavioural attributes of the Nectariniidae. The diversity but general semblance, with which each taxon accomplishes these attributes, reflects their closeness. The Flowerpeckers (70%) and Spiderhunters (98%) are mostly forest dwelling birds. However, Sunbirds (See Figure 5.1, chapter 5) appear to occupy more varying habitat types, ranging from closed forest to semi desert habitats. There is a strong relationship between habitat and bill length at the generic level. With the exception of the Spiderhunters with cup-shaped types of nests, the nests of Flowerpeckers and Sunbirds are purse, oval or pear in shape sometimes with a porch over the nest entrance hole and or a beard, or both. Over 60% of Sunbirds construct their nest with a porch affixed to the entrance, 82.5% suspend their nests on a tree or bush or on artificial objects.

7.6. CONSERVATION IMPLICATIONS

This study has confirmed the role that the vocal phylogeny of the Nectariniidae could play in conservation and management since it has demonstrated that there are evolutionary and taxonomic signals in the vocal phylogenies. This means that vocal phylogenies can be used for the species delimitation and vocalisations used in the field for identifications of unseen birds and for taxonomic purposes when deciding on taxa requiring conservation measures. These attributes may be particularly important when using the phylogeny and acoustic signal techniques in future conservation strategies for the effective conservation and monitoring of some cryptic and elusive species, in particular the Flowerpeckers.

7.7. CONCLUSION

It has been possible from the findings of this study, to draw the following conclusions:

(1) Some members of the Nectariniidae utter simple songs whereas others utter very complex songs.

(2) Acoustic features of the vocalisations of Flowerpeckers, Sunbirds and

Spiderhunters can be used in assessing phylogenetic affinities.

(3) The congruence between the vocal phylogeny and molecular phylogeny of Sunbirds confirms the role that aspects of bird song can play in deriving the lineages of avian species

(4) Analysis of vocalisations supported Bowie's hypothesis of an Asian origin for the sunbirds based on DNA studies contrary to Irwin's suggestion that the sunbirds are of Afrotropical origin.

(5) The trend of song complexity at the generic level further supported Delacour's evolutionary lineage construction of the Nectariniidae based on bright and dull plumage differences.

(6) Analysis of beak morphology and body sizes and the vocalisations indicated significant relationships between bill length and body size and song complexity, with the latter higher in the more advanced genera. Song frequency was lower in forest species than those inhabiting open areas.

7.8. RECOMMENDATIONS FOR FUTURE RESEARCH

Further studies are required to fill the gap that exists in the morphological and behavioural attributes of some members of the Nectariniidae and in particular the breeding biology of most members of the Flowerpeckers.

Possible correlations between tongue types and the vocal ability of members of the Nectariniidae should be investigated.

There is also the need to explore the use of vocalisations of members of the taxa with similar morphology and / or closed forest-dwelling species as a fundamental tool for the conservation and management of such taxa.

Further studies are required on the taxonomic position of the Socotra Sunbird (*Chalcomitra balfouri*) since the results suggested that it would be better placed within *Cinnyris.*

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APPENDICES

APPENDIX 1a RECORDINGS OF FLOWERPECKERS & COMMENTS

Ref. no.	Scientific Name	Common name	Country	Region	Sex	duration	Call	Song	Comments
1	*Prionochilus olivaceus*	Olive-backed Flowerpecker	Philippines	Mindanao	M	0'31"	X		
2	*Prionochilus olivaceus*	Olive-backed Flowerpecker	Philippines	Mindanao	M	0'50"			"tri'ti'ti'ti'"
3	*Prionochilus maculatus*	Yellow-breasted Flowerpecker	Indonesia	West Kalimantan	M	1'11"	X	X	
4	*Prionochilus maculatus*	Yellow-breasted Flowerpecker	Malaysia	Pasoh	M	0'26"	X	X	Foraging with Pygmy Wren-Babbler
5	*Prionochilus percussus*	Crimson-breasted Flowerpecker	Indonesia	West Java	F	1'39"	X		
6	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	Indonesia	East Kalimantan	M	0'57"	X		
7	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	Indonesia	East Kalimantan	M	0'44"	X		Gibbons in the background
8	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	Indonesia	East Kalimantan	M	0'34"	X		Vehicle in the background
9	*Prionochilus thoracicus*	Scarlet-breasted Flowerpecker	Malaya	Paiti forest	M	1'30"	X	X	Grey Jungle fowl in the background
10	*Dicaeum agile*	Thick-billed Flowerpecker	India	South India	M	0'33"	X	X	Purple Sunbird & Jungle crow noise
11	*Dicaeum agile*	Thick-billed Flowerpecker	India	South India	M	1'27"	X		Cicadas in background
12	*Dicaeum agile*	Thick-billed Flowerpecker	Philippines	Palawan	M	1'01"	X		
13	*Dicaeum proprium*	Whiskered Flowerpecker	Philippines	Mindanao	M	0'57"	X		Alarm calls
14	*Dicaeum proprium*	Whiskered Flowerpecker	Philippines	Mindanao	M	1'32"	X		
15	*Dicaeum proprium*	Whiskered Flowerpecker	Philippines	Mindanao	M	1'23"			
16	*Dicaeum nigrilore*	Olive-capped Flowerpecker	Philippines	Mindanao	M	0'42"	X	X	
17	*Dicaeum nigrilore*	Olive-capped Flowerpecker	Philippines	Mindanao	M	0'25"			

18	*Dicaeum quadricolor*	Cebu Flowerpecker	Philippines	Cebu	M	1'38"	X		(Nearly extinct)
19	*Dicaeum quadricolor*	Cebu Flowerpecker	Philippines	Cebu	M	0'50"		X	
20	*Dicaeum australe*	Red-striped Flowerpecker	Philippines	N. Luzon	M	0'36"	X		
21	*Dicaeum australe*	Red-striped Flowerpecker	Philippines	Luzon	M	0'40"	X	X	
22	*Dicaeum australe*	Red-striped Flowerpecker	Philippines	Bohol	M	0'25"	X		
23	*Dicaeum australe*	Red-striped Flowerpecker	Philippines	Negros	M	1'30"	X	X	
24	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker	Philippines	Mindanao	M	0'47"	X		
25	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker	Philippines	Mindanao	M	0'38"	X		
26	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	Philippines	Central Luzon .	M	1'22"	X		Foraging
27	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	Singapore	Tekoug Island	M	1'00"		X	
28	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	Singapore	Tekoug island	M	0'51"		X	
29	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	Philippines	Bohol	M	0'34"	X		
30	*Dicaeum hypoleucum*	Buzzing Flowerpecke	Philippines	Mindanao	M	0'43"	X		
31	*Dicaeum hypoleucum r*	Buzzing Flowerpecke	Philippines	Mindanao	M	1'02"			
32	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	India	Ooty	M	0'43"		X	Song trill with Grey jungle fowl noise
33	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	India	Masinagudi	M	0'55"		X	Responds to playback with Goats noise
34	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	Sri Lanka	Sinharaja	M	0'46"	X		Insects at the background
35	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	Sri Lanka	Hakgala	M	2'12"	X		Voices at the background
36	*Dicaeum concolor*	Plain Flowerpecker	India	S. India	M	3'25"	x		Calls (1&2) same bird with Crows noise
37	*Dicaeum concolor*	Plain Flowerpecker	India	S. India	M	0'20"		X	Alarm call
38	*Dicaeum concolor*	Plain Flowerpecker	India	S. India	M	0'34"		X	Vehicles in the backgrounds
39	*Dicaeum bicolor*	Bicolored Flowerpecker	Phillipines	Luzon	M	0'34"		X	

40	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	Nepal	C. Nepal	M	1'06"	X		Rushing water as background noise
41	*Dicaeum pygmaeum*	Pygmy Flowerpecker	Phillipines	Luzon	M	0'18"	X		
42	*Dicaeum eximium*	Red-banded Flowerpecker	Papua New Guinea	East New Britain	F	2'28"	X		
43	*Dicaeum vincens*	White-throated Flowerpecker	Sri Lanka	Sinharaja	M	1'03"	X		
44	*Dicaeum aeruginosum*	Striped Flowerpecker	Phillipines		M	1'02"	-		
45	*Dicaeum celebicum*	Grey-sided Flowerpecker	Indonesia	Sulawesi	M	1'05"	X		*Oriolus chinensis* in background
46	*Dicaeum celebicum*	Grey-sided Flowerpecker	Indonesia	Lore Lindu	M	0'30"	X		
47	*Dicaeum celebicum*	Grey-sided Flowerpecker	Indonesia	Sulawesi	M	0'44"	-		Spotted Dove in the background
48	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	Malaysia	Buket Kumming Estate	M	0'45"	X		
49	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	Singapore	Layang Layang	M	1'05"		X	Lesser Coucal in the background
50	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	Singapore		M	0'25"		X	School noises
51	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	Singapore	Linden Drive	M	0'15"	X		Flight call
52	*Dicaeum igniferum*	Black-fronted Flowerpecker	Indonesia	Flores	M	0'25"		X	
53	*Dicaeum maugei*	Red-chested Flowerpecker	Timor		M	0'24"	X		
54	*Dicaeum nehrkorni*	Crimson-crowned Flowerpecker	Indonesia	Sulawesi	M	1'13"	-		
55	*Dicaeum pectorale*	Olive-crowned Flowerpecker	Indonesia	Irian Jaya New Guinea	M	0'09"	X		River noise in background
56	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker	Indonesia	Rotang Flores	M	0'10"	X		

57	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker	Indonesia	Sumba	M	0'40"	X		Insects in background
				Manusela N.P					
58	*Dicaeum vulneratum*	Ashy Flowerpecker	Indonesia	Seram	M	0'36"	X		River and Insects in the background
59	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	Bhutan		M	0'25"	X	X	
60	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	Bhutan	Tama	M	1'10"	X	X	Male and Males
61	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	Nepal		M	1'14"	X	X	
62	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	India	N. India	M	1'20"	X		People in the background
63	*Dicaeum igniferum*	Black-fronted Flowerpecker	Indonesia	Flores	M	0'53"	X		
64	*Dicaeum igniferum*	Black-fronted Flowerpecker	Indonesia	Flores	M	0'59"	X		
65	*Dicaeum annae*	Golden-rumped Flowerpecker	Indonesia	Flores	M	1'04"	X	X	
66	*Dicaeum chrysorrheum*	Yellow-vented Flowerpecker	Malay Penin.	Java	M	0'55"	X		
67	*Dicaeum anthonyi*	Flame-crowned Flowerpecker	Philippines	Luzon	M	1'25"	X	X	
68	*Dicaeum aeneum*	Midget Flowerpecker	Solomon Isl.	N. Solomons	M	0'44"	X		
69	*Dicaeum tristrami*	Mottled Flowerpecker	Solomon	Makira	M	0'56"	X	X	Insects in background
70	*Dicaeum hirundinacem*	Mistletoebird	Australia		M	1'29"	X		
71	*Dicaeum monticolum*	Black-sided Flowerpecker	Borneo	Gunung	M	0'42"	X		

APPENDIX 1b. RECORDINGS OF FLOWERPECKERS, RECORDISTS & LOCATIONS

Ref. no.	Scientific Name	Common name	Sp.n	Subsp.	Year	Ref.no.	Copyright holder	Locality
1	*Prionochilus olivaceus*	Olive-backed Flowerpecker	3	3,1	1990	34322	Greensmith, A	PICOP
2	*Prionochilus olivaceus*	Olive-backed Flowerpecker	3	3,1	1994	46663	Morris, P	PICOP
3	*Prionochilus maculatus*	Yellow-breasted Flowerpecker	4	4,1	1993	47804	Van Balen, B	Danu Sentarum Wildlfe Resev.
4	*Prionochilus maculatus*	Yellow-breasted Flowerpecker	4	4,3	1991	44124	Buckton, S	
5	*Prionochilus percussus*	Crimson-breasted Flowerpecker	5	5,2	1989	47805	Van Balen, B	Mt. Halimun NP
6	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	7	None	1992	47801	Van Balen, B	Kayan Mentavrang NP
7	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	7	None	1992	47802	Van Balen, B	Kayan Mentavrang NP
8	*Prionochilus xanthopygius*	Yellow-rumped Flowerpecker	7	None	1992	47803	Van Balen, B	Kayan Mentavrang NP
9	*Prionochilus thoracicus*	Scarlet-breasted Flowerpecker	8	None	1983	33327	Hails, C	Masinagudi (Ooty)
10	*Dicaeum agile*	Thick-billed Flowerpecker	10	1,1	1994	45337	Holt, P	Goa Bondla
11	*Dicaeum agile*	Thick-billed Flowerpecker	10	10,1	1996	65486	Holt, P	
12	*Dicaeum affine*	Thick-billed Flowerpecker	10	10,10	1999	65488	Holt, P	Palawan
13	*Dicaeum proprium*	Whiskered Flowerpecker	12	None	1985	16491	Wassink, A	Mt Apo NP
14	*Dicaeum proprium*	Whiskered Flowerpecker	12	None	1985	16497	Wassink, A	Mt Apo NP

15	*Dicaeum proprium*	Whiskered Flowerpecker	12	None	1995	65209	Morris, P	Baracatan
16	*Dicaeum nigrilore*	Olive-capped Flowerpecker	17	17,2	1990	34304	Greensmith, A	Baracatan
17	*Dicaeum nigrilore*	Olive-capped Flowerpecker	17	17,2	1997	67619	Drijvers, R	Mount Katanglad
18	*Dicaeum quadricolor*	Cebu Flowerpecker	20	None	1993	42603	Gardner, I	Central Cebu NP
19	*Dicaeum quadricolor*	Cebu Flowerpecker	20	None	1997	54863	Drijvers, R	Tabunan
20	*Dicaeum australe*	Red-striped Flowerpecker	21	None	1995	46602	Gardner, N	Angat watershed reserve
21	*Dicaeum australe*	Red-striped Flowerpecker	21	None	1997	54860	Drijvers, R	Mount Makling
22	*Dicaeum australe*	Red-striped Flowerpecker	21	None	1997	54861	Drijvers, R	Rajan Sikatuna NP
23	*Dicaeum australe*	Red-striped Flowerpecker	21	None	1997	54862	Drijvers, R	Casa Roro
24	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker	23	None	1995	65217	Morris, P	Sablayan
25	*Dicaeum retrocinctum*	Scarlet-collared Flowerpecker	23	None	1998	68635	Vercruysse, E	
26	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	24	24,17	1985	16427	Wassink, A	Los banos
27	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	24	24,6	1986	33376	Hails, C	
28	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	24	24,6	1986	33379	Hails, C	
29	*Dicaeum trigonostigma*	Orange-billed Flowerpecker	24	24,9	1997	67620	Drijvers, R	Rajan Sikatuna NP
30	*Dicaeum hypoleucum*	Buzzing Flowerpecker	25	25,3	1985	16473	Wassink, A	Mt Apo NP
31	*Dicaeum hypoleucum*	Buzzing Flowerpecker	25	25,5	1997	67621	Drijvers, R	Mount Katanglad
32	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	26	26,2	1995	51427	Holt, P	Sigur Ghat
33	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	26	26,2	1996	65488	Holt, P	Jungle hut
34	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	26	26,1	1995	52394	Smith, S	Research Centre
35	*Dicaeum erythrorhynchos*	Pale-billed Flowerpecker	26	26,1	1995	52446	Smith,S	Gardens
36	*Dicaeum concolor*	Plain Flowerpecker	27	27,2	1994	45340	Holt, P	Ooty

37	*Dicaeum concolor*	Plain Flowerpecker	27	27,2	1994	45341	Holt, P	-
38	*Dicaeum concolor*	Plain Flowerpecker	27	27,2	1996	65489	Holt, P	Ooty
39	*Dicaeum bicolor*	Bicolored Flowerpecker	19		1997	54859	Drijvers, R	Mt Makling
40	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	40		1996	65325	Holt, P	Kali Gandaki valley
41	*Dicaeum pygmaeum*	Pygmy Flowerpecker	28	28,5	1997	54864	Drijvers, R	Angat
42	*Dicaeum eximium*	Red-banded Flowerpecker	35	35,2	1993	73978	Gunnerson, N	Wild Dog Mining Camp
43	*Dicaeum vincens*	White-throated Flowerpecker	15		1994	52376	Smith, S	-
44	*Dicaeum aeruginosum*	Striped Flowerpecker	10	10,11	1995	65197	Morris, P	Sito Siete
45	*Dicaeum celebicum*	Grey-sided Flowerpecker	42		1980	13188	Watling, D	Palu Valley
46	*Dicaeum celebicum*	Grey-sided Flowerpecker	42		1991	32912	Greensmith, A	Kamaroa
47	*Dicaeum celebicum*	Grey-sided Flowerpecker	42		1991	45888	Smith, S	Tambun
48	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	45		1973	6335	Kersley, R	-
49	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	45		1985	33344	Hails, C	-
50	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	45		1985	33368	Hails, C	-
51	*Dicaeum cruentatum*	Scarlet-backed Flowerpecker	45		-	33408	Hails, C	-
52	*Dicaeum igniferum*	Black-fronted Flowerpecker	38		1991	32980	Greensmith, A	Kisol
53	*Dicaeum maugei*	Red-chested Flowerpecker	39		1992	46763	Lewis, A	Kapan
54	*Dicaeum nehrkorni*	Crimson-crowned Flowerpecker	29	None	1991	45820	Smith, S	Lore Lindu
55	*Dicaeum pectorale*	Olive-crowned Flowerpecker	32	32,2	1991	43170	Smith, S	Afaks Mokwam Village
56	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker	43		1991	33014	Greensmith, A	Pokoranka
57	*Dicaeum sanguinolentum*	Blood-breasted Flowerpecker	43		1991	43389	Smith, S	Lewa

58	*Dicaeum vulneratum*	Ashy Flowerpecker	31	None	1991	43258	Smith, S	Nr Liang 2
59	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	40		1967	15106	Bertram, B	Batashie Camp
60	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	40		1967	15125	Bertram, B	-
61	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	40		1991	44802	Holt, P	Phulchowki
62	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	40		1994	46038	Holt, P	Uttar Pradesh
63	*Dicaeum igniferum*	Black-fronted Flowerpecker	38		1997	33305	Leadley, J	Riung
64	*Dicaeum igniferum*	Black-fronted Flowerpecker	38		1997	33395	Leadley, J	Golo Bilas
65	*Dicaeum annae*	Golden-rumped Flowerpecker	9		1997	33385	Leadley, J	Rana Mese
66	*Dicaeum chrysorrheum*	Yellow-vented Flowerpecker	13	13,2	1998	31246	Hails, C.	-
67	*Dicaeum anthonyi*	Flame-crowned Flowerpecker	18	18,1	2000	43341	Smith, S	Mt Polis
68	*Dicaeum aeneum*	Midget Flowerpecker	36	36,1	1996	33504	Greensmith, A	Ysabel
69	*Dicaeum tristrami*	Mottled Flowerpecker	37	None	1992	46331	Morris, P.	-
70	*Dicaeum hirundinacem*	Mistletoebird	44	44,2	1999	34323	Bertram, B	-
71	*Dicaeum monticolum*	Black-sided Flowerpecker	41	None	1997	54642	Holt, P.	-

APPENDIX 1c RECORDINGS OF ASIAN SPECIES (SUNBIRDS AND SPIDERHUNTERS & COMMENTS)

Ref. no.	Scientific Name	Common name	Country	Region	Sex	duration	Song	Call	Comments
1	*Anthreptes malacensis*	Plain-throated Sunsbird	Indonesia	Maluku province	M	01:08	X		
2	*Anthreptes malacensis*	Plain-throated Sunsbird	Malaysia	Kuala Lumpur	M	00:48		X	
3	*Anthreptes malacensis*	Plain-throated Sunsbird	Indonesia	East Java	M	01:43		X	Human / domestic noise
4	*Anthreptes malacensis*	Plain-throated Sunsbird	Malaysia	Pulan Tioman island	F	01:48		X	Calling in tree
5	*Anthreptes malacensis*	Plain-throated Sunsbird	Indonesia	Sumba	M	01:43	X	X	
6	*Anthreptes malacensis*	Plain-throated Sunsbird	Malaya	Rantau Panjang	M	03:03	X		*Oriolus* sp. in background
7	*Anthreptes malacensis*	Plain-throated Sunsbird	Singapore	Layang Layang	M	01:24	X		
8	*Anthreptes singalensis*	Ruby-cheeked Sunbird	Indonesia	Sulawesi	M	1.02			Domestic fowl noise
9	*Anthreptes singalensis*	Ruby-cheeked Sunbird	Malaysia	Taman nagara NP	M	0.8		X	
10	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	South India (Goa)	M	00:34		X	
11	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	South India (Ooty)	F	02:42		X	Calls from female
12	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	South India (Goa)	M	01:16		X	
13	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	South India (Goa)	M	00:48	X	X	Warbler in background
14	*Nectarinia zeylonica*	Purple-rumped Sunbird	Sri Lanka	Nr Wattala	M	00:43	X		Male perched
15	*Nectarinia zeylonica*	Purple-rumped Sunbird	Sri Lanka	Nr Wattala	M	01:38	X	X	Calls & territorial songs
16	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	Madras City	M	01:16	X		
17	*Nectarinia zeylonica*	Purple-rumped Sunbird	India	South India	M	00:54	X		People in background

18	*Nectarinia minima*	Crimson-backed Sunbird	India	South India (munnar)	M	01:08	X		Babbler noise
19	*Nectarinia minima*	Crimson-backed Sunbird	India	South India (Goa)	M	01:10		X	
20	*Nectarinia minima*	Crimson-backed Sunbird	India	South India (Goa)	M	01:40	X		
21	*Nectarinia minima*	Crimson-backed Sunbird	India	South India (Ooty)	M	00:50		X	Warbler bird in backgro
22	*Nectarinia minima*	Crimson-backed Sunbird	India	South India (Ooty)	M	01:47		X	Response to playback
23	*Nectarinia minima*	Crimson-backed Sunbird	India	Kerela state	M	03:10	X		Male perched
24	*Nectarinia sperata*	Purple-throated Sunbird	Singapore	Sime Road	M	01:01	X		
25	*Nectarinia sperata*	Purple-throated Sunbird	Philippines	Palawan	M	00:57			
26	*Nectarinia sericea*	Black Sunbird	Indonesia	Talaud	M	01:31		X	
27	*Nectarinia sericea*	Black Sunbird	Indonesia	Sangihe	3M	04:31	X	X	
28	*Nectarinia sericea*	Black Sunbird	Indonesia	Maluku province	M	00:43	X		
29	*Nectarinia sericea*	Black Sunbird	BBC?	BBC	M	00:42			
30	*Nectarinia sericea*	Black Sunbird	Indonesia	Halmahera	M	00:58		X	
31	*Nectarinia sericea*	Black Sunbird	Indonesia	Seram	M	00:54		X	
32	*Nectarinia sericea*	Black Sunbird	Indonesia	Seram	M	00:33		X	
33	*Nectarinia calcostetha*	Copper-throated Sunbird	Thailand	Krabi Mangroves	M	00:30		X	
34	*Nectarinia lotenia*	Long-billed Sunbird	Sri Lanka	Colombo District	M	02:06	X	X	Territorial song
35	*Nectarinia lotenia*	Long-billed Sunbird	Sri Lanka	Colombo District	M	01:12	X	X	Territorial song
36	*Nectarinia lotenia*	Long-billed Sunbird	Sri Lanka	Colombo District	M	00:49	X	X	Territorial song
37	*Nectarinia lotenia*	Long-billed Sunbird	Sri Lanka	Altitude C.120	M	01:33		X	Feeding with Barbet
38	*Nectarinia lotenia*	Long-billed Sunbird	India	S. India (Periyar)	F	00:24		X	Grey Junglefowl noise

39	*Nectarinia lotenia*	Long-billed Sunbird	India	South India (Goa)	M	00:48	X		
40	*Nectarinia lotenia*	Long-billed Sunbird	India	South India	M	00:40	X		Response to playback
41	*Nectarinia lotenia*	Long-billed Sunbird	India	South India	M	00:37	X		
42	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Buru (Teluk Bara)	M	00:53		X	
43	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Sulawesi (Palu)	M	01:48		X	
44	*Nectarinia jugularis*	Olive-backed Sunbird	Singapore	Pierce Reserve	M	00:39	X	X	
45	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Ambou (Hills)	M	00:45	X		
46	*Nectarinia jugularis*	Olive-backed Sunbird	India	Andaman Islands	M	01:11		X	Calls from male
47	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Maluku province	M	01:08	X		
48	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Maluku province	M	00:53	X		
49	*Nectarinia jugularis*	Olive-backed Sunbird	Manus Island	Lorengan	M	01:36		X	
50	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Java (Baluran)	M	00:28			
51	*Nectarinia jugularis*	Olive-backed Sunbird	Indonesia	Sulawesi	M	01:58			
52	*Nectarinia jugularis*	Olive-backed Sunbird	Philippines	Luzon	M	00:30	X		
53	*Nectarinia buettikoferi*	Apricot-breasted Sunbird	Indonesia	Sumba	M	00:27		X	
54	*Nectarinia buettikoferi*	Apricot-breasted Sunbird	Indonesia	Sumba	M	00:49	X		
55	*Nectarinia solaris*	Flame-breasted Sunbird	Indonesia	Timor	M	00:51		X	
56	*Nectarinia solaris*	Flame-breasted Sunbird	Indonesia	Flores	M	00:40	X		
57	*Nectarinia solaris*	Flame-breasted Sunbird	Indonesia	Timor (West)	M	00:27			
58	*Nectarinia solaris*	Flame-breasted Sunbird	Indonesia	Flores	M	01:08	X		
CD2									
59	*Nectarinia asiatica*	Purple Sunbird	Iran	Persian Baluchistan	M	02:33	X	X	Perched & flight calls

60	*Nectarinia asiatica*	Purple Sunbird	Thailand	Huai Kha Khaeng	M	01:32		X	
61	*Nectarinia asiatica*	Purple Sunbird	India	Northern India	M	01:28		X	
62	*Nectarinia asiatica*	Purple Sunbird	India	Northern India	M	00:51	X		
63	*Nectarinia asiatica*	Purple Sunbird	Sri Lanka		M	00:25		X	
64	*Nectarinia asiatica*	Purple Sunbird	India	South India (Gao)	M	01:57	X	X	Response to playback
65	*Nectarinia asiatica*	Purple Sunbird	India	South India (Gao)	M	01:27	X		
66	*Nectarinia asiatica*	Purple Sunbird	India	South India (Ooty)	M	00:16		X	Barbet noise
67	*Aethopyga primigenius*	Grey-hooded Sunbird	Philippines	Mindanao	M	00:41	X		
68	*Aethopyga primigenius*	Grey-hooded Sunbird	Philippines	Mindanao	M	00:36	X		
69	*Aethopyga boltoni*	Apo Sunbird	Philippines	Mindanao	M	00:52	X		
70	*Aethopyga boltoni*	Apo Sunbird	Philippines	Mindanao	M	01:48			
71	*Aethopyga boltoni*	Apo Sunbird	Philippines	Mindanao	M	00:49			
72	*Aethopyga flagrans*	Flaming sunbird	Philippines	Panay	M	00:51			
73	*Aethopyga flagrans*	Flaming sunbird	Philippines	Luzon	M	00:34			
74	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Northern Luzon	M	01:18		X	Calls while feeding
75	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Luzon	M	00:28	X	X	
76	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Luzon	M	01:18	X		
77	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Mindanao	M	01:05			
78	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Luzon	M	01:00			
79	*Aethopyga pulcherrima*	Metallic-winged Sunbird	Philippines	Mindanao	M	01:10	X		
80	*Aethopyga duyvenbodei*	Elegant Sunbird	Indonesia	Sangihe	M	00:55	X		
81	*Aethopyga duyvenbodei*	Elegant Sunbird	Indonesia	Sangihe	M	07:06		X	In tree (Ferns)

82	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	Palawan	M	00:48	X		Cicadas in background
83	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	Palawan	M	01:10	X		
84	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	119°E, 10°5'N	M	02:29	X		
85	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	Palawan	M	02:10	X		
86	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	Palawan	M	01:39	X		
87	*Aethopyga shelleyi*	Lovely Sunbird	Philippines	Palawan	M	00:52	X		
88	*Aethopyga gouldiae*	Gould's Sunbird	Bhutan	Central Bhutan	M	01:33	X		Hill partridge in background
89	*Aethopyga gouldiae*	Gould's Sunbird	China	Sichaun province	M	00:41			Flight notes
90	*Aethopyga nipalensis*	Green-tailed Sunbird	Nepal	Gokarna	M	00:39	X		Response to Playback
91	*Aethopyga nipalensis*	Green-tailed Sunbird	India	Nainital	M	02:51		X	
92	*Aethopyga nipalensis*	Green-tailed Sunbird	Nepal	Phulchowki	M	00:41		X	
93	*Aethopyga nipalensis*	Green-tailed Sunbird	Bhutan	Chhuzomsa	M	02:58		X	Robin in background
94	*Aethopyga nipalensis*	Green-tailed Sunbird	India	Meghalaya	M	00:52		X	
95	*Aethopyga eximia*	White-flanked sunbird	Indonesia	Java	M	00:28	X	X	
96	*Aethopyga eximia*	White-flanked sunbird	Indonesia	Java	M	00:59			
97	*Aethopyga christinae*	Forked-tailed Sunbird	Vietnam	Tonkin	M	00:53	X		
98	*Aethopyga christinae*	Forked-tailed Sunbird	China	New territories	M	01:32			
99	*Aethopyga christinae*	Forked-tailed Sunbird	China	New territories	M	00:58			
100	*Aethopyga saturata*	Black-throated Sunbird	Bhutan		M	00:48	X		High pitched notes
101	*Aethopyga saturata*	Black-throated Sunbird	Malaya	Genting	M	01:24	X		
102	*Aethopyga saturata*	Black-throated Sunbird	India	Assam	M	00:49	X		Striped Tit-Babbler noise
103	*Aethopyga saturata*	Black-throated Sunbird	Nepal	Kathmandu Valley	M	00:33	X		Strophe from a male

CD3

104	*Aethopyga siparaja*	Crimson Sunbird	Nepal	Chitwan	M	01:09			Flycatcher in backgroun
105	*Aethopyga siparaja*	Crimson Sunbird	Bhutan	S.Eastern Bhutan	M	00:49	X		Barbet in background
				Long:90'10E					
106	*Aethopyga siparaja*	Crimson Sunbird	Bhutan	Lat:27'00N	M	00:49		X	Clinging to tree trunk
107	*Aethopyga siparaja*	Crimson Sunbird	Bhutan	Rani camp	M	00:57	X		
108	*Aethopyga siparaja*	Crimson Sunbird	Indonesia	Sulawesi	M	01:13		X	Finch-billed Myna noise
109	*Aethopyga siparaja*	Crimson Sunbird	India	Northern India	M	00:53	X		
110	*Aethopyga mystacalis*	Javan Sunbird	Indonesia	Java	M	00:35	X	X	
111	*Aethopyga mystacalis*	Temminck's Sunbird	Indonesia	East Kalimantan	M	00:42			"trrr"s&Ti"s in tree
112	*Aethopyga mystacalis*	Temminck's Sunbird	Borneo	Sabah *	M	01:12		X	
113	*Aethopyga mystacalis*	Temminck's Sunbird	Malaysia	Taman Negara	M	00:54		X	
114	*Aethopyga ignicauda*	Fire-tailed Sunbird	India	Sikkim	M	00:53	X		
115	*Aethopyga ignicauda*	Fire-tailed Sunbird	Bhutan	Dochu la	M	01:01		X	
116	*Aethopyga ignicauda*	Fire-tailed Sunbird	Nepal	Ghorepani	M	00:29			
117	*Arachnothera longirostra*	Little Spiderhunter	Malaysia	Krau	M	02:09			Common in habitat
118	*Arachnothera longirostra*	Little Spiderhunter	Indonesia	East Java	M	01:22		X	Playing with jungle babbler
119	*Arachnothera longirostra*	Little Spiderhunter	Philippines	Palawan	M	01:55		X	Cicadas in background
120	*Arachnothera longirostra*	Little Spiderhunter	Malaya	Paiti forest	M	00:49	X	X	Gibbons insects noise
121	*Arachnothera longirostra*	Little Spiderhunter	India	South India	M	00:56	X	X	
122	*Arachnothera longirostra*	Little Spiderhunter	India	South India	M	00:57	X	X	
123	*Arachnothera longirostra*	Little Spiderhunter	India	Tamil Nadu	M	02:18		X	Alarming call

124	*Arachnothera longirostra*	Little Spiderhunter	India	Assam	M	00:47	X		
125	*Arachnothera robusta*	Long-billed Spiderhunter	Malaysia	Maxwell hill	M	01:10		X	Distress calls
126	*Arachnothera robusta*	Long-billed Spiderhunter	Malaysia	Pahang	M	01:19		X	Alarming / distress calls
127	*Arachnothera robusta*	Long-billed Spiderhunter	Malaysia		M	00:28	X		
128	*Arachnothera flavigaster*	Spectacled Spiderhunter	Malaysia	Prang Besar Estate	M	01:48		X	Feeding
129	*Arachnothera flavigaster*	Spectacled Spiderhunter	Malaysia	Selangor	M	01:58		X	
130	*Arachnothera clarae*	Naked-faced spiderhunter	Philippines	Mindanao	M	00:39		X	
131	*Arachnothera clarae*	Naked-faced spiderhunter	Philippines	Mindanao	M	00:50		X	
132	*Arachnothera clarae*	Naked-faced spiderhunter	Philippines	Luzon	M	00:56		X	Play/pleasure
133	*Arachnothera affinis*	Grey-breasted Spiderhunter	Indonesia	East Java	M	01:39		X	
134	*Arachnothera affinis*	Grey-breasted Spiderhunter	BBC?		M	00:50			
135	*Arachnothera affinis*	Grey-breasted Spiderhunter	Malaysia	Taman Negara	M	00:39		X	
136	*Arachnothera magna*	Streaked Spiderhunter	Malaysia	Pahang	M	02:29		X	Flight calls
137	*Arachnothera magna*	Streaked Spiderhunter	Bhutan	Tama camp	M	00:41		X	Feeding
138	*Arachnothera magna*	Streaked Spiderhunter	Bhutan	Tama	M	00:28		X	

APPENDIX 1d RECORDINGS OF ASIAN SPECIES (SUNBIRDS AND SPIDERHUNTERS & LOCATIONS)

Ref. no.	Scientific Name	Common name	Sp.n.	Sub-sp.no.	Year	Copyright holder	Ref.no.	Locality
1	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,11	1991	Lucking, R	73887	Bobong
2	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,14	1971	Kersley, R	6345	Kuala lumpur
3	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,11	1982	Bartels	13457	Meru Bettri
4	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,14	1988	Dunleavy, S	22373	Pulan tioman
5	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,14	1989	Peters, S	29676	Sumba Alt. C5
6	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,14	1979	Hails, C	34995	Rantau panjang
7	*Anthreptes malacensis*	Plain-throated Sunsbird	53	53,14	1985	Hails, C	33333	Layang Layang
8	*Anthreptes singalensis*	Ruby-cheeked Sunbird	47	47,9	1991	Smith, S	45803	Batimurang
9	*Anthreptes singalensis*	Ruby-cheeked Sunbird	47	47,10	1973	Kersley, R	6307	Taman nagara NP
10	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1996	Holt, P	65490	Bondla
11	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1996	Holt, P	65491	Jungle Hutt (Masingudi)
12	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1996	Holt, P	65492	Bondla
13	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1996	Holt, P	65493	Bondla
14	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,2	1977	Johnson, EDH	11019	Colombo distr.
15	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,2	1977	Johnson, EDH	11020	Colombo distr.
16	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1994	Holt, P	45343	Madras City
17	*Nectarinia zeylonica*	Purple-rumped Sunbird	88	88,1	1994	Holt, P	45344	Madras zoo
18	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1996	Holt, P	65494	Naduvattam

19	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1996	Holt, P	65495	Bondla
20	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1996	Holt, P	65496	Bondla
21	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1994	Holt, P	45345	Masingagudi road
22	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1994	Holt, P	45346	Near Ooty
23	*Nectarinia minima*	Crimson-backed Sunbird	89	None	1992	Sivaprasad, PS	37853	Padagiri
24	*Nectarinia sperata*	Purple-throated Sunbird	90	90,2	1986	Hails, C	33387	Sime Road
25	*Nectarinia sperata*	Purple-throated Sunbird	90	90,5	1997	Drijvers, R	67622	Balsahan trait
26	*Nectarinia sericea*	Black Sunbird	91	91,1	1996	Lambert, F	67689	Karakelong
27	*Nectarinia sericea*	Black Sunbird	91	91,1	1996	Lambert, F	67643	Gunung
28	*Nectarinia sericea*	Black Sunbird	91	91,3	1991	Lucking, R	73829	Menanga
29	*Nectarinia sericea*	Black Sunbird	91	91,19		Greensmith, A	32995	
30	*Nectarinia sericea*	Black Sunbird	91	91,21	1991	Smith, S	43327	Kali Batu Putith
31	*Nectarinia sericea*	Black Sunbird	91	91,21	1991	Smith, S	43238	Manusela NP
32	*Nectarinia sericea*	Black Sunbird	91	91,21	1991	Smith, S	43241	Seram
33	*Nectarinia calcostetha*	Copper-throated Sunbird	92	None 92	1991	Buckton, S	44149	Krabi
34	*Nectarinia lotenia*	Long-billed Sunbird	149	149,1	1977	Johnson, EDH	11017	Wattala
35	*Nectarinia lotenia*	Long-billed Sunbird	149	149,1	1977	Johnson, EDH	11018	Wattala
36	*Nectarinia lotenia*	Long-billed Sunbird	149	149,1	1977	Johnson, EDH	11021	Wattala
37	*Nectarinia lotenia*	Long-billed Sunbird	149	149,1	1992	Gullick, T	38240	Ratnapura
38	*Nectarinia lotenia*	Long-billed Sunbird	149	149,2	1996	Holt, P	65500	Periyar
39	*Nectarinia lotenia*	Long-billed Sunbird	149	149,2	1996	Holt, P	65501	Bondla
40	*Nectarinia lotenia*	Long-billed Sunbird	149	149,2	1996	Holt, P	65502	

41	*Nectarinia lotenia*	Long-billed Sunbird	149	149,2	1996	Holt, P	65503	
42	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,11	1989	Hounsome, M	29667	Teluk Bara
43	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,11	1980	Watling, D	13187	Palu
44	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,10	1985	Hails, C	33353	Pierce Reserve
45	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,10	1991	Smith, S	43096	Soya village
46	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,10	1995	Holt, P	51432	Mt Harriet
47	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,1	1991	Lucking, R	73833	Menanga
48	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,5	1991	Lucking, R	73821	Menanga
49	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,5	1999	Gullick, T	1E+05	Rossum Road
50	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,11	1994	Drijvers, R	67623	Baluram
51	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,11	1996	Corbett, JG	68101	Hoga Island
52	*Nectarinia jugularis*	Olive-backed Sunbird	140	140,9	1990	Greensmith, A	34278	Quezon NP
				None				
53	*Nectarinia buettikoferi*	Apricot-breasted Sunbird	141	141	1996	Verbelen, F	66679	Lewapaku
				None				
54	*Nectarinia buettikoferi*	Apricot-breasted Sunbird	141	141	1991	Smith, S	43393	Lewa Forest
55	*Nectarinia solaris*	Flame-breasted Sunbird	142	142,2	1991	Smith, S	43362	Camplong Forest
56	*Nectarinia solaris*	Flame-breasted Sunbird	142	142,1	1991	Smith, S	43346	Pakandeki
57	*Nectarinia solaris*	Flame-breasted Sunbird	142	142,2	1996	Verbelen, F	66669	Bipolo
58	*Nectarinia solaris*	Flame-breasted Sunbird	142	142,1	1998	Drijvers, R	72360	Cereng
			CD2					
59	*Nectarinia asiatica*	Purple Sunbird	139	139,2	1972	Hollom, P	2928	Nikshahr

60	*Nectarinia asiatica*	Purple Sunbird	139	139,1	1986	Quinnel, R	16895	Wildlife Sanctuary
61	*Nectarinia asiatica*	Purple Sunbird	139	139,1	1992	Holt, P	42618	Bharatpur
62	*Nectarinia asiatica*	Purple Sunbird	139	139,1	1992	Holt, P	42619	Bharatpur
63	*Nectarinia asiatica*	Purple Sunbird	139	139,1	1995	Smith, S	52426	Bundala Village
64	*Nectarinia asiatica*	Purple Sunbird	139	139,1	1996	Holt, P	65497	Baga
65	*Nectarinia asiatica*	Purple Sunbird	139	139,3	1996	Holt, P	65498	Masinagudi(Jungle Hunt)
66	*Nectarinia asiatica*	Purple Sunbird	139	139,3	1996	Holt, P	65499	Masinagudi(Jungle Hunt)
67	*Aethopyga primigenius*	Grey-hooded Sunbird	150	150,2	1997	Drijvers, R	54866	Mount Katanglad
68	*Aethopyga primigenius*	Grey-hooded Sunbird	150	150,2	1990	Morris, P	34302	Baracatan Mt Apo
69	*Aethopyga boltoni*	Apo Sunbird	151	151,1	1997	Morris, P	54865	Mount Katanglad
70	*Aethopyga boltoni*	Apo Sunbird	151	151,1	1997	Vercruysse, E	65279	Mount Katanglad
71	*Aethopyga boltoni*	Apo Sunbird	151	151,3	1994	Morris, P	46685	Sitio Siete
72	*Aethopyga flagrans*	Flaming sunbird	153	153,4	1998	Vercruysse, E	68634	
73	*Aethopyga flagrans*	Flaming sunbird	153	153,3	1997	Morris, P	65923	Quezon Nat. Park
74	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,2	1985	Wassink, A	16418	Ifugao Province
75	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,2	1990	Greensmith, A	34350	Mt Patis
76	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,2	1990	Greensmith, A	34359	Mt Polis
77	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,3	1995	Gardner, N	46624	PICOP
78	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,2	1996	Morris, P	65932	Mt Polis
79	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	154,3	1997	Drijvers, R	54867	PICOP

80	*Aethopyga duyvenbodei*	Elegant Sunbird	155	None 155	1996	Lambert, F	67651	Gunung Sahengbaliva
81	*Aethopyga duyvenbodei*	Elegant Sunbird	155	None 155	1996	Lambert, F	67644	Gunung Awu
82	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1985	Wassink, A	17822	St Paul's Habt. Nat. Park
83	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1985	Wassink, A	17847	St Paul's Habt. Nat. Park
84	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1985	Wassink, A	17866	St Paul's Habt. Nat. Park
85	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1985	Wassink, A	17867	St Paul's Habt. Nat. Park
86	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1990	Greensmith, A	34330	St Paul's Habt. Nat. Park
87	*Aethopyga shelleyi*	Lovely Sunbird	156	156,1	1997	Drijvers, R	54868	St Paul's Habt. Nat. Park
88	*Aethopyga gouldiae*	Goul's Sunbird	157	157,2	1996	Holt, P	65175	Summit of Thrumsingla
89	*Aethopyga gouldiae*	Goul's Sunbird	157	157,2	1994	Greensmith, A	46331	Omei Shan 1750 m.
90	*Aethopyga nipalensis*	Green-tailed Sunbird	158	158,5	1984	Buckingham, R	6194	Royal Game reserve
91	*Aethopyga nipalensis*	Green-tailed Sunbird	158	158,8	1992	Holt, P	42621	
92	*Aethopyga nipalensis*	Green-tailed Sunbird	158	158,8	1991	Holt, P	44801	
93	*Aethopyga nipalensis*	Green-tailed Sunbird	158	158,7	1995	Holt, P	51045	

94	*Aethopyga nipalensis*	Green-tailed Sunbird	158	158,5	2000	Robson, C	1E+05	Shilling Ridge
				None				
95	*Aethopyga eximia*	White-flanked sunbird	159	159	1994	Drijvers, R	54915	Gunung Gede
				None				
96	*Aethopyga eximia*	White-flanked sunbird	159	159	1991	Smith, S	45835	Cibodas water falls
97	*Aethopyga christinae*	Forked-tailed Sunbird	160	160,3	1998	Gardner, N	59319	
98	*Aethopyga christinae*	Forked-tailed Sunbird	160	160,2	1994	Greensmith, A	46424	Tai Po Kau
99	*Aethopyga christinae*	Forked-tailed Sunbird	160	160,2	1994	Greensmith, A	46425	Tai Po Kau
100	*Aethopyga saturata*	Black-throated Sunbird	161	161,9	1967	Bertram, B	15109	Batashi Camp
101	*Aethopyga saturata*	Black-throated Sunbird	161	161,10	1979	Hails, C	34992	
102	*Aethopyga saturata*	Black-throated Sunbird	161	161,2	2000	Robson, C	1E+05	Dirak RF
103	*Aethopyga saturata*	Black-throated Sunbird	161	161,2	1996	Holt, P	65326	Phulchowki
CD3			CD3					
104	*Aethopyga siparaja*	Crimson Sunbird	163	163,6	1996	Holt, P	65329	Chitwan Jungle Lodge
105	*Aethopyga siparaja*	Crimson Sunbird	163	163,6	1996	Holt, P	65178	Sandrup Jonkhar
106	*Aethopyga siparaja*	Crimson Sunbird	163	163,6	1967	Bertram, B	15084	Batashe Camp
107	*Aethopyga siparaja*	Crimson Sunbird	163	163,6	1967	Bertram, B	15101	Altitude 2100
108	*Aethopyga siparaja*	Crimson Sunbird	163	163,3	1990	Redman, N	31663	Dumaga Bone
109	*Aethopyga siparaja*	Crimson Sunbird	163	163,6	1992	Holt, P	42620	Corbett NP
				None				
110	*Aethopyga mystacalis*	Javan Sunbird	164	164	1991	Greensmith, A	33059	Carita
111	*Aethopyga mystacalis*	Temminck's Sunbird	165	None	1993	Van Balen, B	47814	Kayan Mentavrang

112	*Aethopyga mystacalis*	Temminck's Sunbird	165	165 None 165	1994	Harrap, S	56363	Kinabalu
113	*Aethopyga mystacalis*	Temminck's Sunbird	165	None 165	1991	Buckton, S	44100	
114	*Aethopyga ignicauda*	Fire-tailed Sunbird	166	166,2	1979	Corbett, JG	13863	Ranjit river
115	*Aethopyga ignicauda*	Fire-tailed Sunbird	166	166,2	1995	Holt, P	51047	
116	*Aethopyga ignicauda*	Fire-tailed Sunbird	166	166,2	1995	Drijvers, R	67625	
117	*Arachnothera longirostra*	Little Spiderhunter	167	167,2	?	Kersley, R	6364	Ampang reserves
118	*Arachnothera longirostra*	Little Spiderhunter	167	167,9	1982	Bartels Groeneveld	/ 12867	Meru Betiri
119	*Arachnothera longirostra*	Little Spiderhunter	167	167,4	1986	Wassink, A	17841	St Paul's habt. NP
120	*Arachnothera longirostra*	Little Spiderhunter	167	167,3	1983	Hails, C	32654	
121	*Arachnothera longirostra*	Little Spiderhunter	167	167,6	1994	Holt, P	45350	Anaimalai Hills
122	*Arachnothera longirostra*	Little Spiderhunter	167	167,6	1994	Holt, P	45351	Anaimalai Hills
123	*Arachnothera longirostra*	Little Spiderhunter	167	167,6	1995	Holt, P	51442	Anaimalai Hills

124	*Arachnothera longirostra*	Little Spiderhunter	167	167,6	2000	Robson, C	1E+05	Dirak RF
125	*Arachnothera robusta*	Long-billed Spiderhunter	169	169,2		Kersley, R	6209	
126	*Arachnothera robusta*	Long-billed Spiderhunter	169	169,2	1972	Kersley, R	7578	Taman Negara NP
127	*Arachnothera robusta*	Long-billed Spiderhunter	169	169,2	1968	Madge, G	15576	Ampang forest reserve
128	*Arachnothera flavigaster*	Spectacled Spiderhunter	170	None 170	1972	Kersley, R	6255	Pram Besar Estate
129	*Arachnothera flavigaster*	Spectacled Spiderhunter	170	None 170	1972	Kersley, R	6891	
130	*Arachnothera clarae*	Naked-faced spiderhunter	172	172,3	1990	Greensmith, A	34312	PICOP
131	*Arachnothera clarae*	Naked-faced spiderhunter	172	172,2	1990	Greensmith, A	34314	PICOP
132	*Arachnothera clarae*	Naked-faced spiderhunter	172	172,3	1994	Harrap, S	44863	Angat reserve
133	*Aracnothera affinis*	Grey-breasted Spiderhunter	173	173,2	1982	Bartels / Groeneveld	12840	Meru Betiri
134	*Aracnothera affinis*	Grey-breasted Spiderhunter	173	173,3		Bartels / Groeneveld	12842	
135	*Aracnothera affinis*	Grey-breasted Spiderhunter	173	173,3	2000	Robson, C	1E+05	Fraser's hill
136	*Arachnothera magna*	Streaked Spiderhunter	175	175,2	1973	Kersley, R	7284	
137	*Arachnothera magna*	Streaked Spiderhunter	175	175,2	1967	Bertram, B	15121	
138	*Arachnothera magna*	Streaked Spiderhunter	175	175,2	1967	Bertram, B	15142	

APPENDIX 1e RECORDINGS OF SUNBIRDS OF AFRICA (CATEGORISATION AND COMMENTS)

Ref.no.	Latin name	Common name	Country	Region	Sex	Duration	song	call	Comments
1	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome			1'04"	X	X	
2	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		M	0'39"	x		Perched
3	*Anabathmis reichenbachii*	Reichenbach's Sunbird	Congo	Kouilou	M	0'52"	X	X	Grating calls
4	*Anabathmis reichenbachii*	Reichenbach's Sunbird	Congo	Kouilou	M	0'14"		X	Perched
5	*Anabathmis reichenbachii*	Reichenbach's Sunbird	Cameroon	S. Cameroon	M	1'07"	X	X	Perched on bushes
6	*Anthobaphes violacea*	Orange-breasted Sunbird	South Africa	W.Cape Province	M	1'15"	X		Song
7	*Anthreptes anchietae*	Anchieta's Sunbird	Malawi	W. Li;ongwe	M	0'56"	x		
8	*Anthreptes anchietae*	Anchieta's Sunbird	Zambia	Serenje	M	3'09"	X	X	Call then song
9	*Anthreptes anchietae*	Anchieta's Sunbird	Zambia	Chiundaponde	M	0'12"		X	Call notes
10	*Anthreptes gabonicus*	Mouse-brown Sunbird	Ivory Coast	Lamto	M	0'40"		X	
11	*Anthreptes gabonicus*	Mouse-brown Sunbird	Ivory Coast	S. Ivory coast	M	0'25"		X	
12	*Anthreptes longuemarei angolensis*	Western Violet-backed Sunbird	Zambia	C. Zambia	M	0'37"	X		
13	*Anthreptes longuemarei angolensis*	Western Violet-backed Sunbird	Malawi		M				
14	*Anthreptes orientalis*	Kenya Violet-backed Sunbird	Ethiopia	Yavello	M	0'52"			
15	*Anthreptes rectirostris tephrolaema*	Green Sunbird	Kenya		M	1'06"		X	Up on a dead tree
16	*Anthreptes rectirostris tephrolaema*	Green Sunbird	Cameroon	S-W Cameroon	M	0'57"	X	X	

17	*Anthreptes rectirostris tephrolaema*	Green Sunbird	Gabon	N. E. Gabon	M	3'21"	X	X	Calls and song
18	*Anthreptes rectirostris tephrolaema*	Green Sunbird	Congo		M	1'32"			
19	*Anthreptes reichenowi reichenowi*	Plain-backed Sunbird	Kenya		M	1'05"		X	Alarm calls
20	*Anthreptes aurantium*	Violet-tailed Sunbird			M				
21	*Anthreptes seimundi kruensis*	Little Green Sunbird	Gabon	N. E. Gabon	M	0'30"		X	Perched on trees
22	*Anthreptes seimundi traylori*	Little Green Sunbird			M	1'13"			
23	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	Ivory Coast	E. Ivory Coast	M	2'02"	X		Competition
24	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	Ivory Coast	S. Ivory Coast	M	1'47"	X	X	
25	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	Ivory Coast	S. Ivory Coast	M	1'50"			Perched on trees
26	*Chalcomitra rubescens stangerii*	Green-throated Sunbird	Equa. Guinea	Bioko	M	1'10"			Birds in background
27	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	Ivory Coast	S. Ivory Coast	M	0'58"	X		
28	*Chalcomitra amethystina amethystina* 1	Amethyst Sunbird	South Africa		M				
30	*Chalcomitra amethystina amethystina* 2	Amethyst Sunbird	South Africa		M				
31	*Chalcomitra amethystina kirkii* 1	Amethyst Sunbird	Malawi		M	0'36"			
32	*Chalcomitra amethystina kirkii* 1	Amethyst Sunbird	Tanzania		M				
33	*Chalcomitra amethystina kirkii* 2	Amethyst Sunbird	Zambia		M				
34	*Chalcomitra amethystina kirkii* 3	Amethyst Sunbird	Zambia		M				
35	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	Ivory Coast	S. Ivory Coast	M	0'57"			*T. afer* in background
36	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	Ivory Coast	S. Ivory Coast	M	0'41"			
37	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	Ivory Coast	S. Ivory Coast	M	0'34"			
38	*Chalcomitra hunteri*	Hunter's Sunbird	Kenya	Bura	M	0'38"	X	X	Dove in background
39	*Chalcomitra hunteri*	Hunter's Sunbird	Kenya		M	1.16"		X	Wing 'flutter'

40	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	Kenya	Kakamega	M	0'53"	X		Beneath tree
41	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	Cameroon	SW. Cameroon	M	4'34"	X	X	Perched
42	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	Cameroon	SW. Cameroon	M	1'21"	X	X	Alarm call
43	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	Cameroon	S. Cameroon	M	0'48"			
44	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	South Africa		M				
45	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	Swaziland		M				
46	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	Zambia		M				
47	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	Zambia		M				
48	*Chalcomitra senegalensis cruentata*	Scarlet-chested Sunbird	Chad	S.West Chad	M	1'21"	x		Territorial
48	*Chalcomitra senegalensis senegalensis*	Scarlet-chested Sunbird	Gambia		M	0'44"			
50	*Chalcomitra balfouri*	Socotra Sunbird	Yemen	H. Playeau	M	1'34"		x	Territorial
	Double-collared group of *Cinnyris*:								
51	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	South Africa	Natal	M	0'45"	x		
52	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	South Africa	Eastern Cape	M	0'59"		X	Anxiety calls
53	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	South Africa		M				
54	*Cinnyris afer*	Greater Double-Collared Sunbird	Rwanda		M				
55	*Cinnyris ludovicensis whytei*	Montane Double-Collared Sunbird	Zambia		M				
56	*Cinnyris ludovicensis whytei*	Montane Double-Collared Sunbird	Kenya	W. Kenya	M				
57	*Cinnyris chalybeus*	Southern Double-Collared Sunbird	South Africa	SW.Cape Province	M	2'51"	x		
58	*Cinnyris chalybeus chalybeus*	Southern Double-Collared Sunbird	South Africa	E.Cape province	M				

59	*Cinnyris chloropygius chloropygius* 1	Olive-bellied Sunbird	Gabon		M	1'26"	X		Territorial
60	*Cinnyris chloropygius kempi* 1	Olive-bellied Sunbird	Ivory Coast	S. Ivory Coast	M	0'51"		X	
61	*Cinnyris chloropygius kempi* 2	Olive-bellied Sunbird	Ivory Coast	S. Ivory Coast	M	1'57"	X		Territorial
62	*Cinnyris chloropygius kempi* 3	Olive-bellied Sunbird	Ivory Coast	S. Ivory Coast	M	1'40"		X	Alarm call
63	*Cinnyris chloropygius kempi* 4	Olive-bellied Sunbird	Ivory Coast	S. Ivory Coast	M	3'26"	X	X	Background noise
64	*Cinnyris loveridgei*	Loveridge's Sunbird	Tanzania		M				
65	*Cinnyris loveridgei*	Loveridge's Sunbird	Kenya	West Kenya	M				
66	*Cinnyris manoensis*	Miombo Double-Collared Sunbird	Zimbabwe		M				
67	*Cinnyris manoensis*	Miombo Double-Collared Sunbird	Zambia	Chinsali	M	0'34			
68	*Cinnyris mediocris mediocris*	Eastern Double-Collared Sunbird	Kenya		M				
69	*Cinnyris mediocris mediocris*	Eastern Double-Collared Sunbird	Kenya		M				
70	*Cinnyris minullus*	Tiny Sunbird	Congo	Kouilou	M	0'50"	X		High pitched
71	*Cinnyris minullus*	Tiny Sunbird	Gabon	NE. Gabon	M	0'40"			
72	*Cinnyris minullus*	Tiny Sunbird	Gabon	NE. Gabon	M	0'48"	X		Territorial
73	*Cinnyris minullus*	Tiny Sunbird	Gabon	NW. Gabon	M	1'24"			
74	*Cinnyris minullus*	Tiny Sunbird	Benin		M				
75	*Cinnyris neergaardi*	Neergaard's Sunbird	South Africa		M				
75	*Cinnyris neergaardi*	Neergaard's Sunbird	South Africa	N. Zululand	M	1'05"	X		Dove in background
76	*Cinnyris prigoginei*	Prigogine's Double-Collared Sunbird			M				
77	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	Cameroon	C. cameroon	M	3'01	X		Territorial
78	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	Cameroon		M	0'25"	X		One phrase

79	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	Cameroon		M	0'44"	X	X	Bird in the background
80	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	Cameroon		M	2'54"	X		
81	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	Cameroon		M	1'12"	X	X	Anxious calls & song
82	*Cinnyris rockefelleri*	Rockefeller's Sunbird			M				
83	*Cinnyris pulchellus melanogaster* 1	Beautiful Sunbird	Kenya		M				
84	*Cinnyris pulchellus pulchellus* 1	Beautiful Sunbird	Niger		M				
85	*Cinnyris pulchellus pulchellus* 2	Beautiful Sunbird	Chad		M				
86	*Cinnyris pulchellus pulchellus* 3	Beautiful Sunbird	Gambia		M				
87	*Cinnyris congensis*	Congo Sunbird			M				
88	*Cinnyris erythrocerca*	Red-chested Sunbird			M				
89	*Cinnyris regius regius*	Regal Sunbird	Rwanda		M				
90	*Cinnyris regius regius*	Regal Sunbird	Rwanda		M				
	Purple-banded group of *Cinnyris*:								
91	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	South Africa		M				
92	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	Tanzania		M				
93	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	Zambia		M				
94	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	Zambia		M				
95	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	South Africa	Natal	M		x		Territorial
96	*Cinnyris bouvieri*	Orange-tufted Sunbird	Cameroon		M	0'42"	X		Territorial
97	*Cinnyris bouvieri*	Orange-tufted Sunbird	Cameroon		M	1'26"	X		Territorial
98	*Cinnyris bouvieri*	Orange-tufted Sunbird	Cameroon	S.E Cameroon	M	1'21"	X		Territorial

99	*Cinnyris bouvieri*	Orange-tufted Sunbird	Cameroon		M	1'54"	X		Territorial
100	*Cinnyris habessinicus hellmayri*	Shining Sunbird	Yemen	N. Yemen	M	0'22"		X	
101	*Cinnyris mariquensis mariquensis*	Mariqua Sunbird	South Africa		M	1'50"	X		
102	*Cinnyris mariquensis mariquensis*	Mariqua Sunbird	Swaziland		M				
103	*Cinnyris mariquensis suahelicus*	Mariqua Sunbird	Zambia		M				
104	*Cinnyris mariquensis suahelicus*	Mariqua Sunbird	Tanzania		M				
105	*Cinnyris nectarinoides*	Black-bellied Sunbird	Kenya	Taita	2M	1'16"	X		In excited state
106	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	Kenya		M	0'23"	X		Breeding song
107	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	Kenya	Tsavo N.P.	M	0'45"	X		
108	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	Kenya		M	3'30			Cicadas in backgroun
109	*Cinnyris oseus oseus*	Palestine Sunbird	Israel	Tiberias	M&F	2'30"		X	Anxiety calls
110	*Cinnyris oseus oseus*	Palestine Sunbird	Israel		M	1'34"	X		Covid in background
111	*Cinnyris oseus oseus*	Palestine Sunbird	Yemen	N. Yemen	M	0'31"	X	X	
112	*Cinnyris oseus oseus*	Palestine Sunbird	Israel		M	0'50"	X	X	Alarm calls
113	*Cinnyris chalcomelas*	Kenya violet-breasted Sunbird	Kenya		M	1'13"	X	X	Feeding
114	*Cinnyris chalcomelas*	Kenya violet-breasted Sunbird	Kenya		M	0'28"		X	Call from tree
115	*Cinnyris chalcomelas*	Kenya violet-breasted Sunbird	Kenya		M	1'20"	X		On thorn tree
116	*Cinnyris pembae*	Voilet-breasted / Pemba Sunbird	Pemba Island		M		X		
117	*Cinnyris pembae*	Voilet-breasted/ Pemba Sunbird	Pemba Island		M		X		
118	*Cinnyris shelleyi shelleyi*	Shelley's Sunbird	Zambia		M		X		
119	*Cinnyris shelleyi*	Shelley's Sunbird			M		X		

	Maroon group of *Cinnyris*:								
120	*Cinnyris coccinigaster*	Splendid Sunbird	Ghana	S. Ghana	M	1'50	X		Alarm call
121	*Cinnyris coccinigaster*	Splendid Sunbird	Ghana	S. Ghana	M	0'56"	X		Feeding
123	*Cinnyris coccinigaster*	Splendid Sunbird	Ivory Coast	S. Ivory Coast	M	1'28"	X	X	
124	*Cinnyris coccinigaster*	Splendid Sunbird	Ivory Coast	N.Ivory Coast	M	1'04		X	
125	*Cinnyris johannae fasciata* 1	Johanna's Sunbird	Ivory Coast	S.E.IvoryCoast	M	1'40"	X		Perched & Flight
126	*Cinnyris johannae fasciata* 2	Johanna's Sunbird	Ivory Coast	S. Ivory Coast	M	0'40"		X	Perched & Flight
127	*Cinnyris johannae johannae* 3	Johanna's Sunbird	Gabon	S.W. Gabon	M	2'36"		X	
128	*Cinnyris johannae fasciata*	Johanna's Sunbird	Liberia	NE. Liberia	M	1'16"		x	
129	*Cinnyris superbus ashantiensis* 1	Superb Sunbird	Ivory Coast	S. Ivory Coast	M	1'03"	X		
130	*Cinnyris superbus ashantiensis* 2	Superb Sunbird	Ivory Coast	S. Ivory Coast	M	0'29"	Cry		Alarm cry
131	*Cinnyris superbus superbus* 1	Superb Sunbird	Cameroon		M	0'42"	X		Perched
132	*Cinnyris superbus superbus* 1	Superb Sunbird	Gabon	N.E. Gabon	M	2'29"	X		
	White-bellied group of *Cinnyris*:								
133	*Cinnyris fuscus*	Dusky Sunbird	South Africa	Cape Province	M	2'51"	x		Flying
134	*Cinnyris fuscus*	Dusky Sunbird	Namibia		M	3'05"	x		Perching
135	*Cinnyris fuscus*	Dusky Sunbird	Namibia		M		x		
136	*Cinnyris oustaleti rhodesiae*	Oustalet's Sunbird	Zambia		M	1'32"			
137	*Cinnyris oustaleti rhodesiae*	Oustalet's Sunbird	Zambia		M				
138	*Cinnyris talatala*	White-breasted Sunbird	South Africa		M				
139	*Cinnyris talatala*	White-breasted Sunbird	South Africa		M				

140	*Cinnyris talatala*	White-breasted Sunbird	Zambia		M			
141	*Cinnyris talatala*	White-breasted Sunbird	Zambia		M			
142	*Cinnyris talatala*	White-breasted Sunbird	Zambia		M			
143	*Cinnyris talatala*	White-breasted Sunbird	Namibia		M			
144	*Cinnyris venustus falkensteini*	Variable Sunbird	South Africa		M			
145	*Cinnyris venustus falkensteini*	Variable Sunbird	Zambia		M	0'22"	x		
146	*Cinnyris venustus falkensteini*	Variable Sunbird	Zambia		M				
147	*Cinnyris venustus falkensteini*	Variable Sunbird	Zambia		M				
148	*Cinnyris venustus*	Variable Sunbird	Kenya		M	0'20"			
149	*Cinnyris venustus*	Variable Sunbird	Zimbabwe	SE.Zimbabwe	M	0'47"	x		River noise
150	*Cinnyris venustus*	Variable Sunbird	Malawi		M	0'58"		x	Alarm call
151	*Cinnyris venustus*	Variable Sunbird	Benin		M	1'27"	x	x	
152	*Cinnyris venustus*	Variable Sunbird	Nigeria	C.Nigeria	M	2'13"	x		Territorial song
	Olive group of *Cinnyris*:								
153	*Cinnyris batesi*	Bates's Sunbird	Cameroon		M	0'55"		X	
154	*Cinnyris batesi*	Bates's Sunbird	Gabon	NE. Gabon	M	1'26"			And N. *minullus*
155	*Cinnyris batesi*	Bates's Sunbird	Gabon	NE. Gabon	M	1'04"		X	
156	*Cinnyris batesi*	Bates's Sunbird	Ghana	S. Ghana	M	0'35"	X		
157	*Cinnyris ursulae*	Ursula's Sunbird	Cameroon		M	2'07"	X		Background noise
158	*Cinnyris ursulae*	Ursula's Sunbird	Cameroon	SW. Cameroon	M	2'08"	X		Territorial
159	*Cinnyris ursulae*	Ursula's Sunbird	Cameroon	SW. Cameroon	M	0'58"			

					M				
	Miscellaneous *Cinnyris*				M				
160	*Cinnyris cupreus cupreus*	Copper Sunbird	Tanzania		M				
161	*Cinnyris cupreus cupreus*	Copper Sunbird	Ivory Coast		M				
162	*Cinnyris cupreus cupreus*	Copper Sunbird	Ghana		M				
163	*Cinnyris cupreus cupreus*	Copper Sunbird	Chadd	SW.Chad	M				
	Cyanomitra								
164	*Cyanomitra alinae tanganjicae*	Blue-headed Sunbird	Rwanda		M	0'13"	X		Territorial
165	*Cyanomitra alinae tanganjicae*	Blue-headed Sunbird	Rwanda		M	0'31"	X		Territorial
166	*Cyanomitra bannermani*	Bannerman's Sunbird	Zambia		M	0'54"		X	
167	*Cyanomitra cyanolaema magnistrata* 1	Blue-throated Brown Sunbird	Ivory Coast	S. Ivory Coast	M	1'55"	X		Territorial
168	*Cyanomitra cyanolaema octaviae 2*	Blue-throated Brown Sunbird	Congo		M	0'13"	x	X	Sub song & call
169	*Cyanomitra cyanolaema octaviae 3*	Blue-throated Brown Sunbird	Gabon	N.E. Gabon	M				
170	*Cyanomitra cyanolaema octaviae 4*	Blue-throated Brown Sunbird	Gabon	N.E. Gabon	M	1'29"			Two families
171	*Cyanomitra cyanolaema octaviae 5*	Blue-throated Brown Sunbird	Gabon		M	2'24"			Near the top of trees
172	*Cyanomitra olivacea sclateri* 1	Western Olive Sunbird	Zimbabwe		M	0'27"			
173	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	Ghana	S. Ghana	M	0'58"	x		One pitch
174	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	Cameroon	C. cameroon	M	2'19"		x	Call after playback
175	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	Gabon	N.E. Gabon	M	1'09"		x	Alarm calls
176	*Cyanomitra olivacea olivacea* 1	Eastern Olive Sunbird	South Africa		M				
177	*Cyanomitra olivacea olivacea* 2	Eastern Olive Sunbird	South Africa		M				

178	*Cyanomitra olivacea olivacea* 3	Eastern Olive Sunbird	South Africa		M			
179	*Cyanomitra olivacea*	Eastern Olive Sunbird	Zambia		M			
180	*Cyanomitra oritis oritis 1*	Cameroon Sunbird	Cameroon		M			
181	*Cyanomitra oritis oritis 2*	Cameroon Sunbird	Cameroon		M	1'00'	X		Background noise
182	*Cyanomitra oritis oritis 3*	Cameroon Sunbird	Cameroon		M	0'35"		X	Respond to playback
183	*Cyanomitra oritis oritis 4*	Cameroon Sunbird	Cameroon		M	1'35"	X		
184	*Cyanomitra veroxii veroxii 1*	Mouse-coloured Sunbird	South Africa		M	0'44'			Cries
185	*Cyanomitra veroxii 2*	Mouse-coloured Sunbird	South Africa		M				
186	*Cyanomitra verticalis bohndorffii* 1	Green-headed Sunbird	Cameroon		M				
187	*Cyanomitra verticalis bohndorffii* 2	Green-headed Sunbird	Cameroon		M	0'49"	X	X	Flying song
188	*Cyanomitra verticalis viridisplendens 3*	Green-headed Sunbird	Kenya		M	1'00"	X		
189	*Cyanomitra verticalis viridisplendens 4*	Green-headed Sunbird	Kenya	S. Kenya		1'10"		X	Call from a tree
	Deleornis					2'05"	X		Song & cries
190	*Deleornis fraseri cameroonensis* 1	Scarlet-tufted Sunbird	Chad	S. West Chad	M				
191	*Deleornis fraseri idius 1*	Scarlet-tufted Sunbird	Ivory Coast	S. Ivory Coast	M	1'04"		X	
192	*Deleornis fraseri cameroonensis* 3	Scarlet-tufted Sunbird	Gabon	N. East Gabon	M	o'56"	X		
193	*Deleornis fraseri cameroonensis 2*	Scarlet-tufted Sunbird	Gabon		M	0'40"		X	Faint calls
						3'50"	X		
	Anthodiaeta								
194	*Anthodiaeta collaris collaris* 1	Collared Sunbird	South Africa		M				
195	*Anthodiaeta collaris elachior* 1	Collared Sunbird	Kenya		M				

196	*Anthodiaeta collaris elachior* 2	Collared Sunbird	Tanzania		M	1'27"			And insects
197	*Anthodiaeta collaris zuluensis* 1	Collared Sunbird	South Africa		M				
198	*Anthodiaeta collaris zambesiana* 1	Collared Sunbird	Zambia	SW. Zambia	M				
199	*Anthodiaeta collaris hypodila* 1	Collared Sunbird	Bioko		M	1'20"	X		
200	*Anthodiaeta collaris somereni* 1	Collared Sunbird	Cameroon	SW. Cameroon	M	0'52"			Bird in the backgroun
201	*Anthodiaeta collaris subcollarris* 1	Collared Sunbird	Ivory Coast		M	0'41"			
202	*Anthodiaeta collaris somereni 1*	Collared Sunbird	Gabon	N.East Gabon	M	0'42"	x		
203	*Anthodiaeta pallidigaster*	Amani Sunbird	Tanzania		M	0'35"			
204	*Anthodiaeta platura*	Pygmy Sunbird	Ivory Coast	S. Ivory Coast	M				
205	*Anthodiaeta platura*	Pygmy Sunbird	Nigeria	Comoe	M	0'28"		X	Alarm calls
206	*Anthodiaeta platura*	Pygmy Sunbird	Nigeria	C. Negeria	M	1'59"	X		
207	*Anthodiaeta platura*	Pygmy Sunbird	Cameroon	C. Cameroon	M	0'55"		X	
208	*Anthodiaeta metallica*	Nile valley Sunbird	Yemen		M	0'56"	X		
	Nectarinia								
209	*Nectarinia famosa famosa*	Malachite Sunbird	South Africa	Natal	M				
210	*Nectarinia famosa famosa*	Malachite Sunbird	South Africa	Natal	M	1'32"	x		
211	*Nectarinia famosa cupreonitens*	Malachite Sunbird	Zambia		M	0'24	x		And animals & crows
212	*Nectarinia famosa cupreonitens*	Malachite Sunbird	Kenya	SW. Kenya	M		x	x	
213	*Nectarinia johnstoni johnstoni* 1	Red-tufted Sunbird	Rwanda	Kivu	M				
214	*Nectarinia johnstoni johnstoni* 2	Red-tufted Sunbird	Rwanda	Kivu	M				
215	*Nectarinia johnstoni nyikensis* 1	Red-tufted Sunbird	Malawi		M				

216	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	Tanzania		M	0'30"	X	X	Territorial
217	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	Kenya		M	0'08		x	
218	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	Kenya	W. Kenya	M	1'10		x	
219	*Nectarinia bocagei*	Bocage's Sunbird			M	0'58"		x	
220	*Nectarinia purpureiventris*	Purple-breasted Sunbird	Uganda		M				
221	*Nectarinia purpureiventris*	Purple-breasted Sunbird	Uganda		M	0'11"	X		Water in the backgrou
222	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	Kenya		M	0'36"	X	X	
223	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	Kenya	Molo	M	2'25		X	Birds in the backgroun
224	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	Kenya		M	1'08"	X		And Insects
225	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	Kenya	C. Kenya	M	2'11"	X	X	Call and song

Where, **n** is the order of the species or subspecies recording.

APPENDIX 1f RECORDINGS OF AFRICAN SUNBIRDS (RECORDISTS & LOCATIONS)

Ref. no.	Latin name	Common name	Sp. n.	Sub-sp.n.	Year	Ref. No.	Copyright holder	Locality
1	*Anabathmis newtoni*	Newton's Sunbird	70	None		cc3112	Tye, A.	-
2	*Anabathmis newtoni*	Newton's Sunbird	70	None	2002	116285	Chappuis, Claude	Bom Sucesso
3	*Anabathmis reichenbachii*	Reichenbach's Sunbird	68	None	1990	35621	Dowsett-Lemaire, F.	Mpinde Marsh,
4	*Anabathmis reichenbachii*	Reichenbach's Sunbird	68	None	1990	35626	Dowsett-Lemaire, F.	Menengue,
5	*Anabathmis reichenbachii*	Reichenbach's Sunbird	68	None	1972	cc3106	Chappuis, Claude	South Douala
6	*Anthobaphes violacea*	Orange-breasted Sunbird	72	None	1974	60915	Gillard, Len	(Knysna) Near the Heads
7	*Anthreptes anchietae*	Anchieta's Sunbird	51	None	1980	cc23031	Chappuis, Claude	West Li;ongwe
8	*Anthreptes anchietae*	Anchieta's Sunbird	51	None	1989	26073	Stjernstedt, R	Kasanka
9	*Anthreptes anchietae*	Anchieta's Sunbird	51	None		26369	Stjernstedt, R	
10	*Anthreptes gabonicus*	Mouse-brown Sunbird	55	None	1992	35097	Greensmith, A	
11	*Anthreptes gabonicus*	Mouse-brown Sunbird	55	None	1968	cc3072	Chappuis, Claude	N'Douci
12	*Anthreptes longuemarei angolensis*	Western Violet-backed Sunbird	56	56,1	1973	cc3073	Stjernstedt, R	Moumbua
13	*Anthreptes longuemarei angolensis*	Western Violet-backed Sunbird	56	56,1			Gibbon, G.	
14	*Anthreptes orientalis*	Kenya Violet-backed Sunbird	57	None	1995	68858	Smith, S.	Campsite, Lake Stefanie

15	*Anthreptes rectirostris tephrolaema*	Green Sunbird	61	61,2		27886	McVicker, R.	Kakamega
16	*Anthreptes rectirostris tephrolaema*	Green Sunbird	61	61,2	1972	cc3075	Chappuis, Claude	Kribi,
17	*Anthreptes rectirostris tephrolaema*	Green Sunbird	61	61,2	1970	cc3076	Chappuis, Claude	Makokou
18	*Anthreptes rectirostris tephrolaema*	Green Sunbird	61	61,2	1994	cc25884	Dowsett-Lemaire, F.	Odzala
19	*Anthreptes reichenowi reichenowi*	Plain-backed Sunbird	50	50,2	1993	55960	Keith, Stuart	Sokoke forest
20	*Anthreptes aurantium*	Violet-tailed Sunbird	59	None			Chappuis, Claude	
21	*Anthreptes seimundi kruensis*	Little Green Sunbird	60	60,2		cc3090	Chappuis, Claude	Makokou
22	*Anthreptes seimundi traylori*	Little Green Sunbird	60	60,2	1971	cc3091	Keith, Stuart	-
23	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	81	81,1	1968	cc3132	Chappuis, Claude	Ayame
24	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	81	81,1	1976	cc20239	Chappuis, Claude	Adiopodoume
25	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	81	81,1	1968	cc3134	Chappuis, Claude	N'Douci
26	*Chalcomitra rubescens stangerii*	Green-throated Sunbird	83	83,3	1996	cc26454	Chappuis, Claude	
27	*Chalcomitra adelberti adelberti*	Buff-throated Sunbird	81	81,1	1968	cc3133	Thiollay, J.M.	N'Douci
28	*Chalcomitra amethystina amethystina* 1	Amethyst Sunbird	84	84,1			Gillard, Len	-
30	*Chalcomitra amethystina amethystina* 2	Amethyst Sunbird	84	84,1			Skead, C. J	Eastern Cape
31	*Chalcomitra amethystina kirkii* 1	Amethyst Sunbird	84	84,3	1980	cc23105	Chappuis, Claude	West Lilongwe
32	*Chalcomitra amethystina kirkii* 1	Amethyst Sunbird	84	84,3			Stjernstedt, R	Machiya
33	*Chalcomitra amethystina kirkii* 2	Amethyst Sunbird	84	84,2			Stjernstedt, R	-
34	*Chalcomitra amethystina kirkii* 3	Amethyst Sunbird	84	84,2			Stjernstedt, R	-

35	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	82	82,1	1968	cc3123	Thiollay, J.M.	Adiopodoume
36	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	82	82,1	1968	cc3124	Thiollay, J.M.	N'Douci
37	*Chalcomitra fuliginosa aurea*	Carmelite Sunbird	82	82,1	1976	cc20408	Chappuis, Claude	North Guitry
38	*Chalcomitra hunteri*	Hunter's Sunbird	86	86,2	1983	27541	McVicker, R.	Taita Hills Lodge
39	*Chalcomitra hunteri*	Hunter's Sunbird	86	86,2	1990	48875	Pearson, D.	Ndara Ranch
40	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	83	83,2	1990	27889	McVicker, R.	
41	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	83	83,1	1975	cc20053	Chappuis, Claude	N'Kunden
42	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	83	83,1	1976	cc20153	Chappuis, Claude	Top of Mt Manengouba
43	*Chalcomitra rubescens rubescens*	Green-throated Sunbird	83	83,1	1971	cc3125	Chappuis, Claude	South Douala
44	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	85	85,3			Gillard, Len	-
45	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	85	85,3			Skead, C. J	-
46	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	85	85,3			Stjernstedt, R	-
47	*Chalcomitra senegalensis gutturalis*	Scarlet-chested Sunbird	85	85,3			Stjernstedt, R	Rufunsa
48	*Chalcomitra senegalensis cruentata*	Scarlet-chested Sunbird	85	85,2	1972	cc3129	Chappuis, Claude	Moundou
48	*Chalcomitra senegalensis senegalensis*	Scarlet-chested Sunbird	85	85,5	1994	52176	Smith, Steve	Abuko
50	*Chalcomitra balfouri*	Socotra Sunbird			1972	cc3128	Pearson, D	yemen
51	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	109	109,2		20897	Gillard, Len	natal national park
52	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	109	109,2	1984	61612	Skead, C. J	Addo Elephant Park
53	*Cinnyris afer saliens*	Greater Double-Collared Sunbird	109	109,2			Macaulay, L.	Zululand
54	*Cinnyris afer*	Greater Double-Collared Sunbird	109	109,2			Dowsett-Lemaire, F.	Nyungwe

55	*Cinnyris ludovicensis whytei*	Montane Double-Collared Sunbird	107	107,2		26380	Stjernstedt, R	Nyika
56	*Cinnyris ludovicensis whytei*	Montane Double-Collared Sunbird		107,2			Chappuis, Claude	Kakamega
57	*Cinnyris chalybeus*	Southern Double-Collared Sunbird	103	103,1			Gillard, Len	
58	*Cinnyris chalybeus chalybeus*	Southern Double-Collared Sunbird	103	103,2			Skead, C. J	
59	*Cinnyris chloropygius chloropygius* 1	Olive-bellied Sunbird	100	100,4		cc3150	Chappuis, Claude	Libreville
60	*Cinnyris chloropygius kempi* 1	Olive-bellied Sunbird	100	100,3	1968	cc3144	Thiollay, J.M.	N'Douci
61	*Cinnyris chloropygius kempi* 2	Olive-bellied Sunbird	100	100,3	1976	cc20301	Chappuis, Claude	Adiopodoume
62	*Cinnyris chloropygius kempi* 3	Olive-bellied Sunbird	100	100,4	1976	cc20277	Chappuis, Claude	Adiopodoume
63	*Cinnyris chloropygius kempi* 4	Olive-bellied Sunbird	100	100,3	1976	cc20293	Chappuis, Claude	Adiopodoume
64	*Cinnyris loveridgei*	Loveridge's Sunbird	114	None			Stjernstedt, R.	Uluguru Mts
65	*Cinnyris loveridgei*	Loveridge's Sunbird	114	None			Chappuis, Claude	Kakamega
66	*Cinnyris manoensis*	Miombo Double-Collared Sunbird	102	102,2	1986	38298	Stjernstedt, R	Ndzalanyama/Gt Dyke
67	*Cinnyris manoensis*	Miombo Double-Collared Sunbird	102	102,3	1991	81095	Chappuis, Claude	Shiwa Ngandu
68	*Cinnyris mediocris mediocris*	Eastern Double-Collared Sunbird	112	112,3			Stjernstedt, R	Aberdare
69	*Cinnyris mediocris mediocris*	Eastern Double-Collared Sunbird	112	112,3			Chappuis, Claude	Aberdare
70	*Cinnyris minullus*	Tiny Sunbird	101	None	1990	35606	Dowsett-Lemaire, F.	Goumina,
71	*Cinnyris minullus*	Tiny Sunbird	101	None	1970	cc3140	Chappuis, Claude	Makokou
72	*Cinnyris minullus*	Tiny Sunbird	101	None	1970	cc3141	Chappuis, Claude	Mt Bengoue
73	*Cinnyris minullus*	Tiny Sunbird	101	None	1972	cc3142	Chappuis, Claude	Bitam
74	*Cinnyris minullus*	Tiny Sunbird	101	None			Chappuis, Claude	Cotonou
75	*Cinnyris neergaardi*	Neergaard's Sunbird	104	None			Gillard, Len	-

75	*Cinnyris neergaardi*	Neergaard's Sunbird	104	None	1974	61279	Watts, David	Mkusi Game Reserve
76	*Cinnyris prigoginei*	Prigogine's Double-Collared Sunbird	106	None			Chappuis, Claude	
77	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	108	108,1	1971	cc3155	Chappuis, Claude	Ngaoundere
78	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	108	108,1	1974	cc3159	Chappuis, Claude	Mt Cameroon(1500m)
79	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	108	108,1	1974	cc3160	Chappuis, Claude	Mt Cameroon
80	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	108	108,1	1974	cc3164	Chappuis, Claude	Mt Cameroon(1100m)
81	*Cinnyris preussi preussi*	Northern Double-Collared Sunbird	108	108,1	1976	cc20204	Chappuis, Claude	Mt Cameroon(2500m)
82	*Cinnyris rockefelleri*	Rockefeller's Sunbird	111	None			Chappuis, Claude	
83	*Cinnyris pulchellus melanogaster* 1	Beautiful Sunbird	115	115,1	1986	48882	Pearson, D.	Meto Road
84	*Cinnyris pulchellus pulchellus* 1	Beautiful Sunbird	115	115,2	1971	cc3184	Chappuis, Claude	E. Tahoua
85	*Cinnyris pulchellus pulchellus* 2	Beautiful Sunbird	115	115,2	1972	cc3185	Chappuis, Claude	-
86	*Cinnyris pulchellus pulchellus* 3	Beautiful Sunbird	115	115,2		52148	Smith, Steve	Kotu area
87	*Cinnyris congensis*	Congo Sunbird	118	None			Chappuis, Claude	
88	*Cinnyris erythrocerca*	Red-chested Sunbird	119	None			Chappuis, Claude	
89	*Cinnyris regius regius*	Regal Sunbird	110	110,2	1989	30586	Dowsett-Lemaire, F.	Nyungwe Forest
90	*Cinnyris regius regius*	Regal Sunbird	110	110,2	1989	cc26207	Dowsett-Lemaire, F.	Nyungwe Forest
91	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	121	121,2			Gillard, Len	-
92	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	121	121,2		26386	Stjernstedt, R	Shughuri
93	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	121	121,2		80552	Stjernstedt, R	-

94	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	121	121,2		24044	Stjernstedt, R	-
95	*Cinnyris bifasciatus microrhynchus*	Purple-banded Sunbird	121	121,2	1972	12036	Gibbon, G.	Hluhluwe
96	*Cinnyris bouvieri*	Orange-tufted Sunbird	125	None	1974	cc3166	Chappuis, Claude	10km North Yaounde
97	*Cinnyris bouvieri*	Orange-tufted Sunbird	125	None	1975	cc20004	Chappuis, Claude	Yaounde
98	*Cinnyris bouvieri*	Orange-tufted Sunbird	125	None	1972	cc3167	Chappuis, Claude	Bertoua
99	*Cinnyris bouvieri*	Orange-tufted Sunbird	125	None	1974	cc3168	Chappuis, Claude	Yaounde
100	*Cinnyris habessinicus hellmayri*	Shining Sunbird	127	127,3	1985	10613	Hollom, P.	Ma'bar
101	*Cinnyris mariquensis mariquensis*	Mariqua Sunbird	116	116,1			Gillard, Len	-
102	*Cinnyris mariquensis mariquensis*	Mariqua Sunbird	116	116,1			Skead, C. J	-
103	*Cinnyris mariquensis suahelicus*	Mariqua Sunbird	116	116,3		52688	Stjernstedt, R	-
104	*Cinnyris mariquensis suahelicus*	Mariqua Sunbird	116	116,3		26385	Stjernstedt, R	Rukwa
105	*Cinnyris nectarinoides*	Black-bellied Sunbird	120	120,2	1986	18002	McVicker, R.	
106	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	120	120,2	1986	18003	McVicker, R.	Tsavo Safari Camp
107	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	120	120,2	1990	27175	Fisher, D.	Tsavo.Safari Camp,
108	*Cinnyris nectarinoides nectarinoides*	Black-bellied Sunbird	120	120,2	1989	48886	Pearson, D.	Tsavo Safari Camp
109	*Cinnyris oseus oseus*	Palestine Sunbird	126	126,2	1986	19494	Waite, Brian D.	Sea of Galilee
110	*Cinnyris oseus oseus*	Palestine Sunbird	126	126,2	1980	38089	Hollom, P.	Tel Aviv
111	*Cinnyris oseus oseus*	Palestine Sunbird	126	126,2	1985	38086	Hollom, P.	Near Kawkoban
112	*Cinnyris oseus oseus*	Palestine Sunbird	126	126,2	1993	47608	Svensson, L.	Wadi Sholomo
113	*Cinnyris chalcomelas*	Kenya Violet-breasted Sunbird	123	None	1988	27843	McVicker, R.	Sokoke Forest
114	*Cinnyris chalcomelas*	Kenya Violet-breasted Sunbird	123	None	1981	27798	McVicker, R.	Sokoke Forest
115	*Cinnyris chalcomelas*	Kenya Violet-breasted Sunbird	123	None	1981	30045	McVicker, R.	Galana Ranch

116	*Cinnyris pembae*	Voilet-breasted / Pemba Sunbird	124	None			Mellanby, R.	-
117	*Cinnyris pembae*	Voilet-breasted / Pemba Sunbird	124	None			Mellanby, R.	-
118	*Cinnyris shelleyi shelleyi*	Shelley's Sunbird	117	117,2		26384	Stjernstedt, R	Mawanda
119	*Cinnyris shelleyi*	Shelley's Sunbird	117				Chappuis, Claude	
120	*Cinnyris coccinigaster*	Splendid Sunbird	128	None	1975	10080	Grimes, L. I	Accra Plains
121	*Cinnyris coccinigaster*	Splendid Sunbird	128	None	1986	27896	Watson, C. R.	Shai Hills Nature reserve
123	*Cinnyris coccinigaster*	Splendid Sunbird	128	None	1968	cc3175	Chappuis, Claude	N'douci
124	*Cinnyris coccinigaster*	Splendid Sunbird	128	None	1968	cc3181	Chappuis, Claude	Korhogo
125	*Cinnyris johannae fasciata* 1	Johanna's Sunbird	129	129,1	1968	cc3187	Thiollay, J.M.	Ayame
126	*Cinnyris johannae fasciata* 2	Johanna's Sunbird	129	129,1	1976	cc20321	Chappuis, Claude	Divo Forest
127	*Cinnyris johannae johannae* 3	Johanna's Sunbird	129	129,2	1991	cc25701	Sargeant, D.	Gamba
128	*Cinnyris johannae fasciata*	Johanna's Sunbird	129	129,1	1971	cc3188	S. Keith	
129	*Cinnyris superbus ashantiensis* 1	Superb Sunbird	130	130,1	1968	cc3192	Chappuis, Claude	N'Douci
130	*Cinnyris superbus ashantiensis* 2	Superb Sunbird	130	130,1	1976	cc20302	Chappuis, Claude	West Abidjan
131	*Cinnyris superbus superbus* 1	Superb Sunbird	130	130,4	1975	cc20005	Chappuis, Claude	Yaounde
132	*Cinnyris superbus superbus* 1	Superb Sunbird	130	130,4	1970	cc3190	Chappuis, Claude	Makokou
133	*Cinnyris fuscus*	Dusky Sunbird	135	135,1	1979	60500	Gillard, Len	Karoo N.P.
134	*Cinnyris fuscus*	Dusky Sunbird	135	135,1		60563	Skead, C. J	Mariental
135	*Cinnyris fuscus*	Dusky Sunbird	135	135,1		60566	Skead, C. J	Mariental
136	*Cinnyris oustaleti rhodesiae*	Oustalet's Sunbird	132	132,2	1995	80907	Carter, Clide	Isoka
137	*Cinnyris oustaleti rhodesiae*	Oustalet's Sunbird	132	132,2		80907	Stjernstedt, R	-

138	*Cinnyris talatala*	White-breasted Sunbird	133	None			Gillard, Len	-
139	*Cinnyris talatala*	White-breasted Sunbird	133	None			Skead, C . J	Zululand
140	*Cinnyris talatala*	White-breasted Sunbird	133	None		26376	Stjernstedt, R	Lusaka, Mutulanganga
141	*Cinnyris talatala*	White-breasted Sunbird	133	None		26377	Stjernstedt, R	-
142	*Cinnyris talatala*	White-breasted Sunbird	133	None		52689	Stjernstedt, R	-
143	*Cinnyris talatala*	White-breasted Sunbird	133	None			Chappuis, Claude	
144	*Cinnyris venustus falkensteini*	Variable Sunbird	134	134,?.			Gillard, Len	-
145	*Cinnyris venustus falkensteini*	Variable Sunbird	134	134,2		26378	Stjernstedt, R	Zambesi valley
146	*Cinnyris venustus falkensteini*	Variable Sunbird	134	134,2		26379	Stjernstedt, R	-
147	*Cinnyris venustus falkensteini*	Variable Sunbird	134	134,2			Stjernstedt, R	-
148	*Cinnyris venustus*	Variable Sunbird	134	134,1	1976		Skead, C. J	Langata
149	*Cinnyris venustus*	Variable Sunbird	134	134,2	1968	54554	Chappuis, Claude	
150	*Cinnyris venustus*	Variable Sunbird	134	134,2	1980	cc22966	Chappuis, Claude	Lilongwe
151	*Cinnyris venustus*	Variable Sunbird	134	134,5	1969	cc3136	Chappuis, Claude	Ndali
152	*Cinnyris venustus*	Variable Sunbird	134	134,5	1971	cc3137	Chappuis, Claude	South-East Zaria
153	*Cinnyris batesi*	Bates's Sunbird	137	None	1997	59290	Gardner,N.	Mount kupe (Nyasoso)
154	*Cinnyris batesi*	Bates's Sunbird	137	None	1970	cc3173	Chappuis, Claude	Makokou
155	*Cinnyris batesi*	Bates's Sunbird	137	None	1970	cc3174	Chappuis, Claude	
156	*Cinnyris batesi*	Bates's Sunbird	137	None	1996	cc26467	Chappuis, Claude	Kakum Forest
157	*Cinnyris ursulae*	Ursula's Sunbird	136	None	1974	cc3105	Chappuis, Claude	Mt Cameroon(1100m)
158	*Cinnyris ursulae*	Ursula's Sunbird	136	None	1992	cc26082	Rodewald, P.	
159	*Cinnyris ursulae*	Ursula's Sunbird	136	None	1992	cc26083	Rodewald, P.	

160	*Cinnyris cupreus cupreus*	Copper Sunbird	138	138,1			Stjernstedt, R	Tatanda
161	*Cinnyris cupreus cupreus*	Copper Sunbird	138	138,2			Chappuis, Claude	
162	*Cinnyris cupreus cupreus*	Copper Sunbird	138	138,2			Moyer, D.	
163	*Cinnyris cupreus cupreus*	Copper Sunbird	138	138,2			Brunel, J.	
164	*Cyanomitra alinae tanganjicae*	Blue-headed Sunbird	77	77,5	1989	30599	Dowsett-Lemaire, F.	Nyungwe Forest
165	*Cyanomitra alinae tanganjicae*	Blue-headed Sunbird	77	77,5	1989	cc26220	Dowsett-Lemaire, F.	Nyungwe
166	*Cyanomitra bannermani*	Bannerman's Sunbird	74	None	1990	cc25924	Carter, Clide	Isombu stream
167	*Cyanomitra cyanolaema magnistrata* 1	Blue-throated Brown Sunbird	75	75,2	1968	cc3117	Thiollay, J.M.	Adiopodoume
168	*Cyanomitra cyanolaema octaviae 2*	Blue-throated Brown Sunbird	75	75,3	1989	40026	Dowsett-Lemaire, F.	Mayombe
169	*Cyanomitra cyanolaema octaviae 3*	Blue-throated Brown Sunbird	75	75,3	1977	cc3122	Erand, Chrstian	Mokokou
170	*Cyanomitra cyanolaema octaviae 4*	Blue-throated Brown Sunbird	75	75,3	1970	cc3120	Brosset, A.	Mokokou
171	*Cyanomitra cyanolaema octaviae 5*	Blue-throated Brown Sunbird	75	75,3	1972	cc3121	Chappuis, Claude	Libreville
172	*Cyanomitra olivacea sclateri*1	Western Olive Sunbird	79	79,6		26373	Stjernstedt, R.	Vumba
173	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	79	79,1	1996	cc26444	Chappuis, Claude	Kakum Forest
174	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	79	79,1	1976	cc20166	Chappuis, Claude	Nkonsamba
175	*Cyanomitra olivacea cephaelis*	Western Olive Sunbird	79	79,1	1972	cc3100	Chappuis, Claude	Makokou
176	*Cyanomitra olivacea olivacea* 1	Eastern Olive Sunbird	78	78,4			Gillard, Len	-
177	*Cyanomitra olivacea olivacea* 2	Eastern Olive Sunbird	78	78,5			Skead, C. J	Zululand
178	*Cyanomitra olivacea olivacea* 3	Eastern Olive Sunbird	78	78,5			Skead, C. J	Natal

179	*Cyanomitra olivacea*	Eastern Olive Sunbird	78	78,1		37579	Stjernstedt, R.	-
180	*Cyanomitra oritis oritis 1*	Cameroon Sunbird	76	76,2	1974	6074	Chappuis, Claude	Mt Cameroon
181	*Cyanomitra oritis oritis 2*	Cameroon Sunbird	76	76,2	1976	6075	Chappuis, Claude	Mt Cameroon
182	*Cyanomitra oritis oritis 3*	Cameroon Sunbird	76	76,2	1974	cc3113	Chappuis, Claude	Mt Cameroon(1300m)
183	*Cyanomitra oritis oritis 4*	Cameroon Sunbird	76	76,2	1976	cc20226	Chappuis, Claude	Mt Cameroon
184	*Cyanomitra veroxii veroxii 1*	Mouse-coloured Sunbird	80	80,1			Skead, C. J	Eastern Cape
185	*Cyanomitra veroxii 2*	Mouse-coloured Sunbird	80	80,1			Gillard, Len	
186	*Cyanomitra verticalis bohndorffii* 1	Green-headed Sunbird	73	73,1	1976	cc20131	Chappuis, Claude	Mt Manangouba
187	*Cyanomitra verticalis bohndorffii* 2	Green-headed Sunbird	73	73,1	1976	cc20218	Chappuis, Claude	Mt Cameroon
188	*Cyanomitra verticalis viridisplendens 3*	Green-headed Sunbird	73	73,4	1982	27632	McVicker, R.	Mlaba Forest
189	*Cyanomitra verticalis viridisplendens 4*	Green-headed Sunbird	73	73,4	1976	cc22642	Chappuis, Claude	South Kericho
190	*Deleornis fraseri cameroonensis* 1	Scarlet-tufted Sunbird	48	48,1	1972	cc3070	Chappuis, Claude	Moundou
191	*Deleornis fraseri idius 1*	Scarlet-tufted Sunbird	48	48,3	1976	cc20417	Chappuis, Claude	Adiapodoumi
192	*Deleornis fraseri cameroonensis* 3	Scarlet-tufted Sunbird	48	48,1	1970	cc3071	Keith, Stuart	Makokou
193	*Deleornis fraseri cameroonensis 2*	Scarlet-tufted Sunbird	48	48,1	/2003	cc26547	Chappuis, Claude	Detais in LNS Cornell
194	*Anthodiaeta collaris collaris* 1	Collared Sunbird	63	63,9			Skead, C. J	
195	*Anthodiaeta collaris elachior* 1	Collared Sunbird	63	63,4	1988	48865	Keith, Stuart	
196	*Anthodiaeta collaris elachior* 2	Collared Sunbird	63	63,8		26371	Stjernstedt, R	Sokoke forest
197	*Anthodiaeta collaris zuluensis* 1	Collared Sunbird	63	63,9			Gillard, Len	Eastern Cape
198	*Anthodiaeta collaris zambesiana* 1	Collared Sunbird	63	63,8	1997	52624	Stjernstedt, R	-
199	*Anthodiaeta collaris hypodila* 1	Collared Sunbird	63	63,5	1992	cc25633	Chappuis, Claude	Sindabezi
200	*Anthodiaeta collaris somereni* 1	Collared Sunbird	63	63,6	1992	cc26088	Chappuis, Claude	Ureka, 400m.

201	*Anthodiaeta collaris subcollarris* 1	Collared Sunbird	63	63,7	1968	cc3082	Chappuis, Claude	
202	*Anthodiaeta collaris somereni* 1	Collared Sunbird	63	?.	1970	cc3078	Chappuis, Claude	Makokou
203	*Anthodiaeta pallidigaster*	Amani Sunbird	66	None			Keith, Stuart	Usambara Mts
204	*Anthodiaeta platura*	Pygmy Sunbird	64	None	1992	35301	Greensmith, A	N'Douci
205	*Anthodiaeta platura*	Pygmy Sunbird	64	None	1971	cc3086	Chappuis, Claude	South-East Zaria
206	*Anthodiaeta platura*	Pygmy Sunbird	64	None	1971	cc3087	Chappuis, Claude	Jos
207	*Anthodiaeta platura*	Pygmy Sunbird	64	None	1971	cc3088	Chappuis, Claude	Ngaoundere
208	*Anthodiaeta metallica*	Nile valley Sunbird	Yemen	None			Smith, Steve	Tendaba
209	*Nectarinia famosa famosa*	Malachite Sunbird	97	97,2	1984	62824	Gillard, Len	
210	*Nectarinia famosa famosa*	Malachite Sunbird	97	97,2	1974	61094	Skead, C. J	
211	*Nectarinia famosa cupreonitens*	Malachite Sunbird	97	97,1		26288	Stjernstedt, R	
212	*Nectarinia famosa cupreonitens*	Malachite Sunbird	97	97,1			Chappuis, Claude	Mau Forest Near Kericho
213	*Nectarinia johnstoni johnstoni* 1	Red-tufted Sunbird	98	98,1	1978		BBC	Virunga Volcanoes
214	*Nectarinia johnstoni johnstoni* 2	Red-tufted Sunbird	98	98,1	1978		BBC	-
215	*Nectarinia johnstoni nyikensis* 1	Red-tufted Sunbird	98	98,4	1980	19782	Dowsett-Lemaire, F.	Nyika Plateau
216	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	96	96,1		10923	Stjernstedt, R	Arusha
217	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	96	96,3		6936	Skead, C. J	Nairobi
218	*Nectarinia kilimensis kilimensis*	Bronze Sunbird	96	96,3	1976	cc22643	Chappuis, Claude	Kericho
219	*Nectarinia bocagei*	Bocage's Sunbird	93	None			Chappuis, Claude	
220	*Nectarinia purpureiventris*	Purple-breasted Sunbird	94	None	1990	30651	Dowsett-Lemaire,	Bwindi Forest

							F.	
221	*Nectarinia purpureiventris*	Purple-breasted Sunbird	94	None	1990	cc26265	Dowsett-Lemaire, F.	Bwindi Forest
222	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	99	99,1	1964	3798	North, M.E.W.	Kivulini
223	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	99	99,1	1981	30076	McVicker, R.	Thika
224	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	99	99,2	1980	cc23178	Chappuis, Claude	Nyahururu
225	*Nectarinia reichenowi reichenowi*	Golden-winged Sunbird	99	99,2	1980	cc24560	Chappuis, Claude	Mt Kenya

APPENDIX 1g RECORDINGS OF SUNBIRDS OF INDIAN OCEAN AND GULF OF GUINEA ISLAND SPECIES

Ref. no.	Latin name	Common name	Country	Region	Sex	Duration	song	call	Comments.
1	*Anabathmis hartlaubii*	Principe Sunbird	Principe		M	0'45"	X	X	
2	*Anabathmis hartlaubii*	Principe Sunbird	Principe		M	2'15"	X		
3	*Anabathmis hartlaubii*	Principe Sunbird	Principe		M	2'25"	X	X	Calls of party of sunbirds
4	*Anabathmis hartlaubii*	Principe Sunbird	Principe		M	0'39"	X	x	
5	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		M	0'50"	X	X	
6	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		M	1'09"	X	X	
7	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		2 M	3'08"	X		Counter singing
8	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		M	1'04"	X		
9	*Anabathmis newtoni*	Newton's Sunbird	Sao Tome		M	0'39"	x		Perched at dawn
10	*Dreptes thomensis*	SaoTome Sunbird	Sao Tome		M		X		
11	*Dreptes thomensis*	SaoTome Sunbird	Sao Tome		M	2'45"	X		
12	*Cinnyris dussumieri*	Seychelles Sunbird	Seychelles Islands		M	2'00"	X	X	Adult alarm call & song
13	*Cinnyris dussumieri*	Seychelles Sunbird	Seychelles Islands		M	1'50"	X	X	Hammering sound
14	*Cinnyris dussumieri*	Seychelles Sunbird	Seychelles Islands		M	3'05"	X		Response to playback
15	*Cinnyris dussumieri*	Seychelles Sunbird	Seychelles Islands	Grand Comore	M	0'55"	X		
16	*Cinnyris notatus moebii*	Madagascar Sunbird	Comoros Is		M			X	Feeding on nectar.
17	*Cinnyris notatus notatus*	Madagascar Sunbird	Madagascar		M		X		
18	*Cinnyris notatus notatus*	Madagascar Sunbird	Madagascar		M	0'26"	X	X	

19	*Cinnyris notatus notatus*	Madagascar Sunbird	Madagascar		M	0'41"		X	
20	*Cinnyris n. voeltzkwowi*	Moheli Sunbird	Moheli Island	Aldabra	M	0'54"	X		
21	*Cinnyris souimanga*	Souimanga Sunbird	Indian Ocean	Aldabra	M	00:52		X	Territorial song
22	*Cinnyris souimanga*	Souimanga Sunbird	Indian Ocean	Ankarara	M	01:32	X		Excited (raps) & alarm
23	*Cinnyris souimanga*	Souimanga Sunbird	Madagascar	Mandeny-Antsahanade	M	01:39	X	X	Courtship
24	*Cinnyris souimanga*	Souimanga Sunbird	Madagascar	Analamazaotra	M	00:45		X	
25	*Cinnyris souimanga*	Souimanga Sunbird	Madagascar	Marojejy	M	01:46	X		
26	*Cinnyris souimanga*	Souimanga Sunbird	Madagascar	BBC	M	01:41	X	X	
27	*Cinnyris souimanga*	Souimanga Sunbird	BBC		M	02:50:00	X		
28	*Cinnyris humbloti mohelicus*	Humblot's Sunbird	Moheli Island		M	0'53"	X		
29	*Cinnyris humbloti humbloti*	Humblot's Sunbird	Comoros Island		M	0'52"	X		
30	*Cinnyris coquerellii*	Mayotte Sunbird			M	0'57"	X		

*Sp. n. – Species number

*Sub-sp.n. – Subspecies number

APPENDIX 1h RECORDINGS OF SUNBIRDS OF INDIAN OCEAN AND GULF OF GUINEA ISLAND SPECIES

Ref.no.	Latin name	Common name	Sp. n.	Sub-sp.n.	Year	Ref. No.	Copyright holder	Locality
1	*Anabathmis hartlaubii*	Principe Sunbird	69	None	1980	31426	Jones, P.	Porto Real
2	*Anabathmis hartlaubii*	Principe Sunbird	69	None	1987	cc3107	Tye, A.	
3	*Anabathmis hartlaubii*	Principe Sunbird	69	None	1987	24199	Tye, A.	
4	*Anabathmis hartlaubii*	Principe Sunbird	69	None	1996	113010	Chappuis, Claude	
5	*Anabathmis newtoni*	Newton's Sunbird	70	None	1990	30767	Alexander-Marrack, P.	Lagoa Amelia trail
6	*Anabathmis newtoni*	Newton's Sunbird	70	None	1990	cc3108	Alexander-Marrack, P.	-
7	*Anabathmis newtoni*	Newton's Sunbird	70	None	1990	cc3109	Alexander-Marrack, P.	-
8	*Anabathmis newtoni*	Newton's Sunbird	70	None		cc3112	Tye, A.	-
9	*Anabathmis newtoni*	Newton's Sunbird	70	None	2002	116285	Chappuis, Claude	Bom Sucesso
10	*Dreptes thomensis*	SaoTome Sunbird	71	None	1988	31445	Jones, Peter	
11	*Dreptes thomensis*	SaoTome Sunbird	71	None			Chappuis, Claude	L Amelia
12	*Cinnyris dussumieri*	Seychelles Sunbird	145	None	1976	3888	Turner, D.	Cousin Island
13	*Cinnyris dussumieri*	Seychelles Sunbird	145	None	1976	17700	Stjernstedt, R.	Mahe
14	*Cinnyris dussumieri*	Seychelles Sunbird	145	None	1976	23712	Stjernstedt, R.	Mahe
15	*Cinnyris dussumieri*	Seychelles Sunbird	145	None	1991	33928	Sinclair, I.	Cousin Island
16	*Cinnyris notatus moebii*	Madagascar Sunbird	144	144,1	1992	36022	Safford, R.	La Convalescence
17	*Cinnyris notatus notatus*	Madagascar Sunbird	144	144,2			Harrap, S.	Perinet
18	*Cinnyris notatus notatus*	Madagascar Sunbird	144	144,2	1993	54724	Lambert, F.	Ranomafana N. P.
19	*Cinnyris notatus notatus*	Madagascar Sunbird	144	144,2	1993	54728	Lambert, F.	Ranomafana N. P.

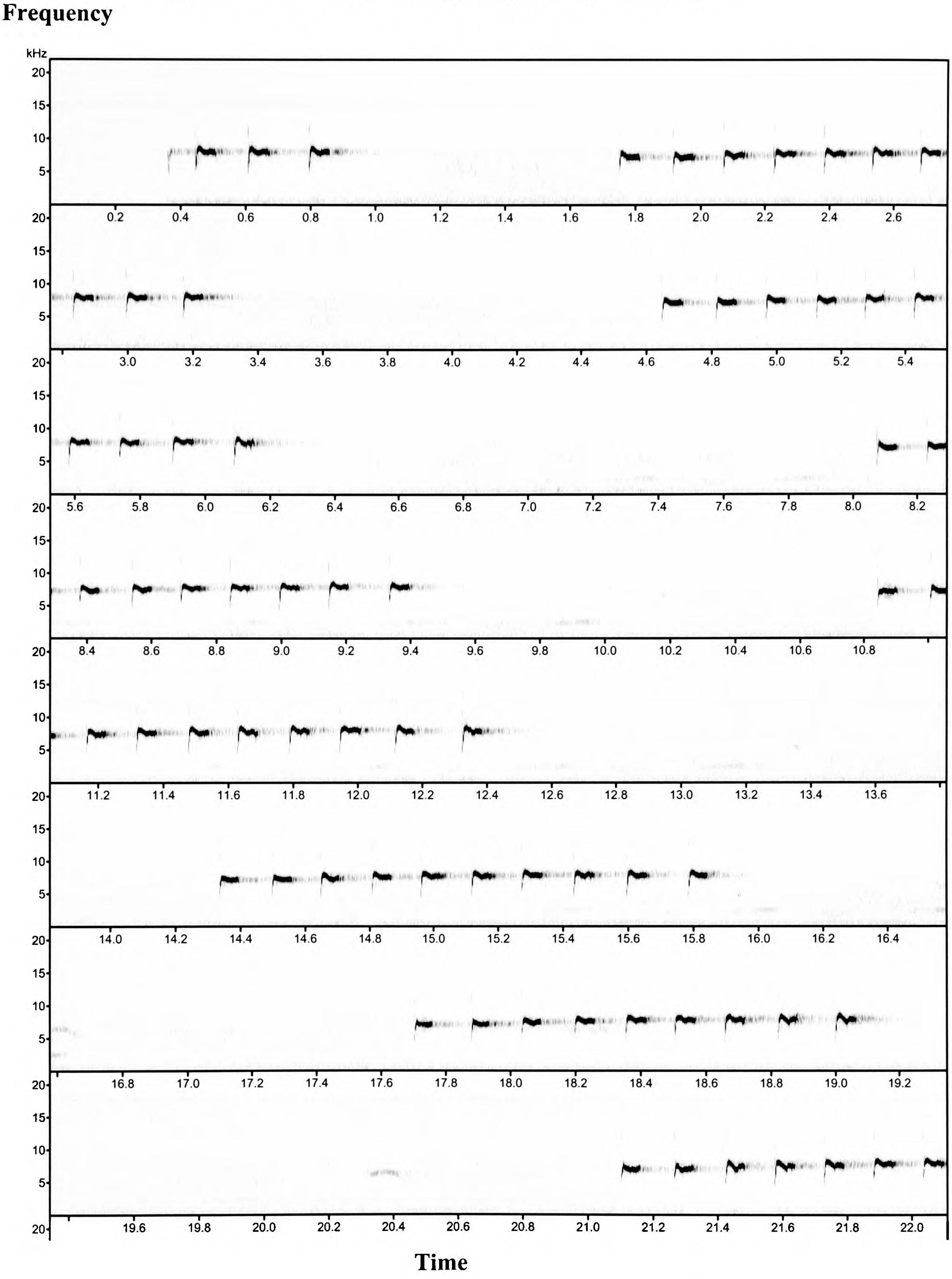
20	*Cinnyris n.voeltzkwowi*	Moheli Sunbird	144	144,3	2002	55826	Lambert, F.	
21	*Cinnyris souimanga*	Souimanga Sunbird	143	143,2	1974	4035	Snow, D	
22	*Cinnyris souimanga*	Souimanga Sunbird	143	143,2	1974	4059	Snow, D	
23	*Cinnyris souimanga*	Souimanga Sunbird	143	143,3	1987	22204	Stewart, P	
24	*Cinnyris souimanga*	Souimanga Sunbird	143	143,3	1976	17672	Stjernstedt, R	
25	*Cinnyris souimanga*	Souimanga Sunbird	143	143,3	1993	45122	Holt, P	
26	*Cinnyris souimanga*	Souimanga Sunbird	143	143,5	1996	52539	Hawkins, F	
27	*Cinnyris souimanga*	Souimanga Sunbird	143	143,6	2000			BBC
28	*Cinnyris humbloti mohelicus*	Humbloti's Sunbird	146	146'2	2000	53533	Lambert, F.	
29	*Cinnyris humbloti humbloti*	Humbloti's Sunbird	146	146'1	2000	55543	Lambert, F.	
30	*Cinnyris coquerellii*	Mayotte Sunbird	148	None	2000	565772	Lambert, F.	Mayotte

SONOGRAMS

Appendix 2

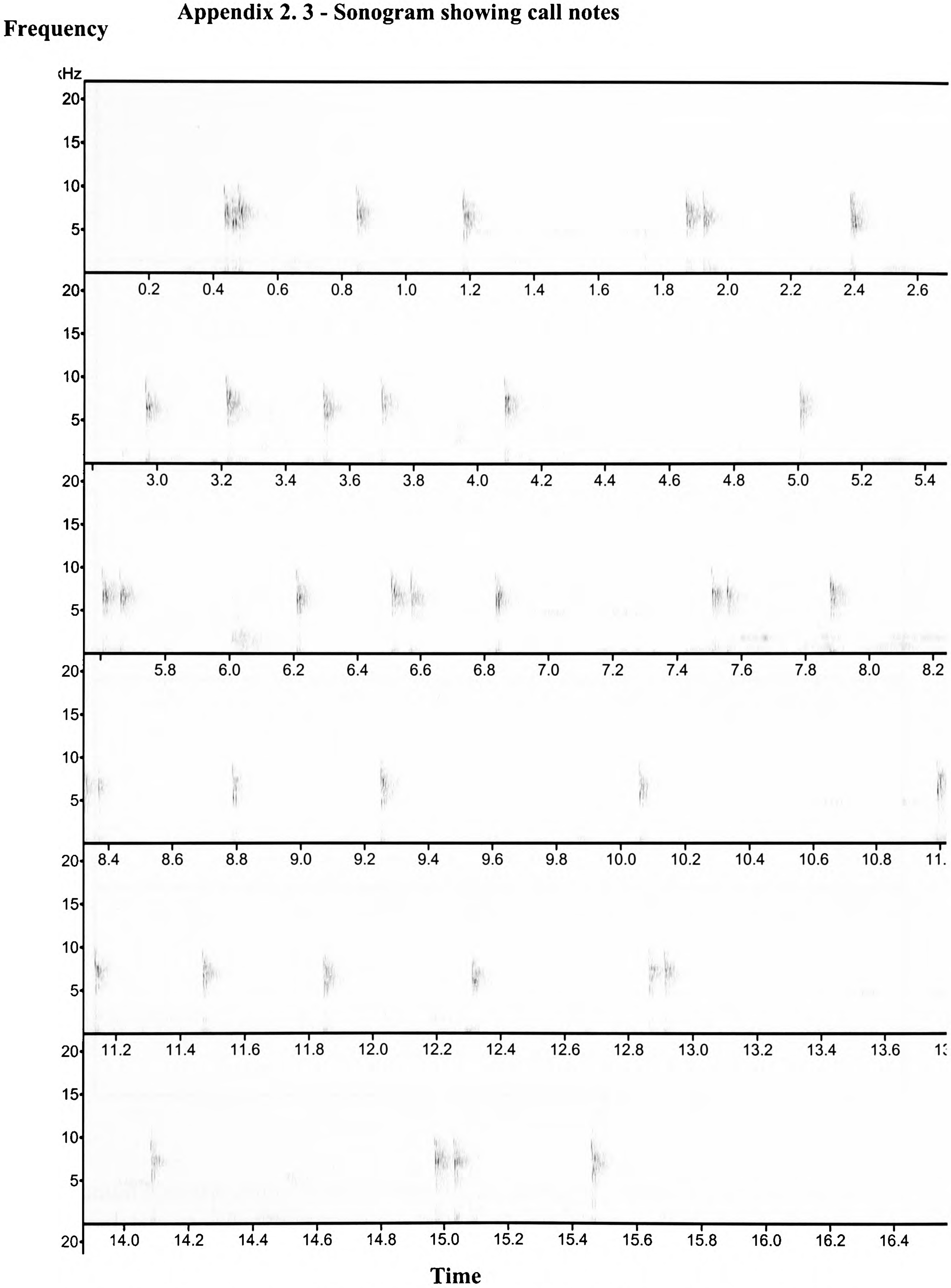
Examples of sonograms for flowerpeckers

Appendix 2. 2 - Sonogram depicting series of call notes



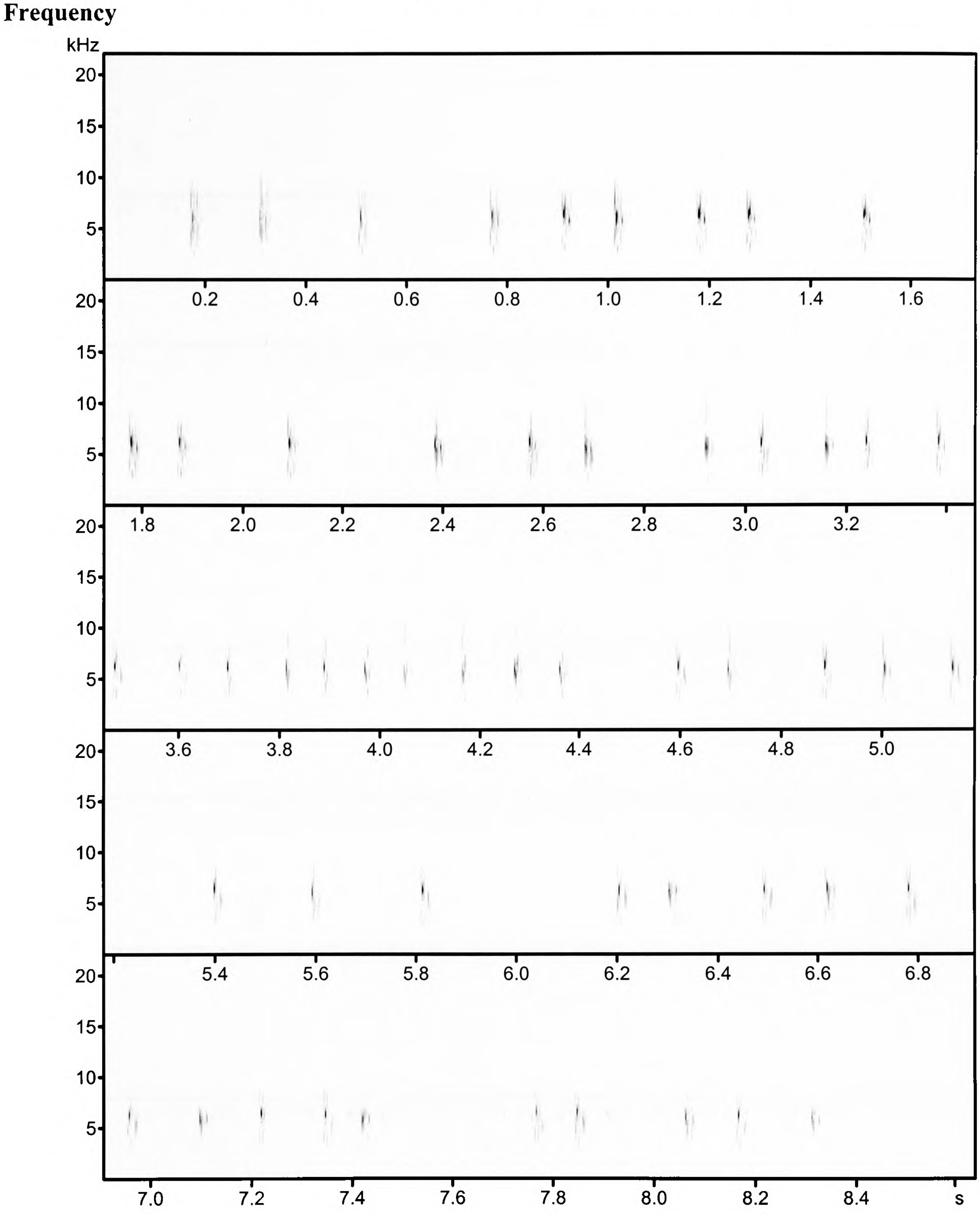
Olive-backed Flowerpecker *Prionochilus olivaceus* recorded in Mindanao, Philippines by P. Morris.

Appendix 2. 3 - Sonogram showing call notes



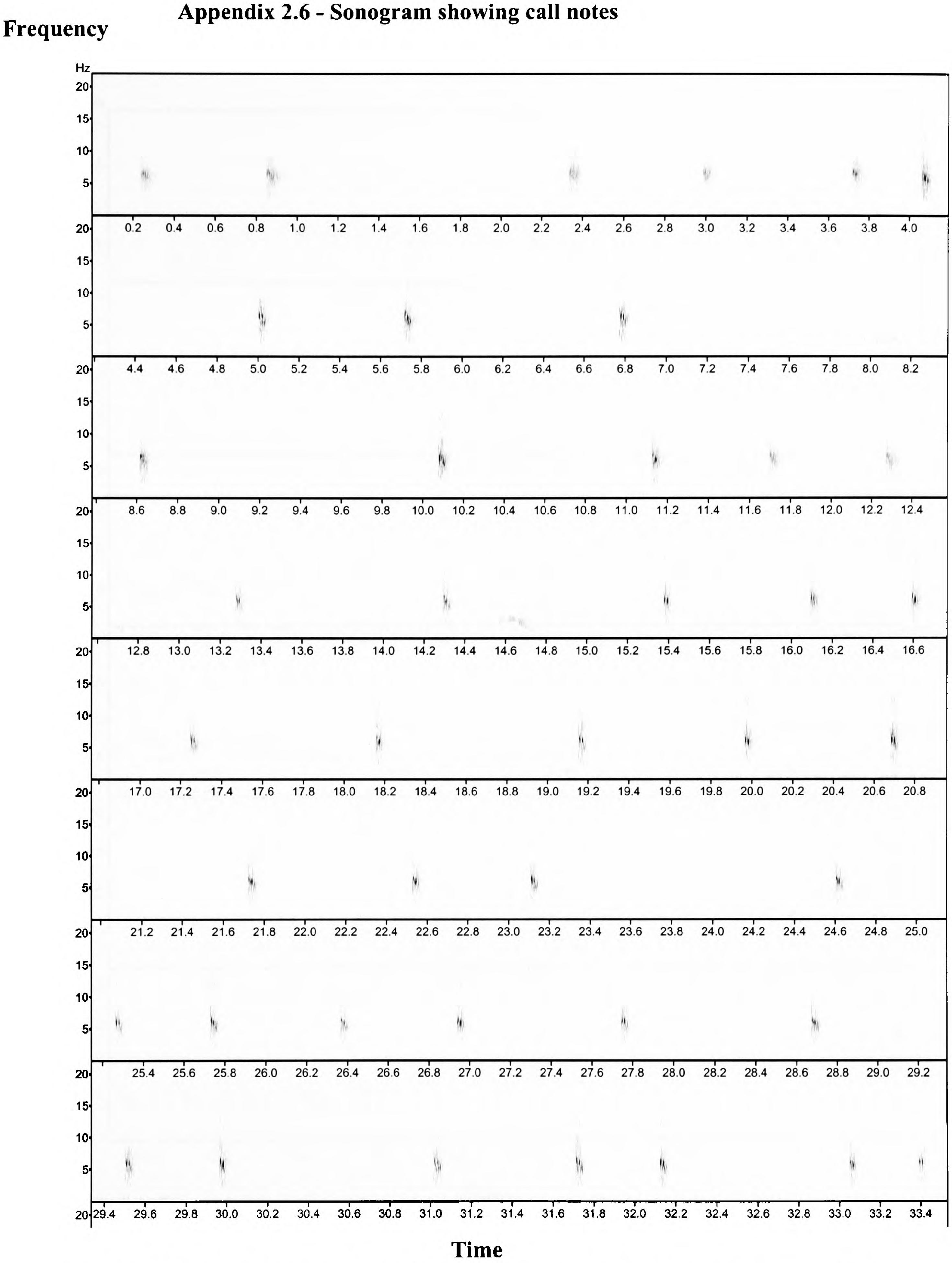
Yellow-breasted Flowerpecker *Prionochilus maculatus oblitus* recorded in Pasoh, Malaysia by S. Buckton.

Appendix 2.5 - Sonogram depicting series of call notes



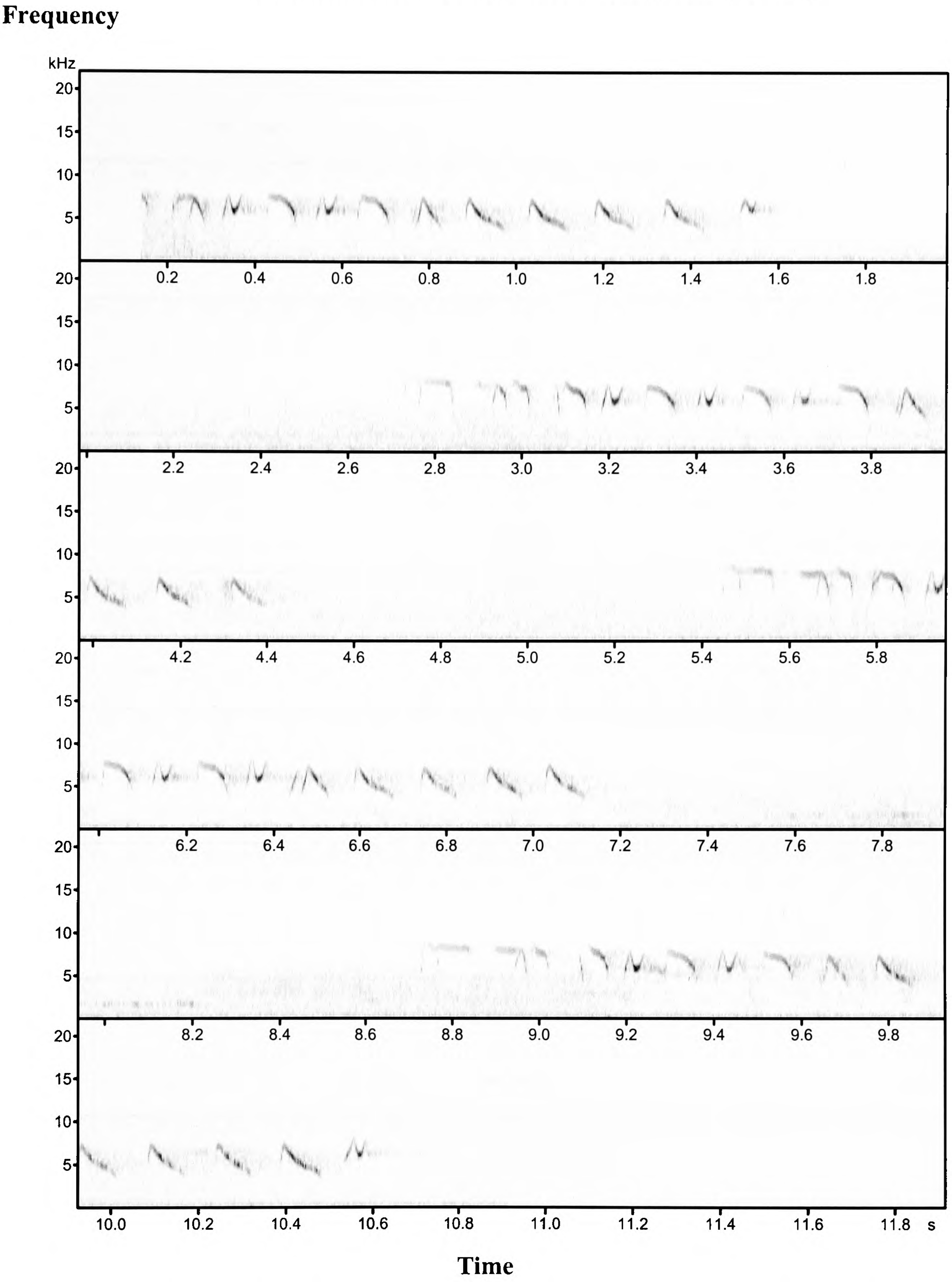
Crimson-breasted Flowerpecker *Prionochilus percussus* recorded in West Java, Indonesia by B. van Balen.

Appendix 2.6 - Sonogram showing call notes



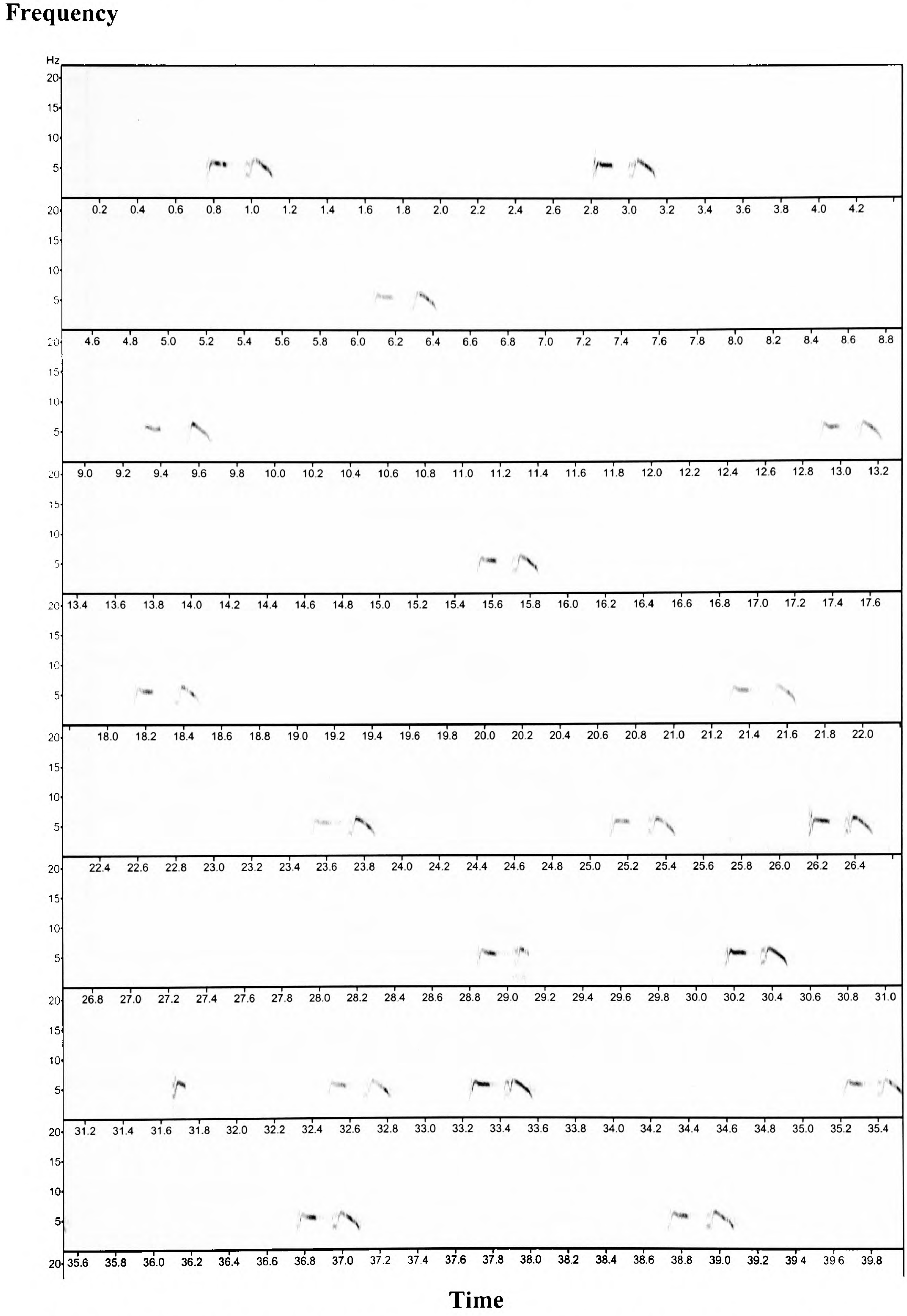
Yellow-rumped Flowerpecker *Prionochilus xanthopygius* recorded at East Kalimantan, Indonesia by B. van Balen.

Appendix 2. 13 - Sonogram depicting a simple song



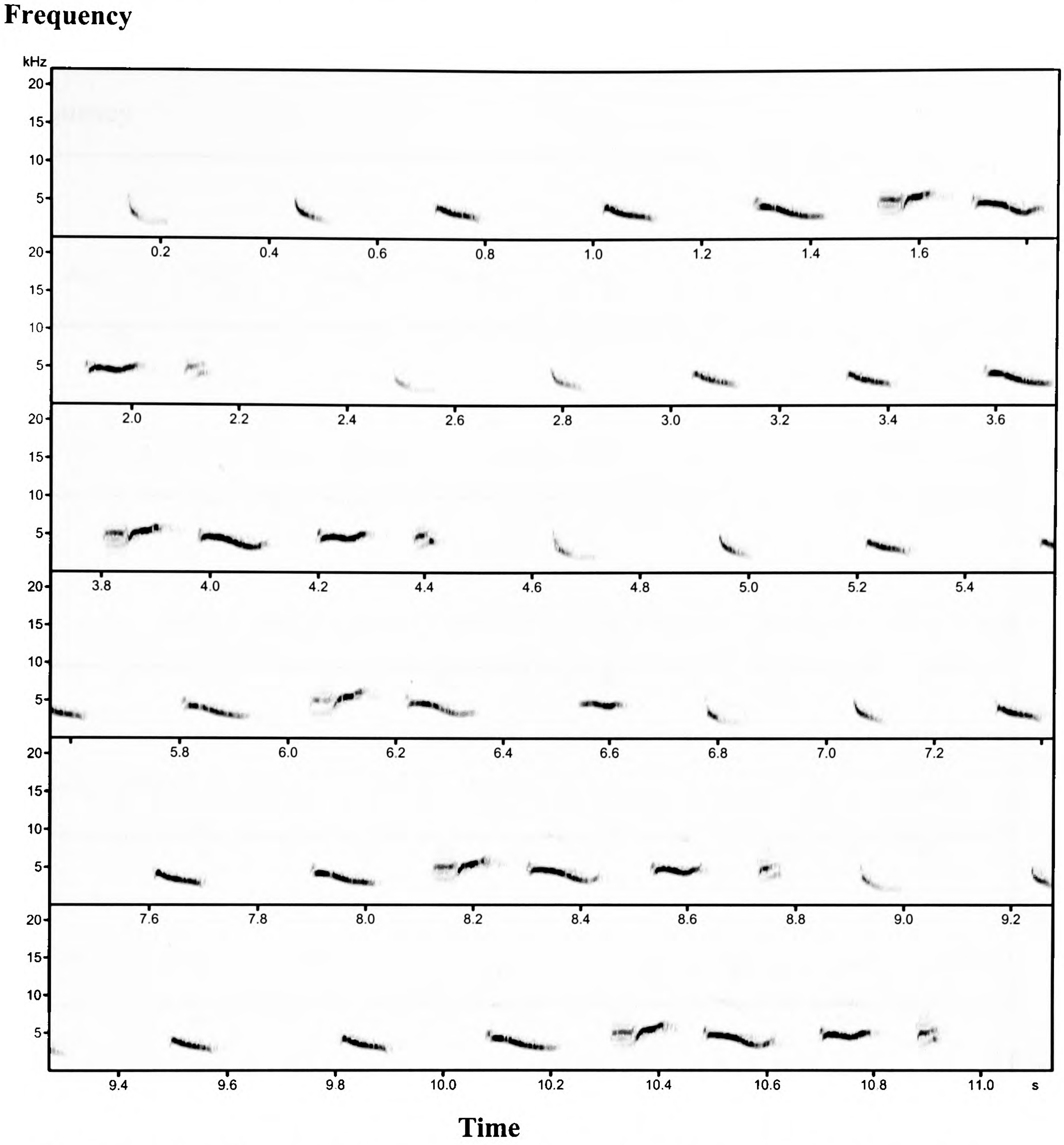
Whiskered Flowerpecker *Dicaeum proprium* recorded on Mt Apo, Mindanao Philippines by A. Wassink.

Appendix 2.29 - Sonogram showing call notes



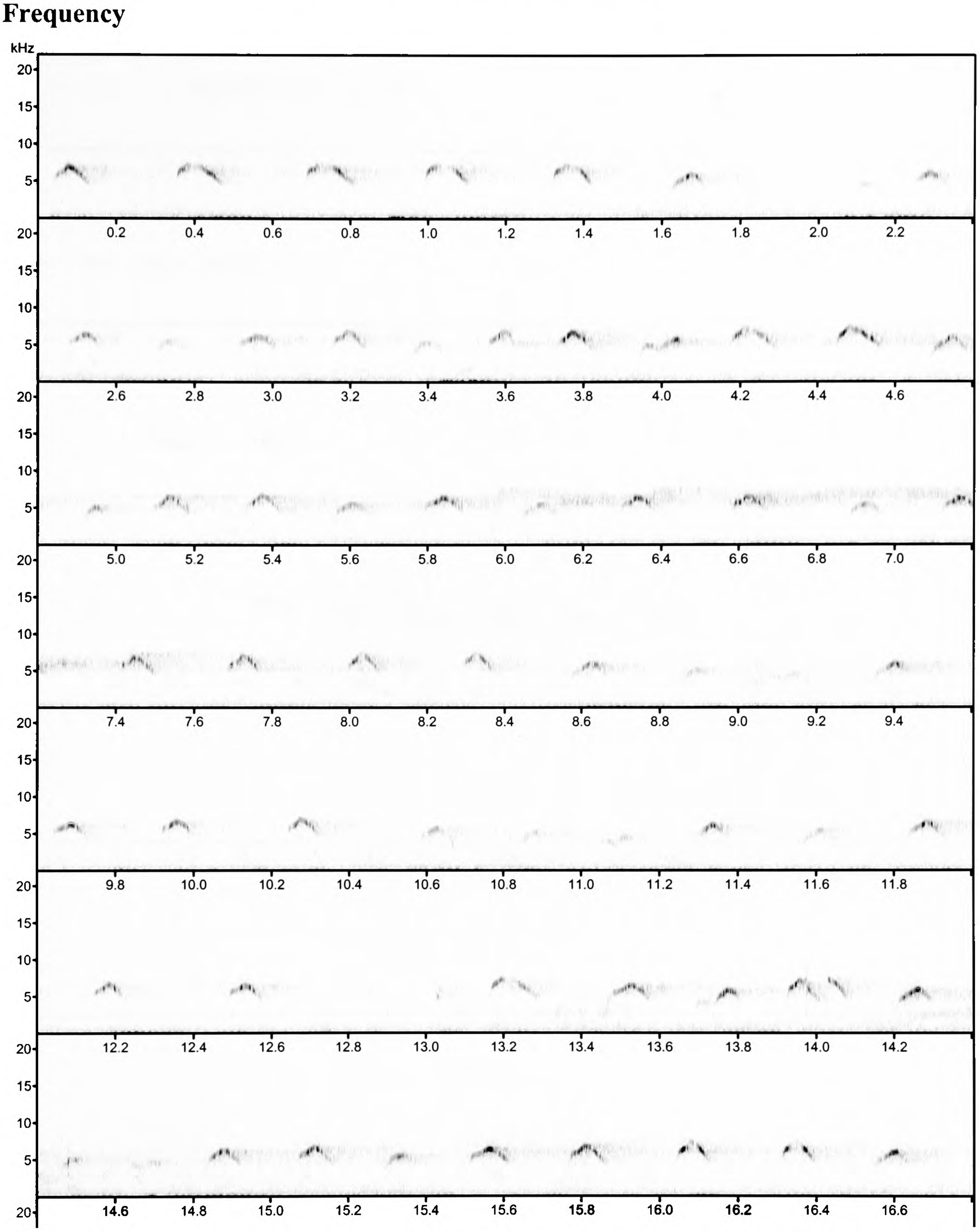
Orange-bellied Flowerpecker *Dicaeum trigonostigma cinereigulare* recorded in Bohol, Philippines by C. Hails.

Appendix 2. 57 - Sonogram showing a simple song



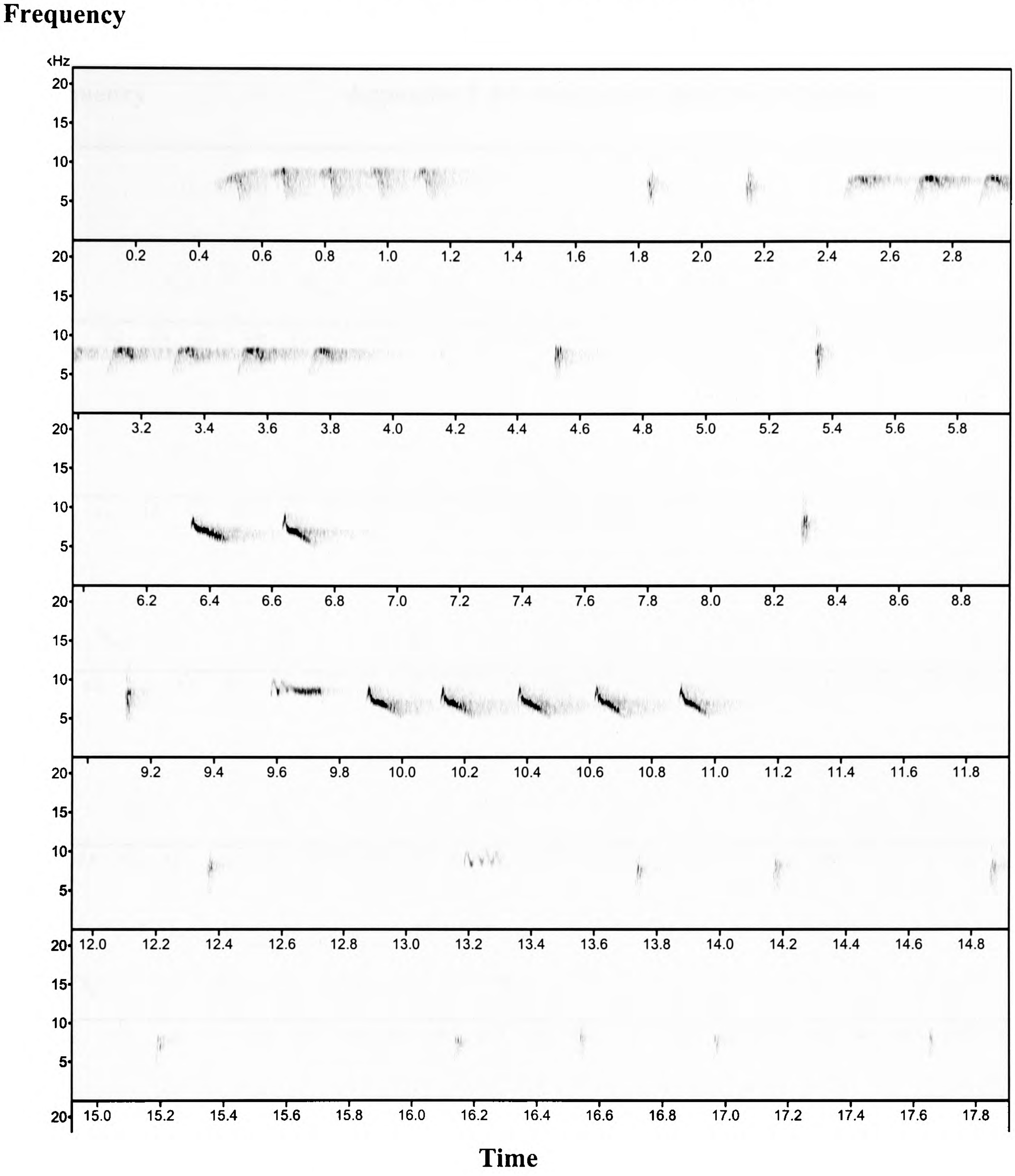
Blood-breasted Flowerpecker *Sanguinolentum whihelmonae* recorded in Sumba, Indonesia by S. Smith.

Appendix 2. 60 -Sonogram showing a simple song



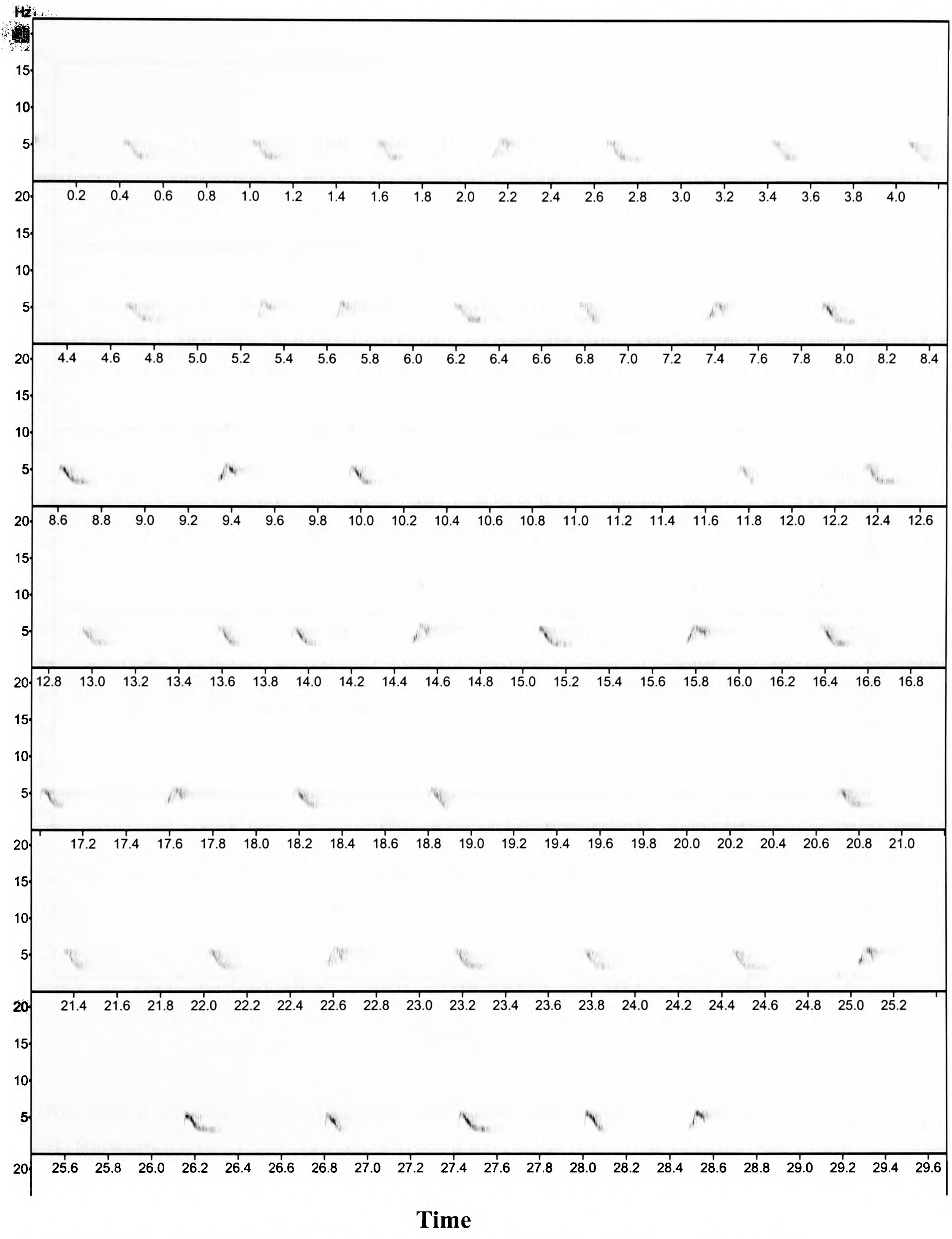
Fire-breasted Flowerpecker *Dicaeum ignipectum dolichorhynchum* recorded in South India by P. Holt.

Appendix 2. 66 - Sonogram showing a simple song



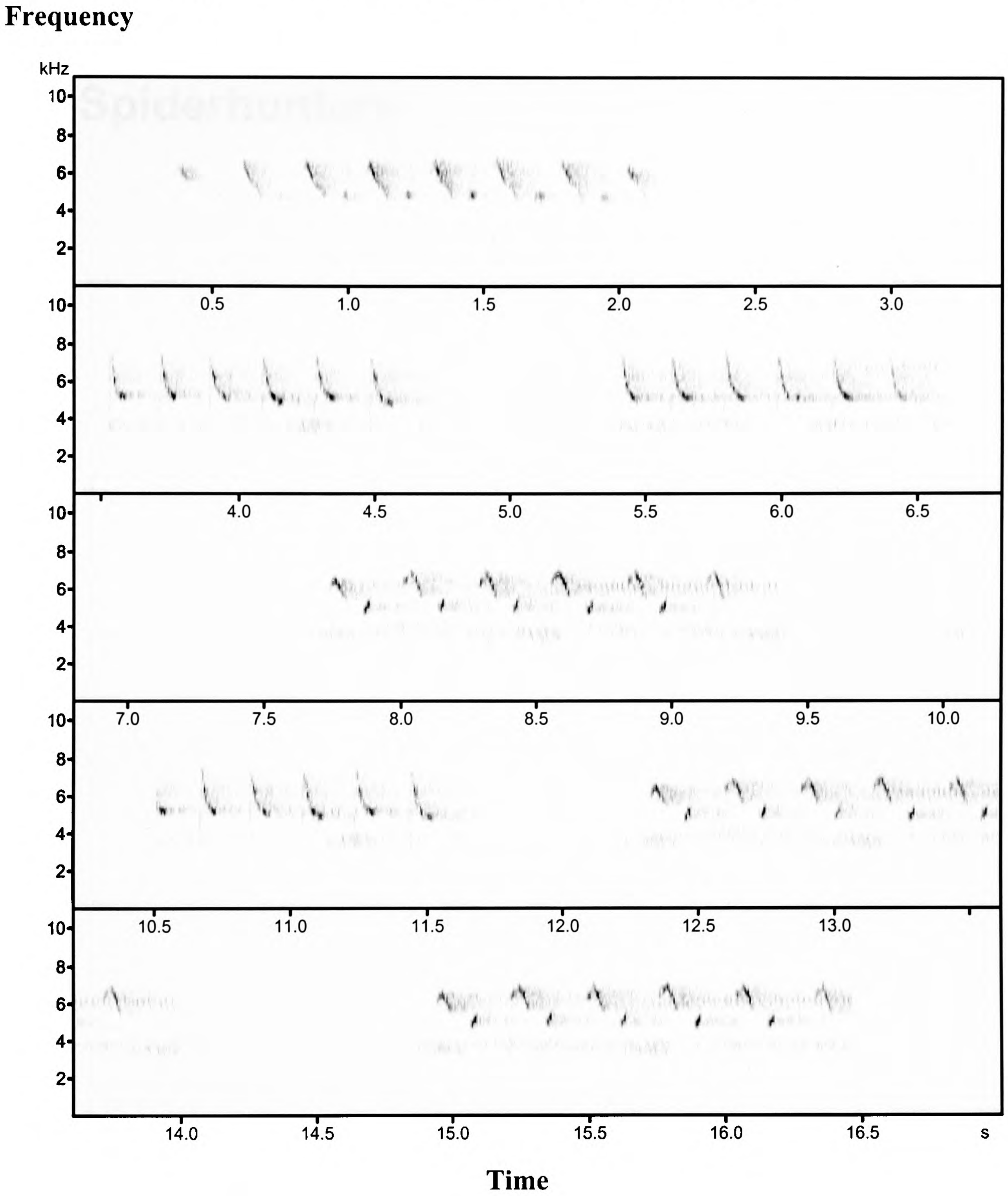
Yellow-vented Flowerpecker *Dicaeum chrysorrheum chrysorrheum* recorded in East Java, Indonesia by Groeneveld Henri, W.

Appendix 2 .69 - Sonogram showing call notes



Mottled Flowerpecker *Dicaeum tristrami* recorded in the Solomon Islands by P. Morris.

Appendix 2.70 - sonogram showing a simple song

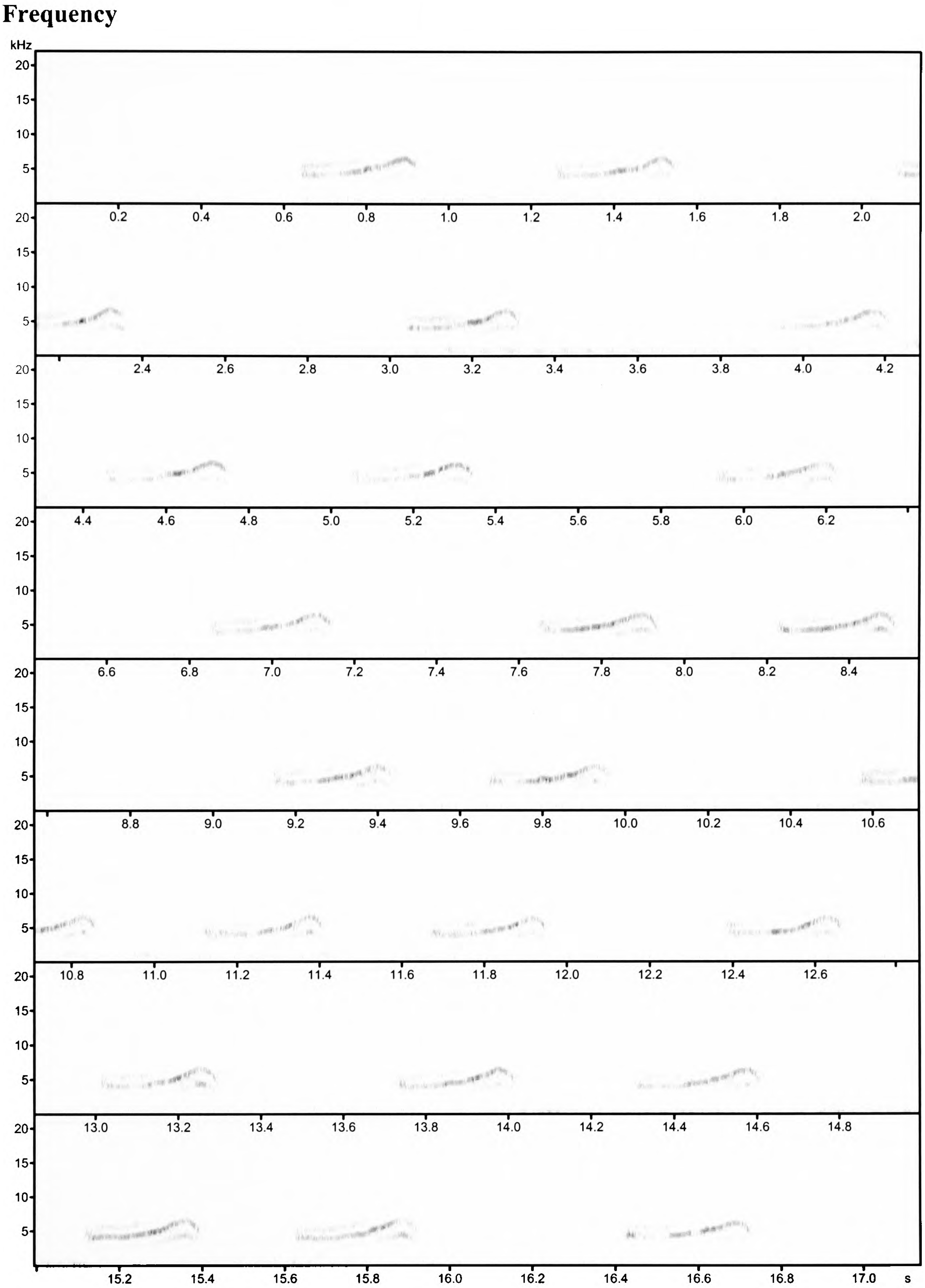


Mistletoebird *Dicaeum hirundinaceum hirundinaceum* recorded in Eastern Australia by B. Bertram.

APPENDIX 3.

Examples of sonograms of Asian Sunbirds & Spiderhunters

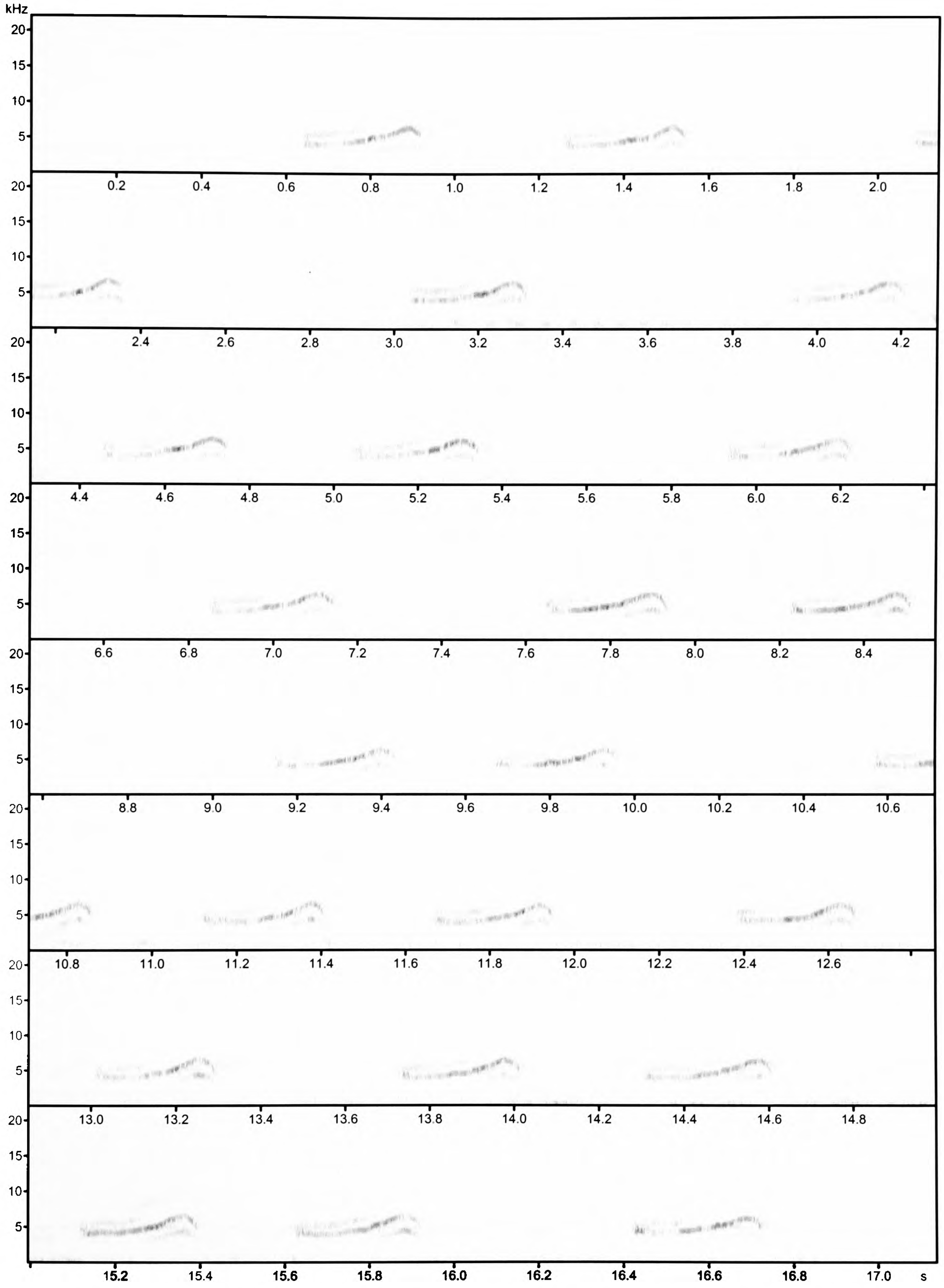
Appendix 3. 20 - Sonogram showing a simple song with harmonics



Crimson-backed *Sunbird Leptocoma minima* recorded in Kerela State, India by P. S. Sivaprasad.

Appendix 3. 39 - Sonogram showing a simple song with harmonics

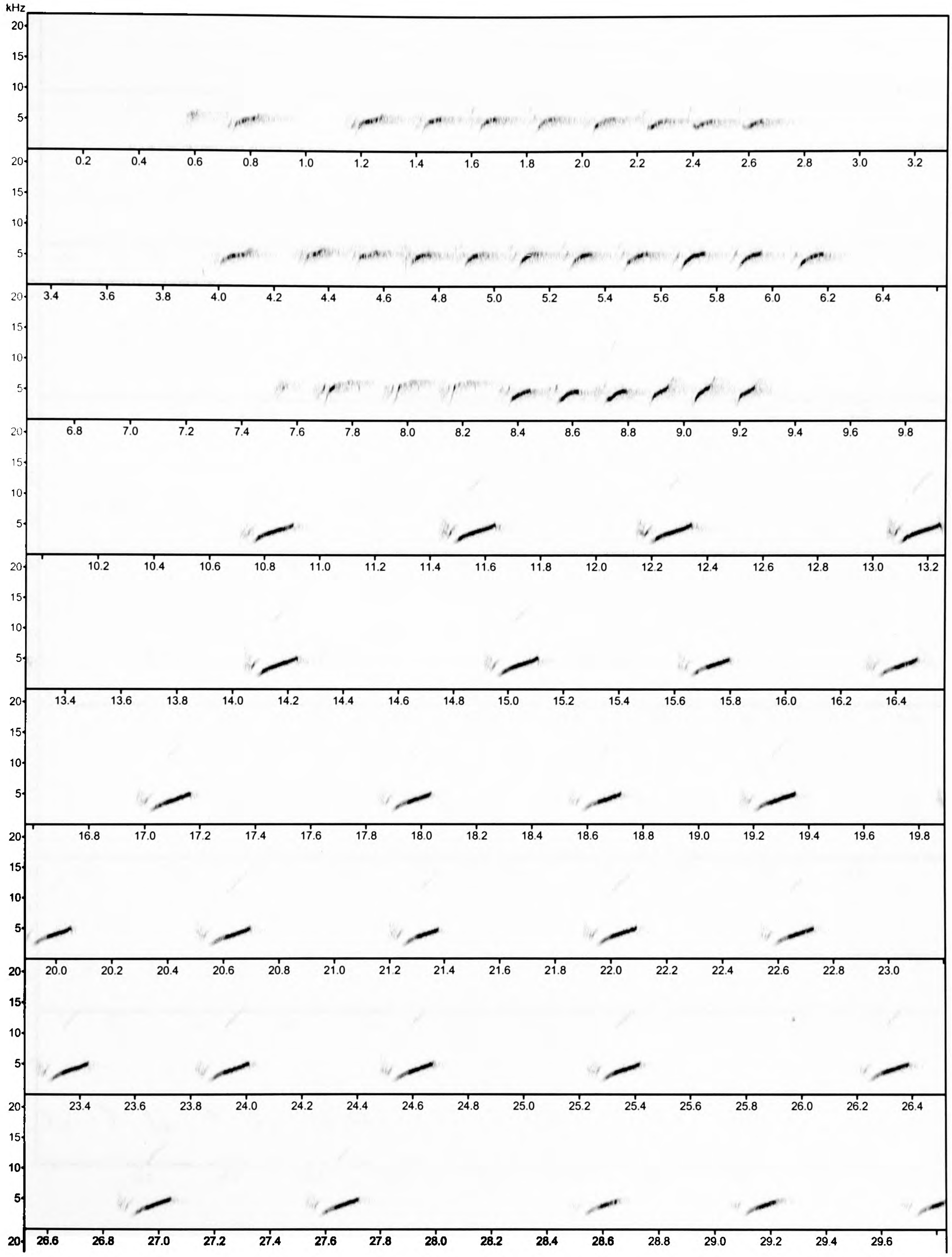
Frequency



Long-billed Sunbird *Cinnyris lotenius lotenius* recorded in Goa, South India, by P. Holt.

Appendix 3. 44 - Sonogram showing a complex song

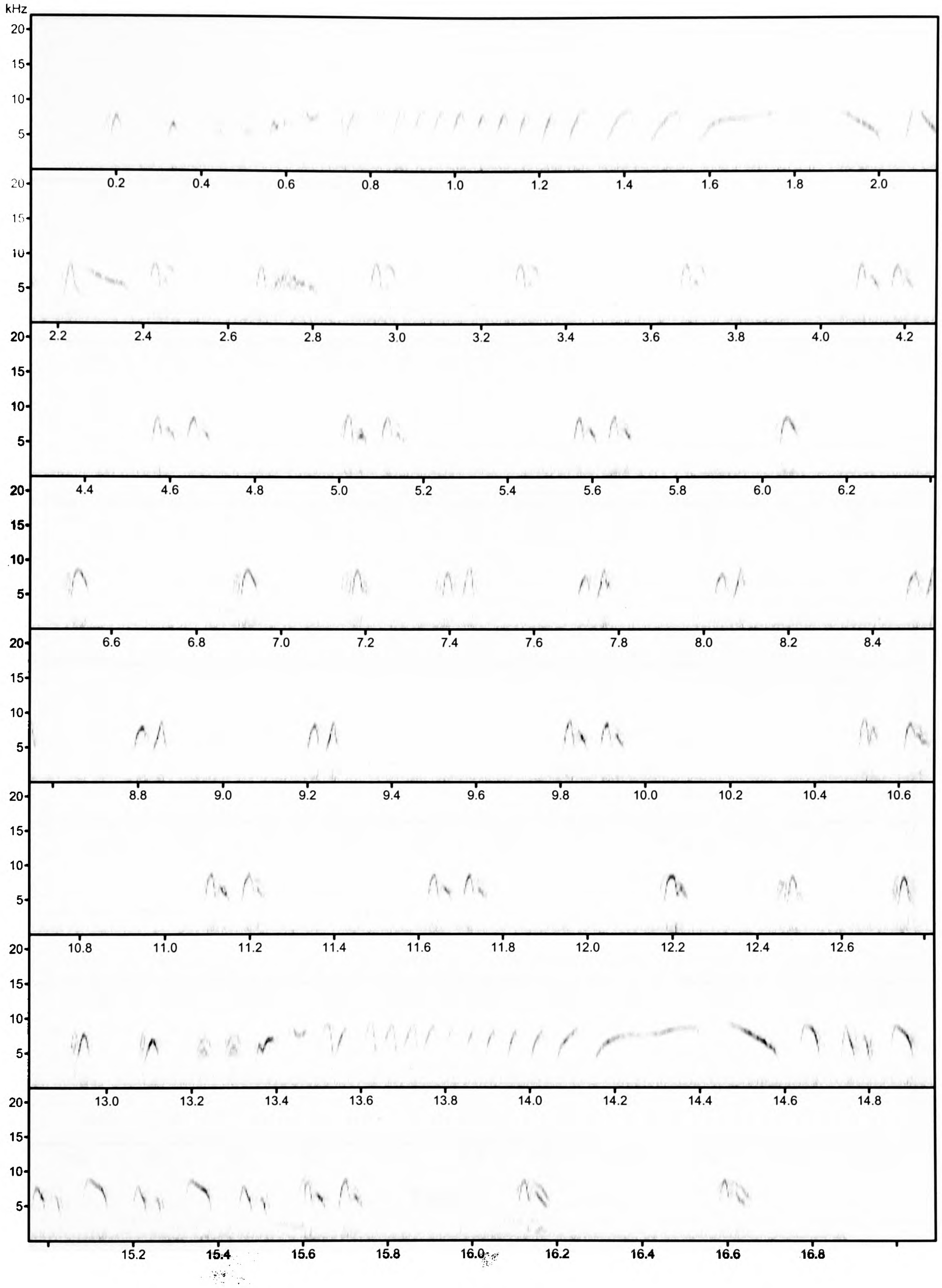
Frequency



Olive-backed Sunbird *Cinnyris jugularis bruensis* recorded in Buru, Indonesia, by M. Hounsome.

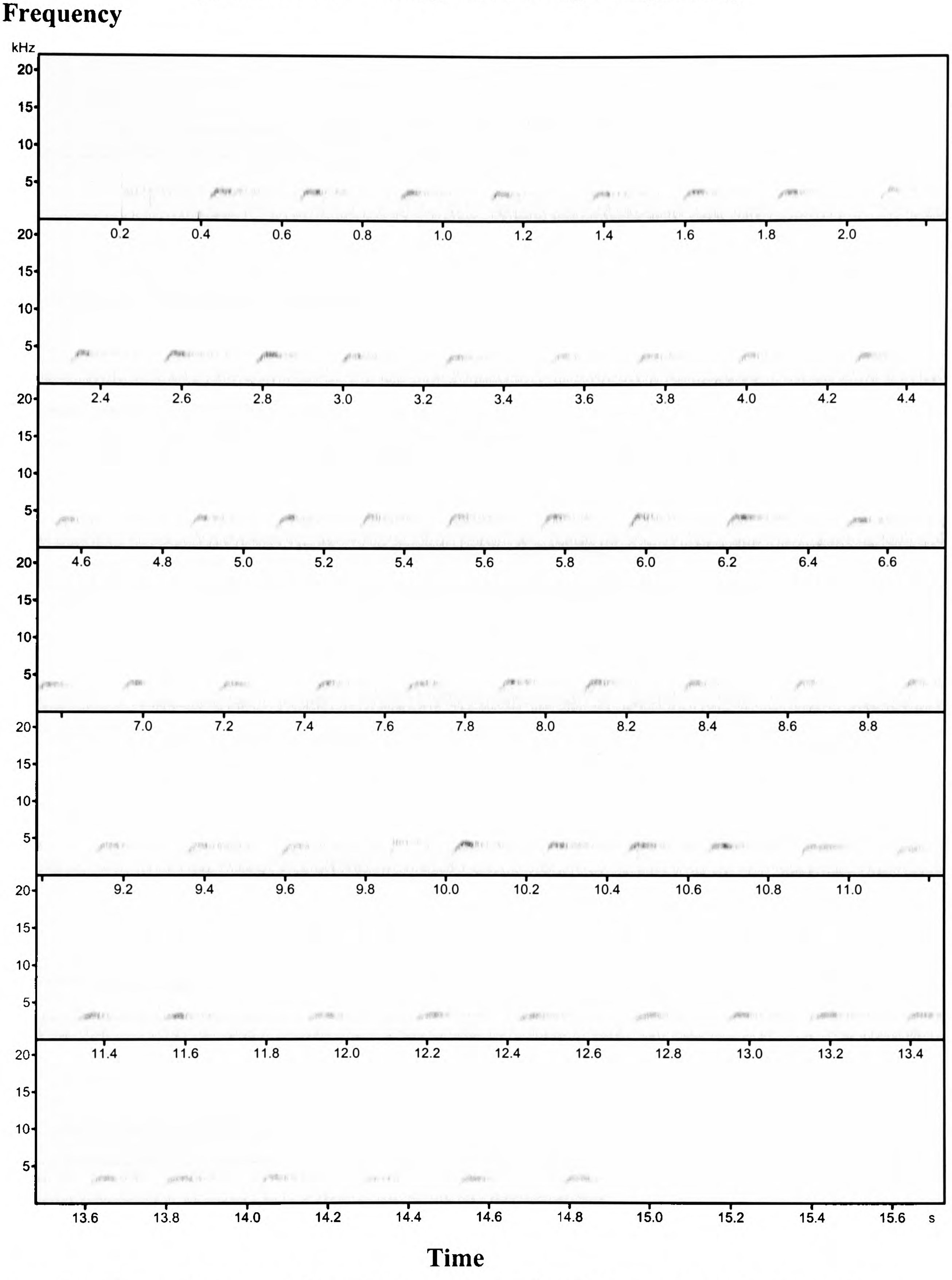
Appendix 3. 47 - Sonogram showing a complex song

Frequency



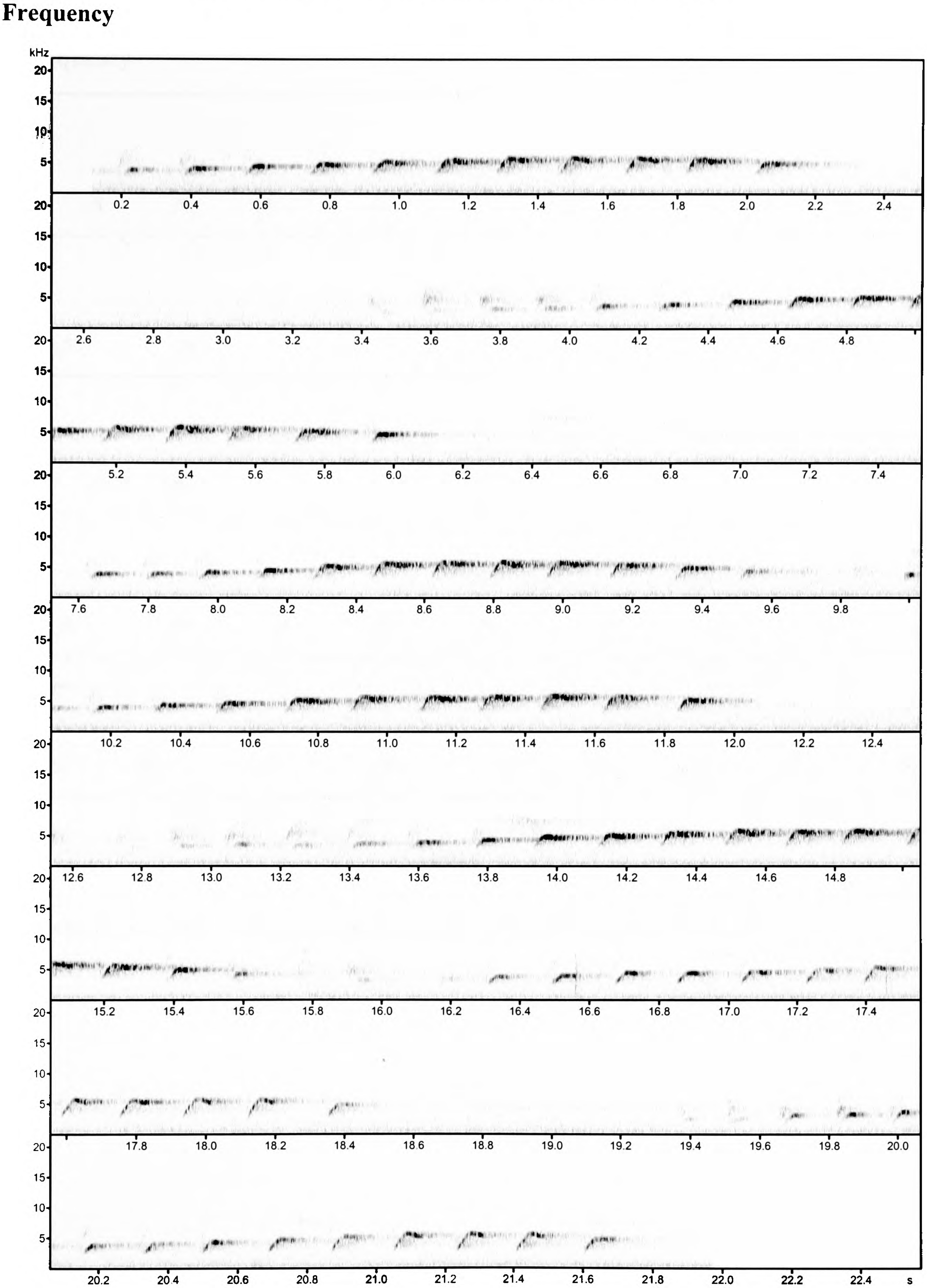
Olive-backed Sunbird *Cinnyris jugularis plateni* recorded in Baluran, Indonesia by R. Drijvers.

Appendix 3. 69 - Sonogram showing a simple song



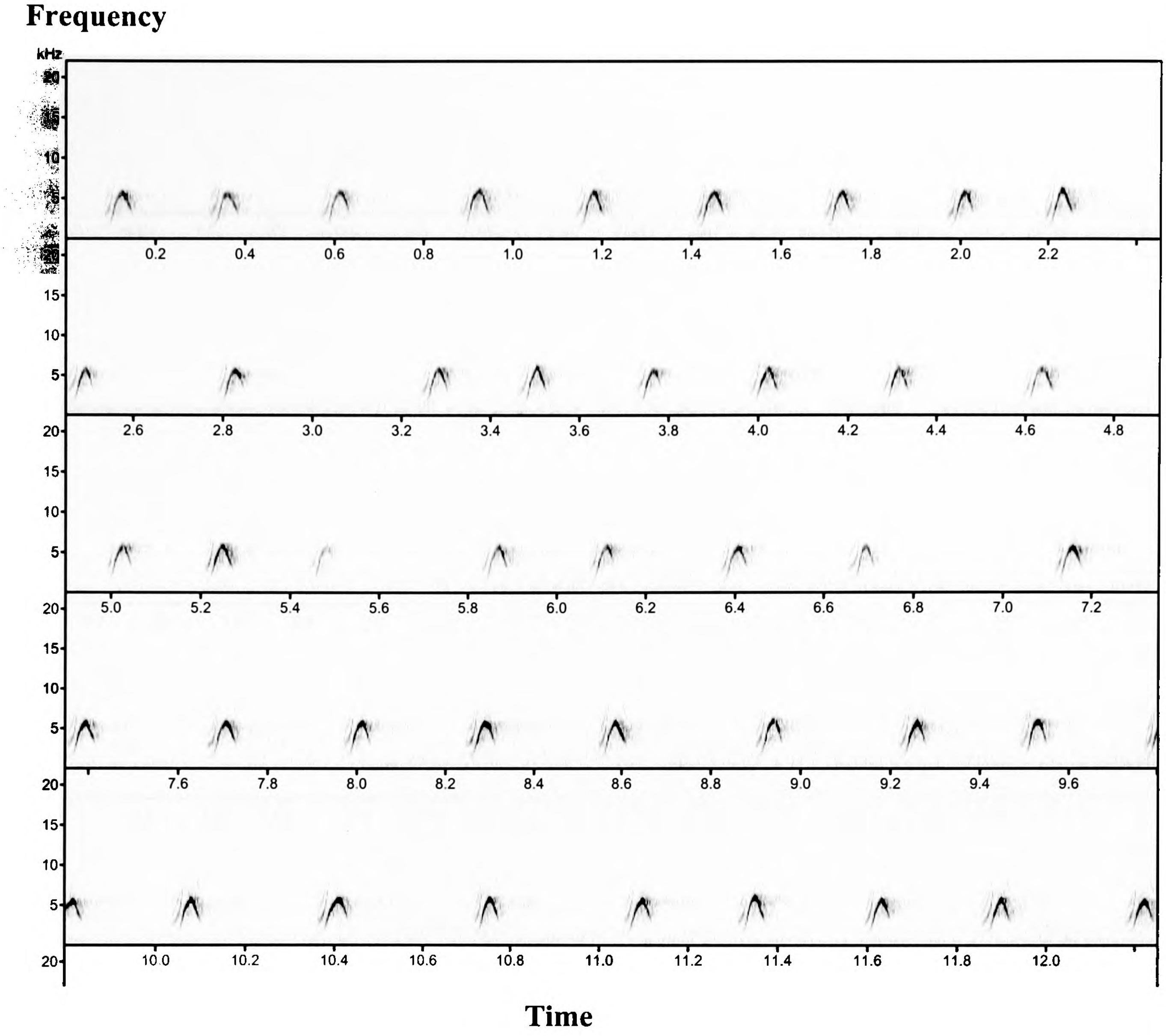
Apo Sunbird *Aethopyga boltoni boltoni* recorded on Mount Katanglad, Mindanao, Philippines by P. Morris.

Appendix 3. 70 - Sonogram showing a simple song



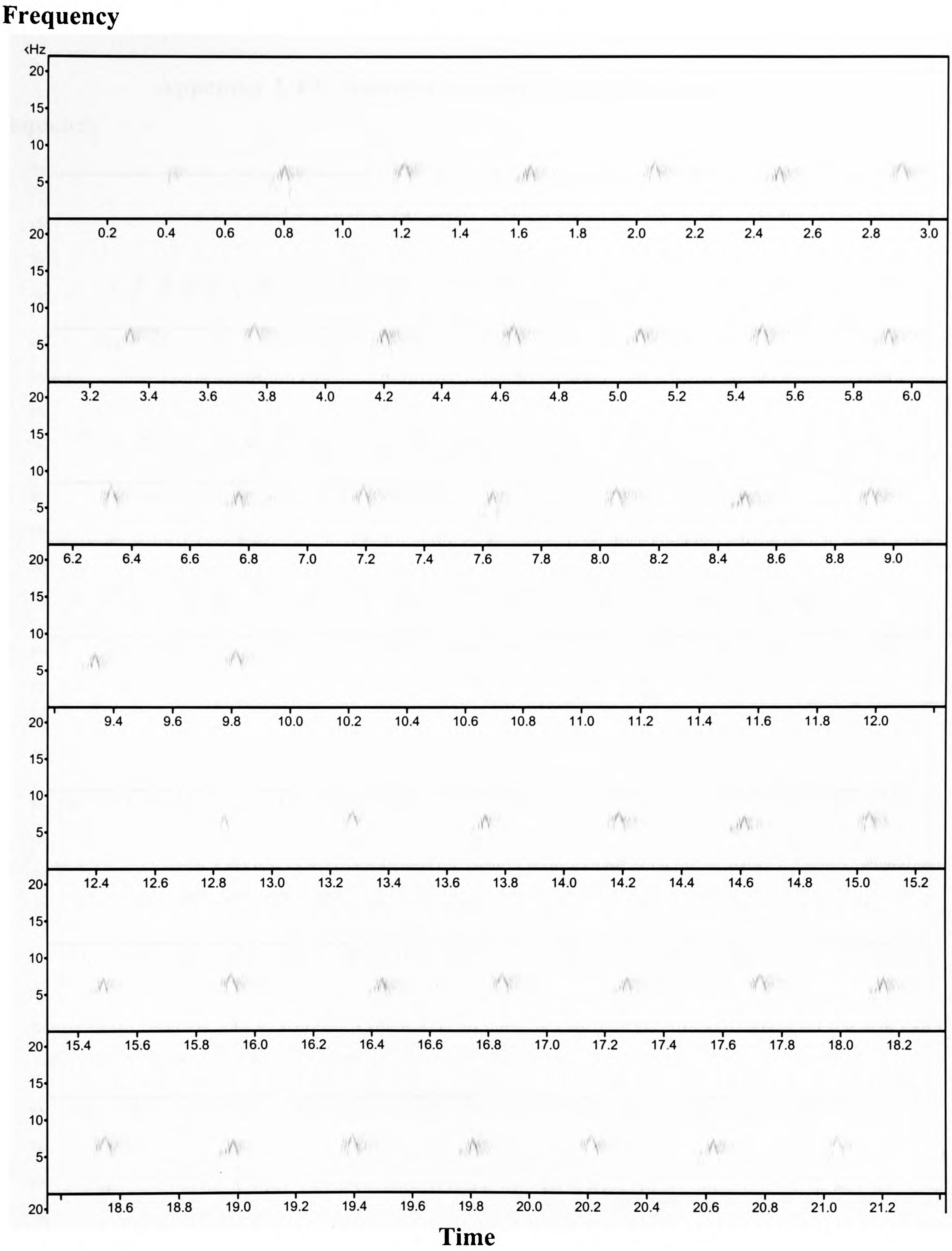
Apo Sunbird *Aethopyga boltoni tibolii* recorded in Sito Siete, Mindanao, Philippines by P. Morris.

Appendix 3. 80 -Sonogram showing call notes



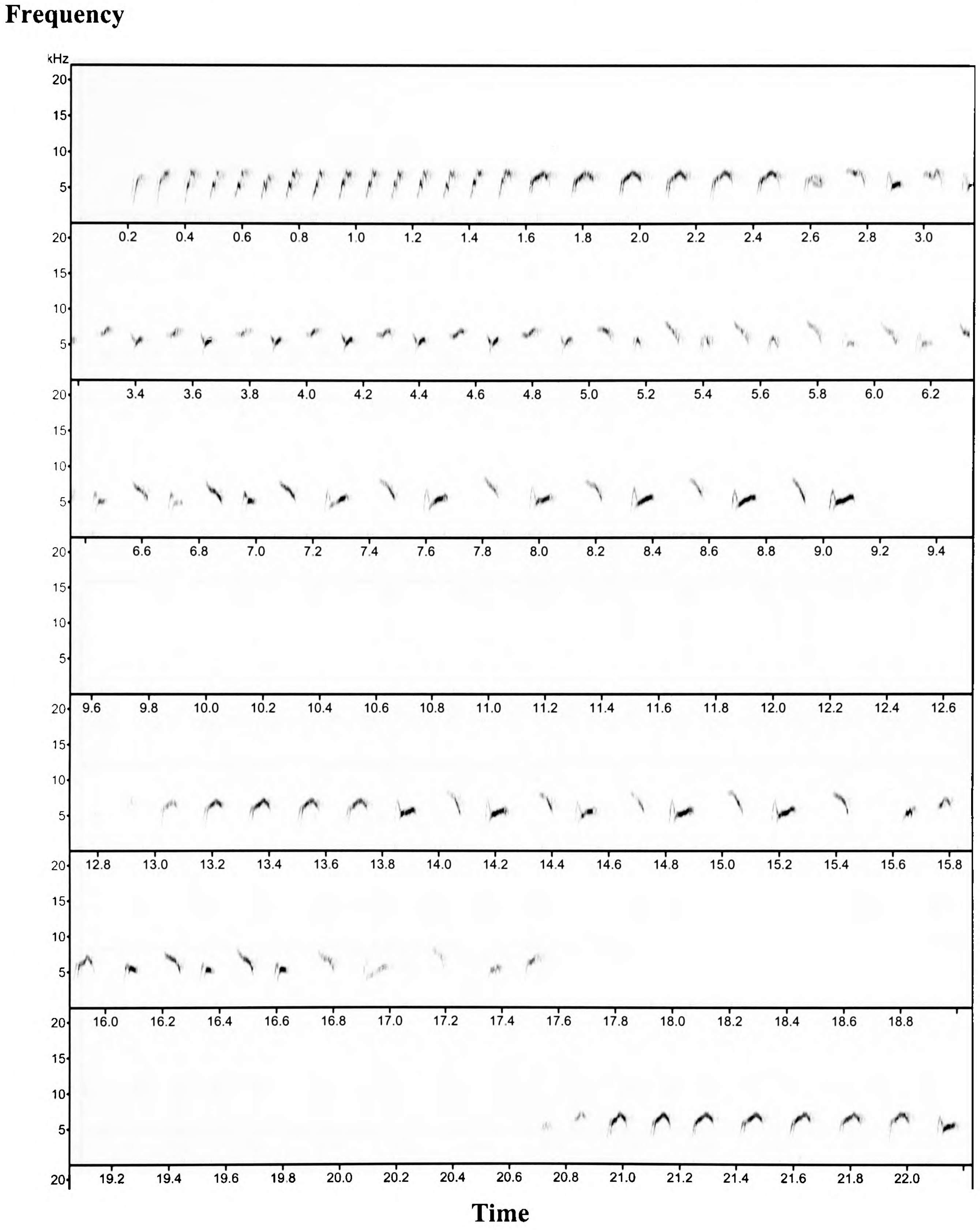
Elegant Sunbird *Aethopyga duyvenbodei* recorded Sangihe, Indonesia, by F. Lambert.

Appendix 3. 83 - Sonogram call notes



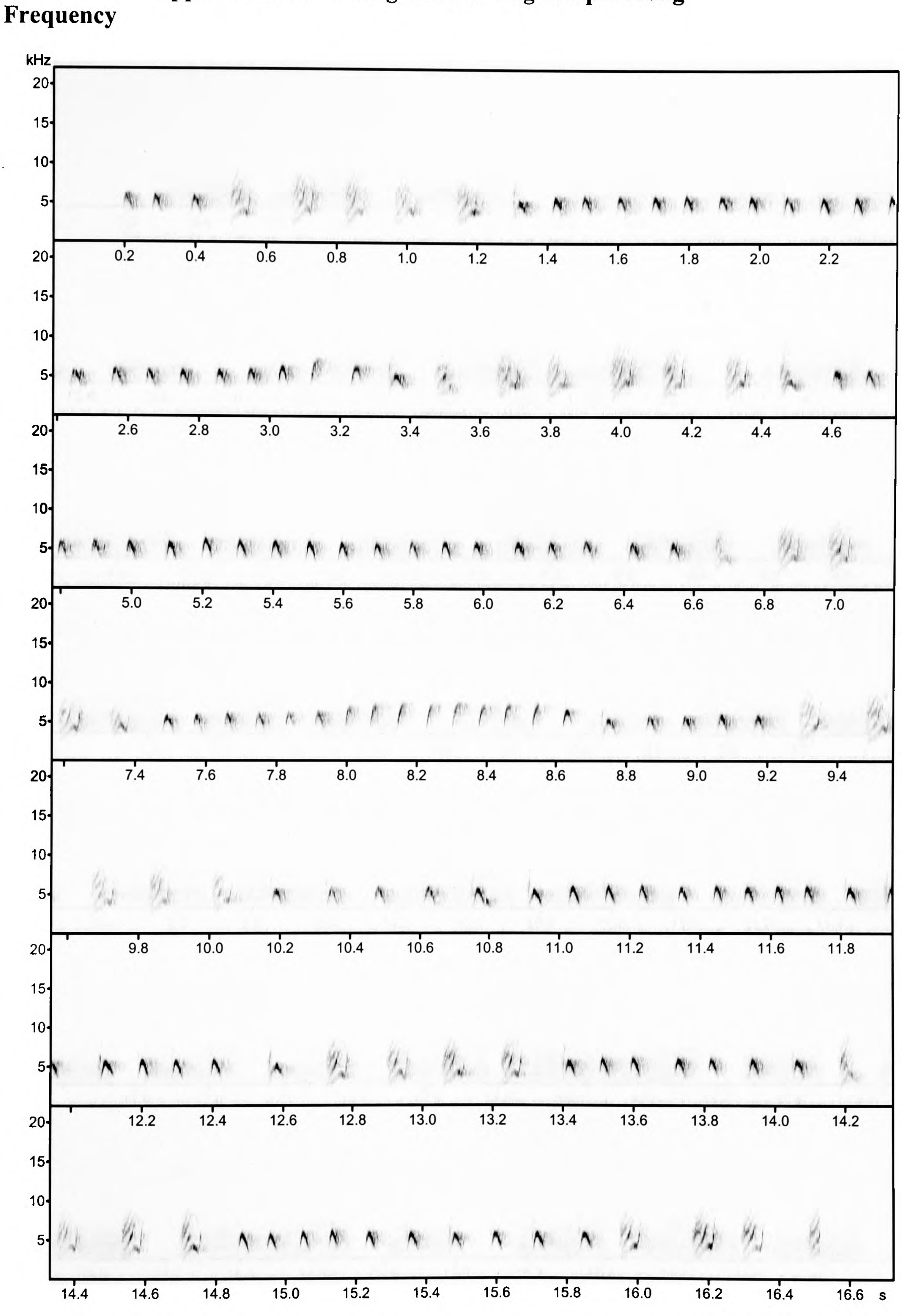
Lovely Sunbird *Aethopyga shelleyi shelleyi* recorded in Palawan, Philippines by A. Wassink.

Appendix 3. 88 - Sonogram showing complex song



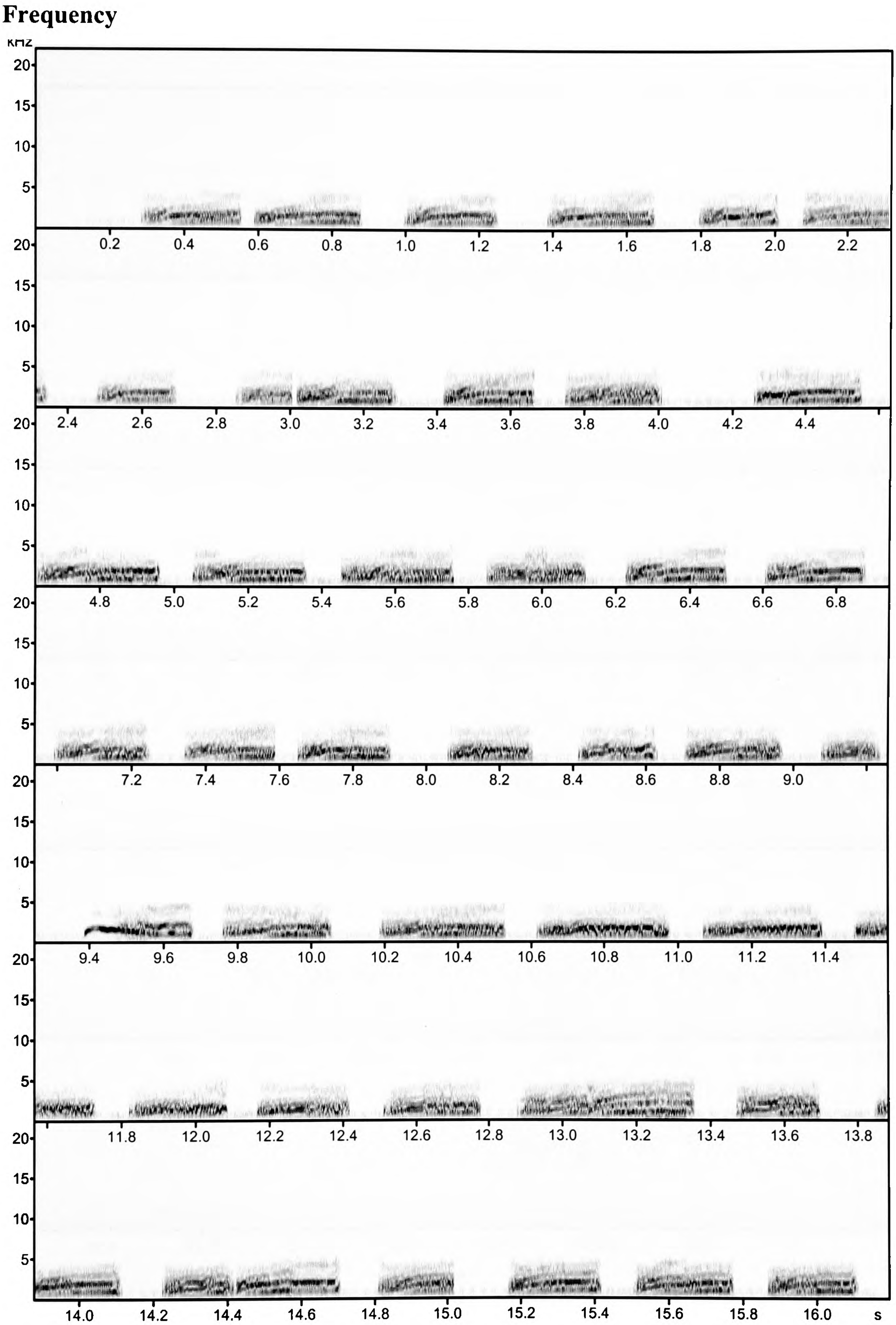
Gould’s Sunbird *Aethopyga gouldiae gouldiae* recorded in Central Bhutan by P. Holt.

Appendix 3. 93 - Sonogram showing complex song



Green-tailed Sunbird *Aethopyga nipalensis koelzi* recorded in Chhuzomsa, Bhutan, by P. Holt.

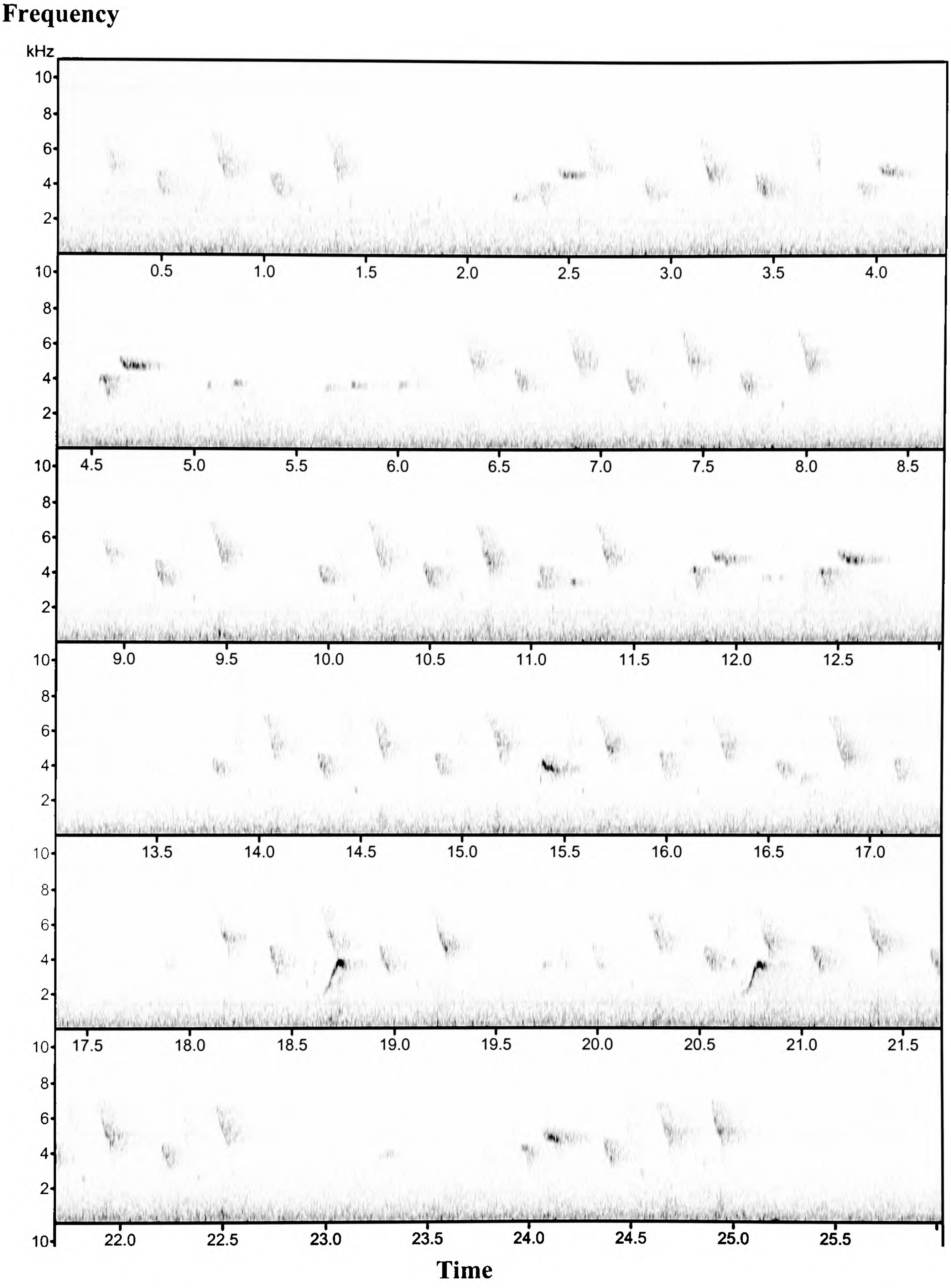
Appendix 3. 125 - Sonogram showing a simple son with harmonics



Time

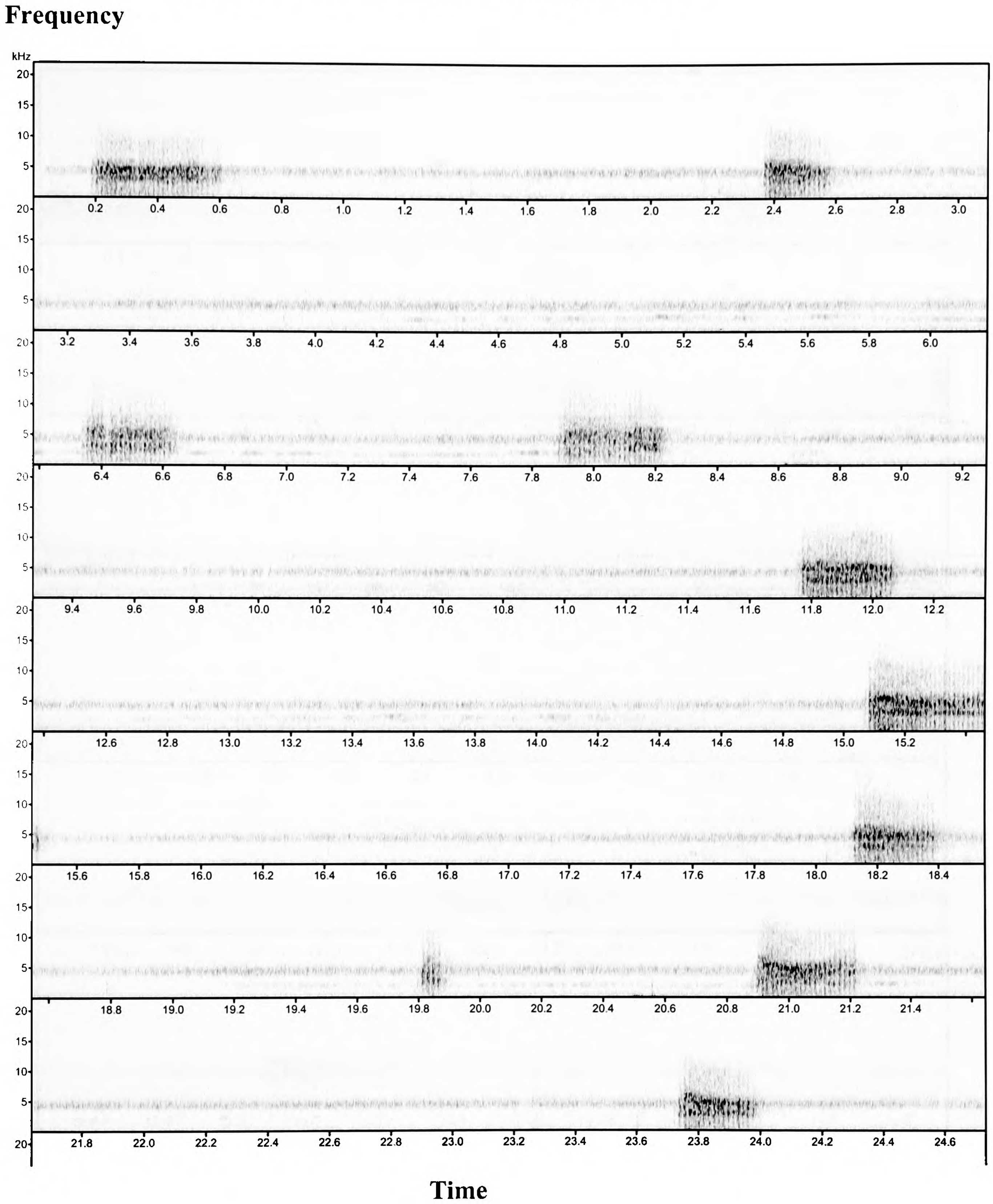
Long-billed Spiderhunter *Arachnothera robusta robusta* recorded in Sumatra by R. Kersley.

Appendix 3. 128 - Sonogram showing a complex song



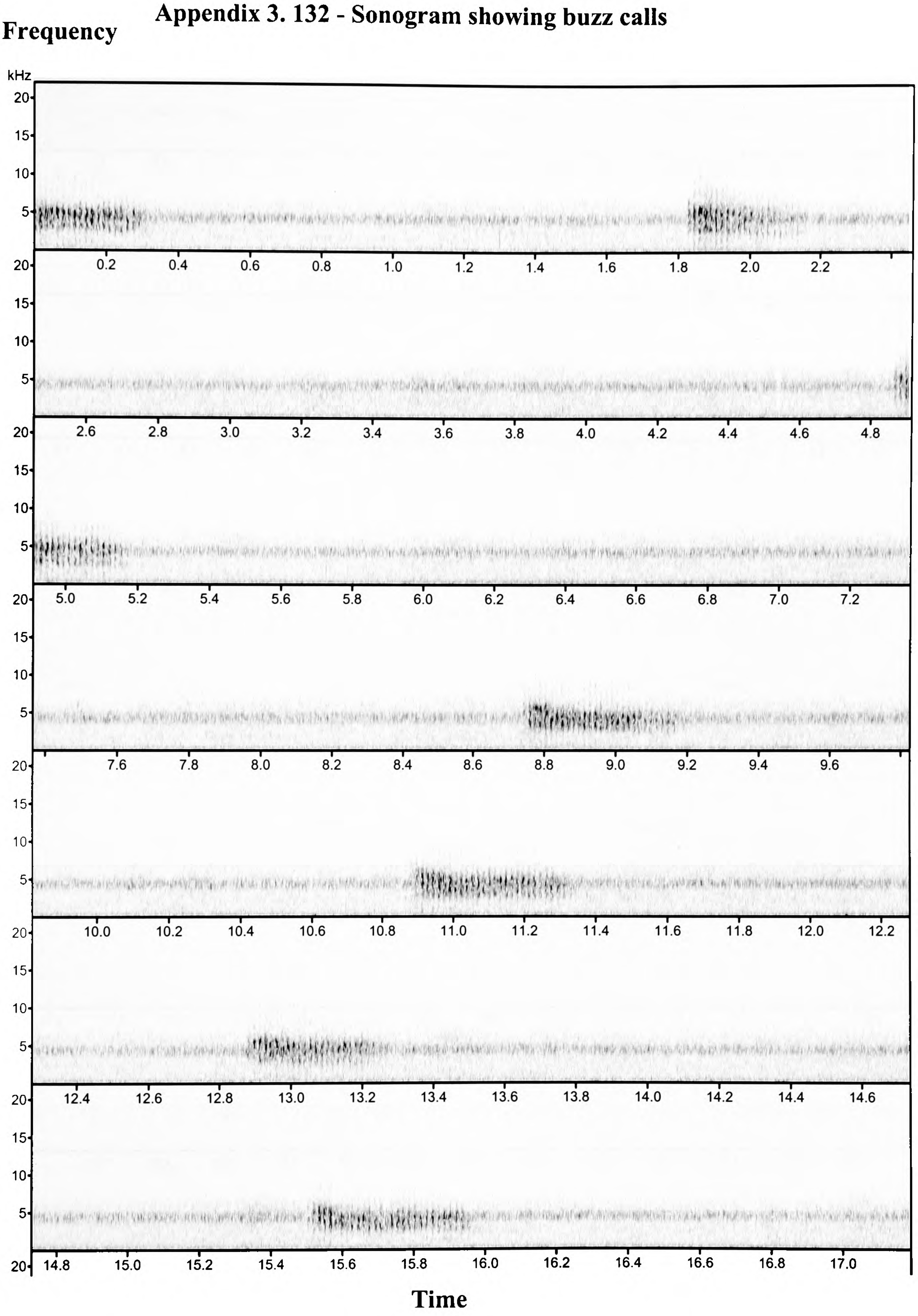
Spectacled Spiderhunter *Arachnothera flavigaster* recorded in Malaysia by R. Kersley.

Appendix 3. 131 - Sonogram showing buzz calls



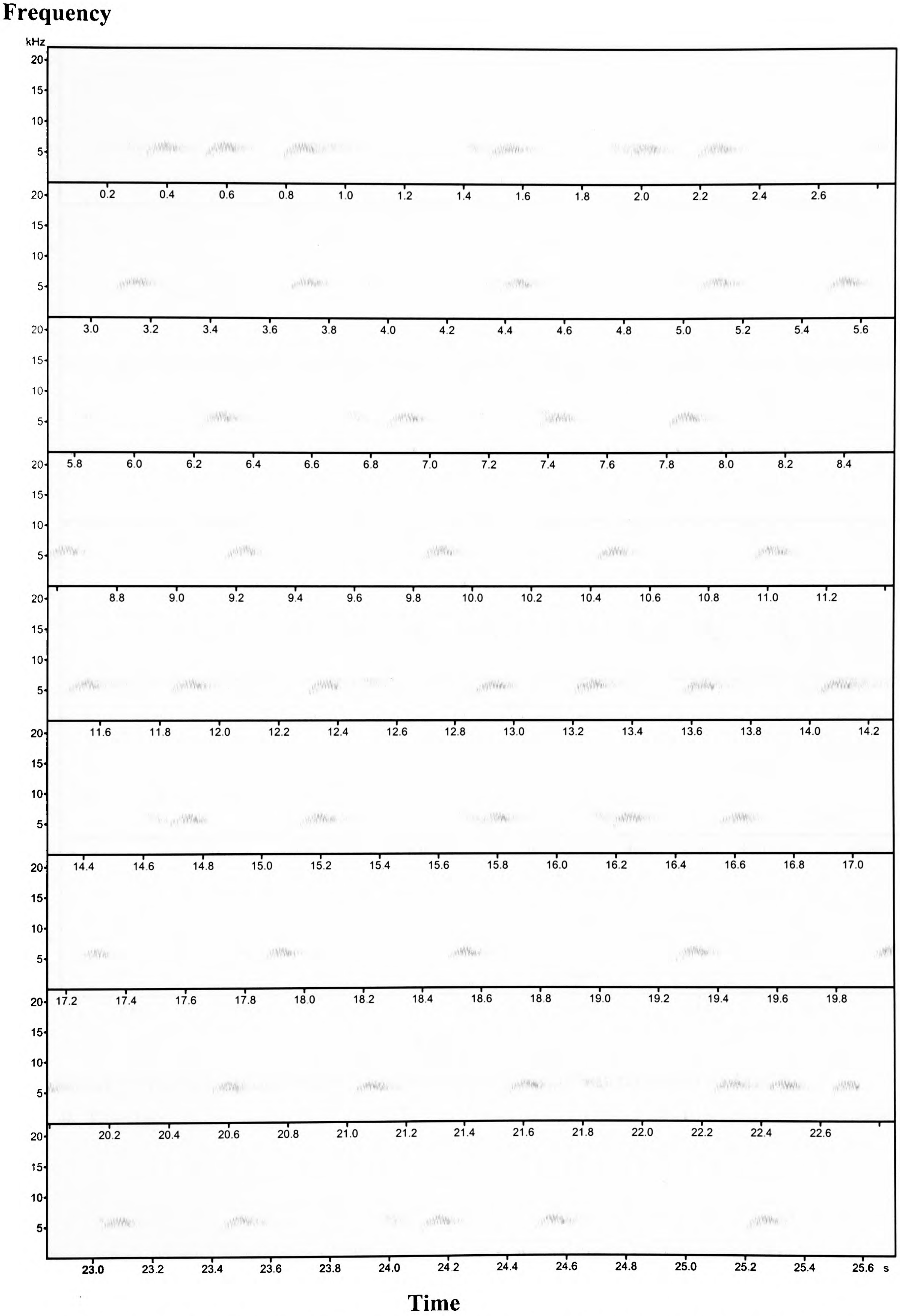
Naked-faced Spiderhunter *Arachnothera clarae malindangensis* recorded in Mindanao by A. Greensmith.

Appendix 3. 132 - Sonogram showing buzz calls



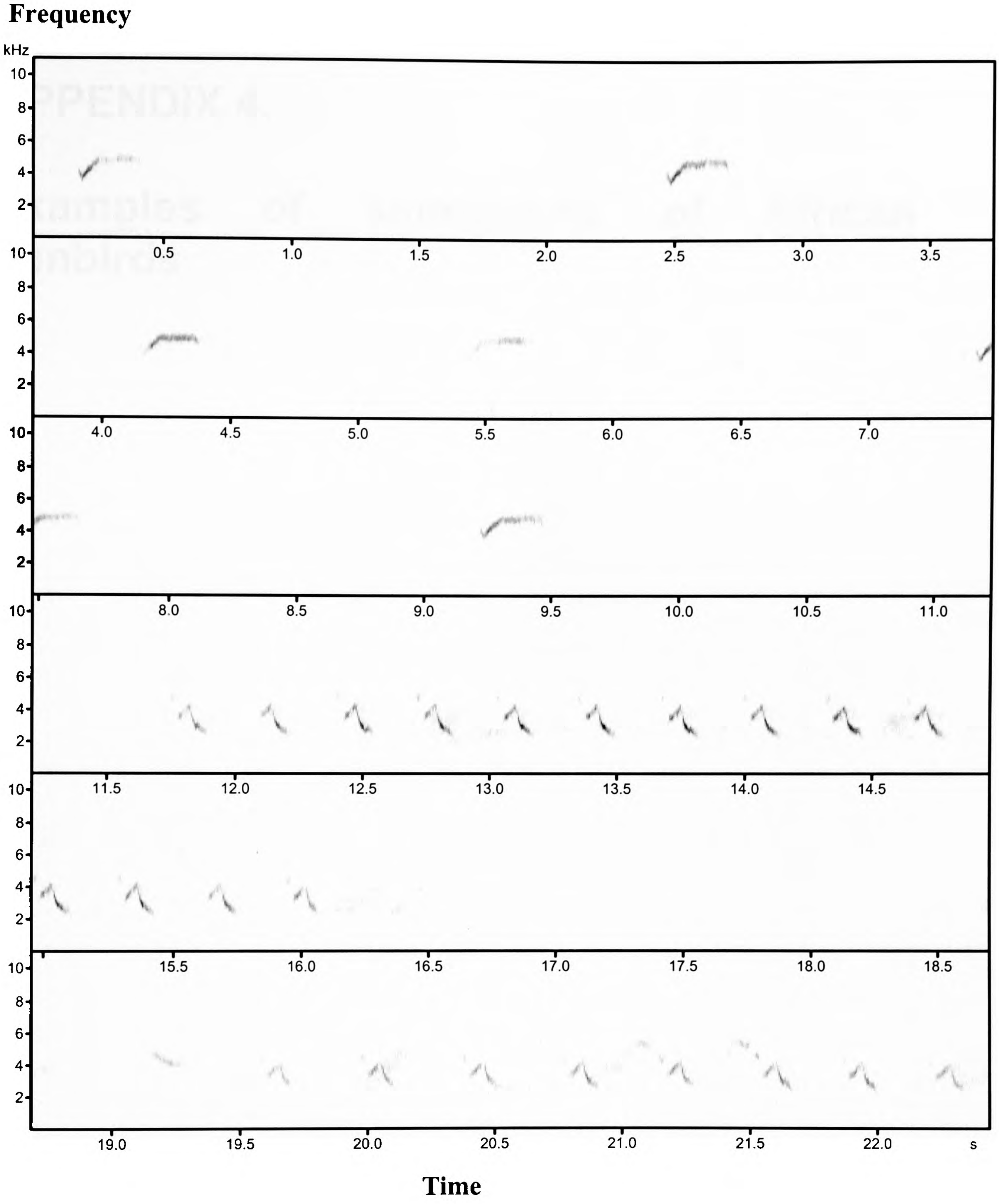
Naked-faced Spiderhunter *Arachnothera clarae luzonensis* record in Luzon by A. Greensmith.

Appendix 3. 139 - Sonogram showing a simple song



Grey-breasted Spiderhunter *Arachnothera modesta modesta* recorded in Thailand by G. Bartels.

Appendix 3. 133 - Sonogram showing a complex song

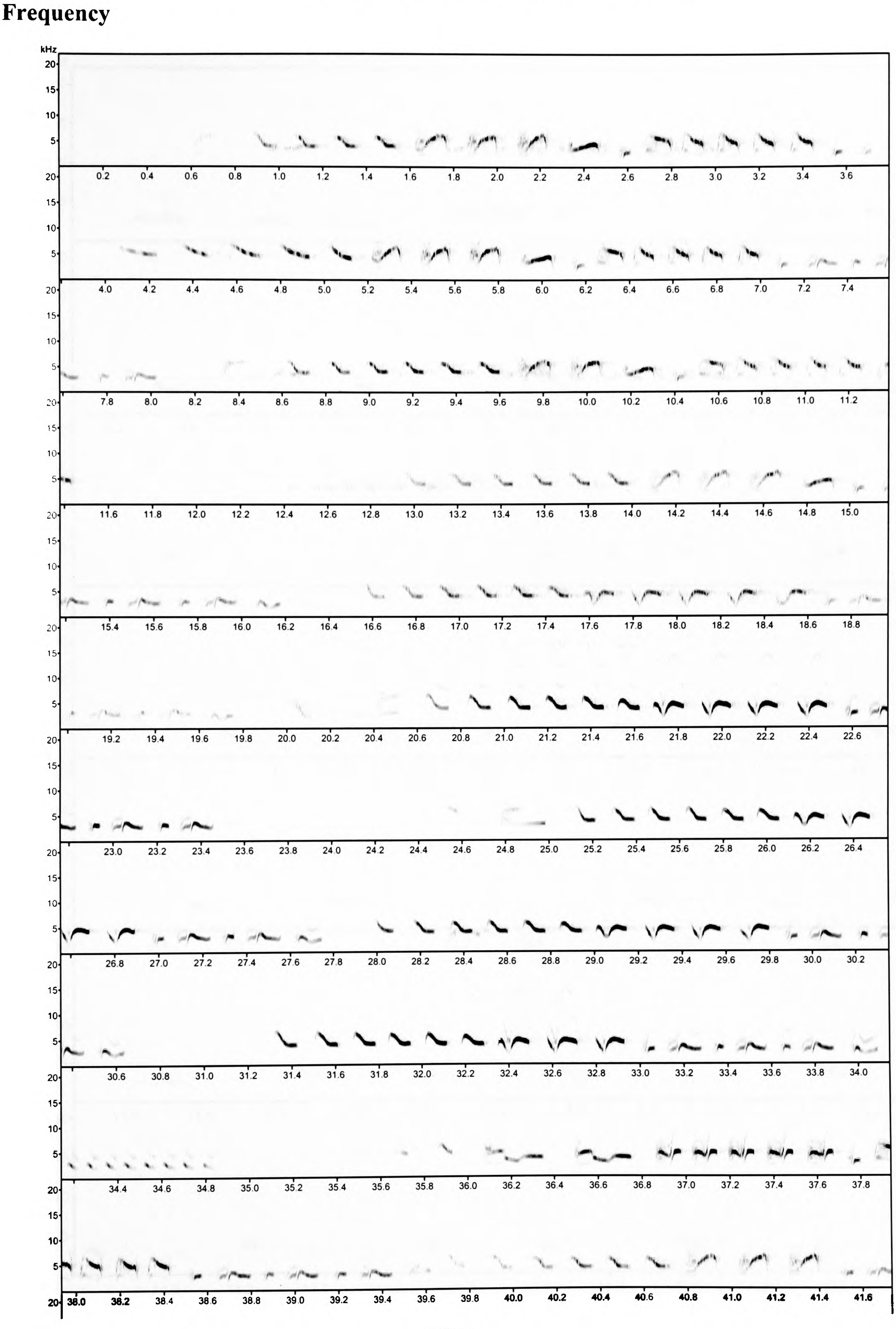


Streaky-breasted Spiderhunter *Arachnothera affinis affinis* recorded in Java by R. Kersley.

APPENDIX 4.

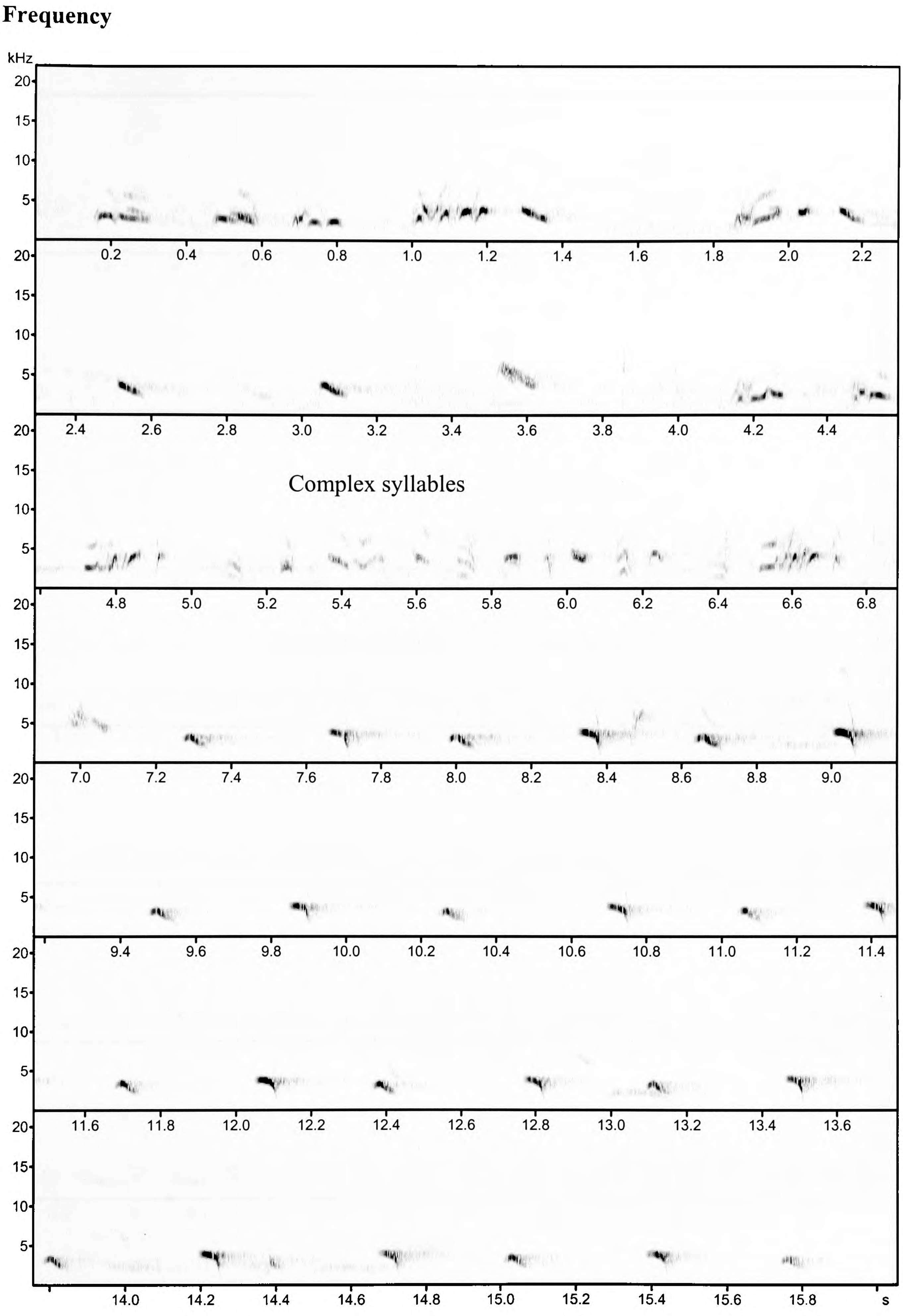
Examples of sonograms of African sunbirds

Appendix 4.19-Sonogram showing a complex song



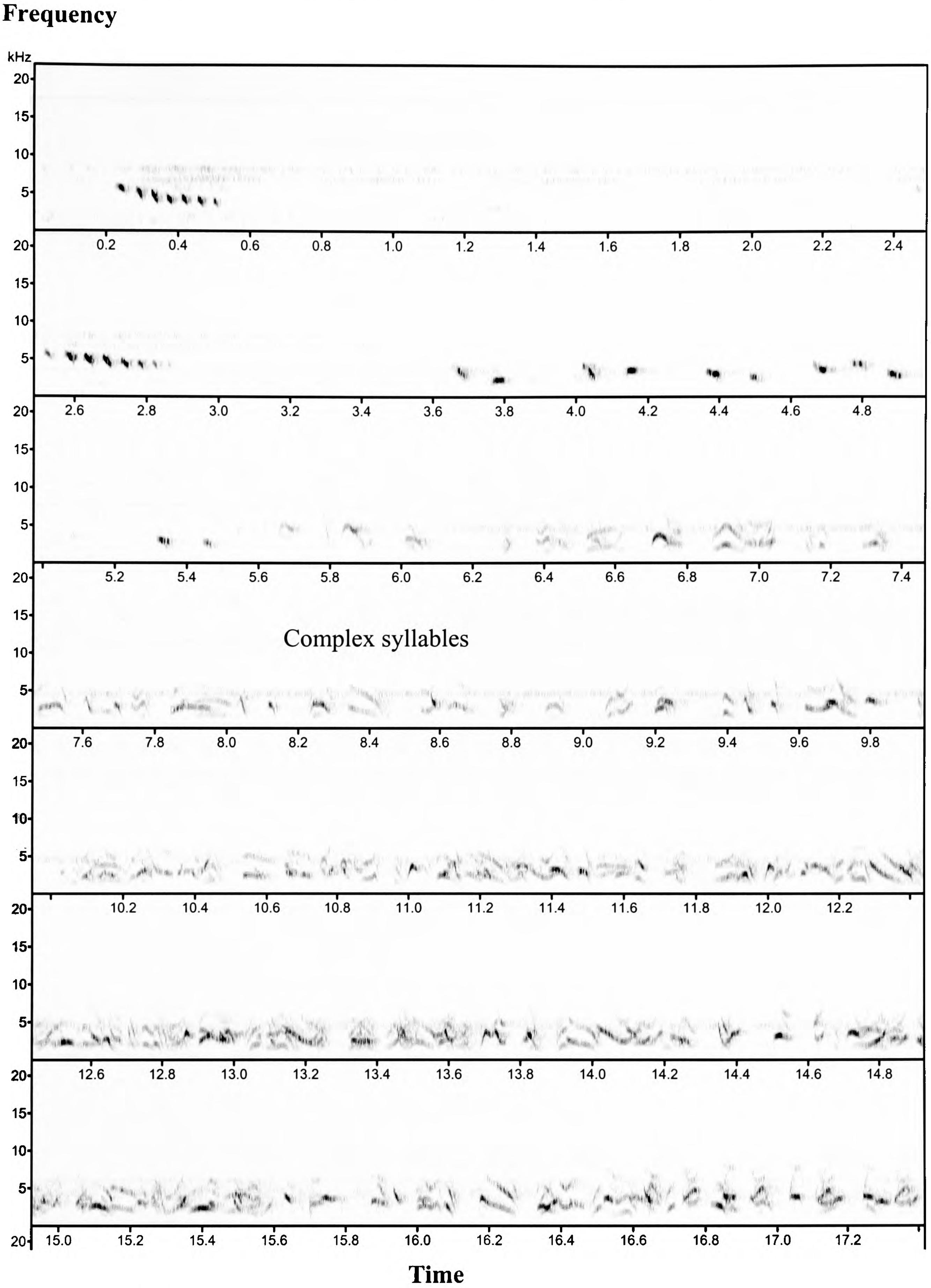
Plain-backed Sunbird *Anthreptes reichenowi reichenowi* recorded in Ndumu Game Reserve, South Africa, by J. Stannard.

Appendix 4. 28 -Sonogram showing a complex song



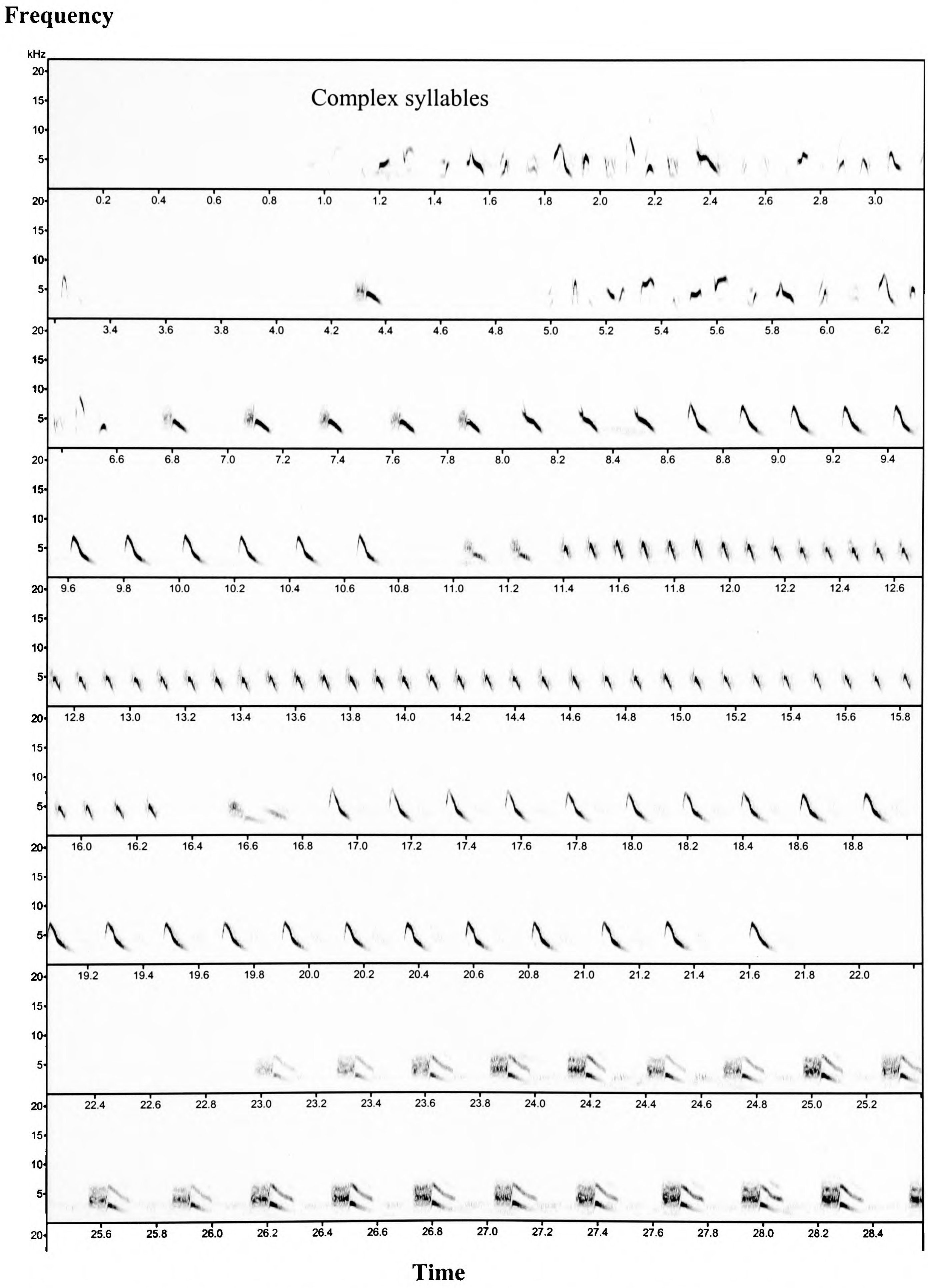
Amethyst Sunbird *Chalcomitra amethystina amethystina* recorded in Eastern Cape, South Africa, by C. J. Skead.

Appendix 4. 35 - Sonogram showing a complex song



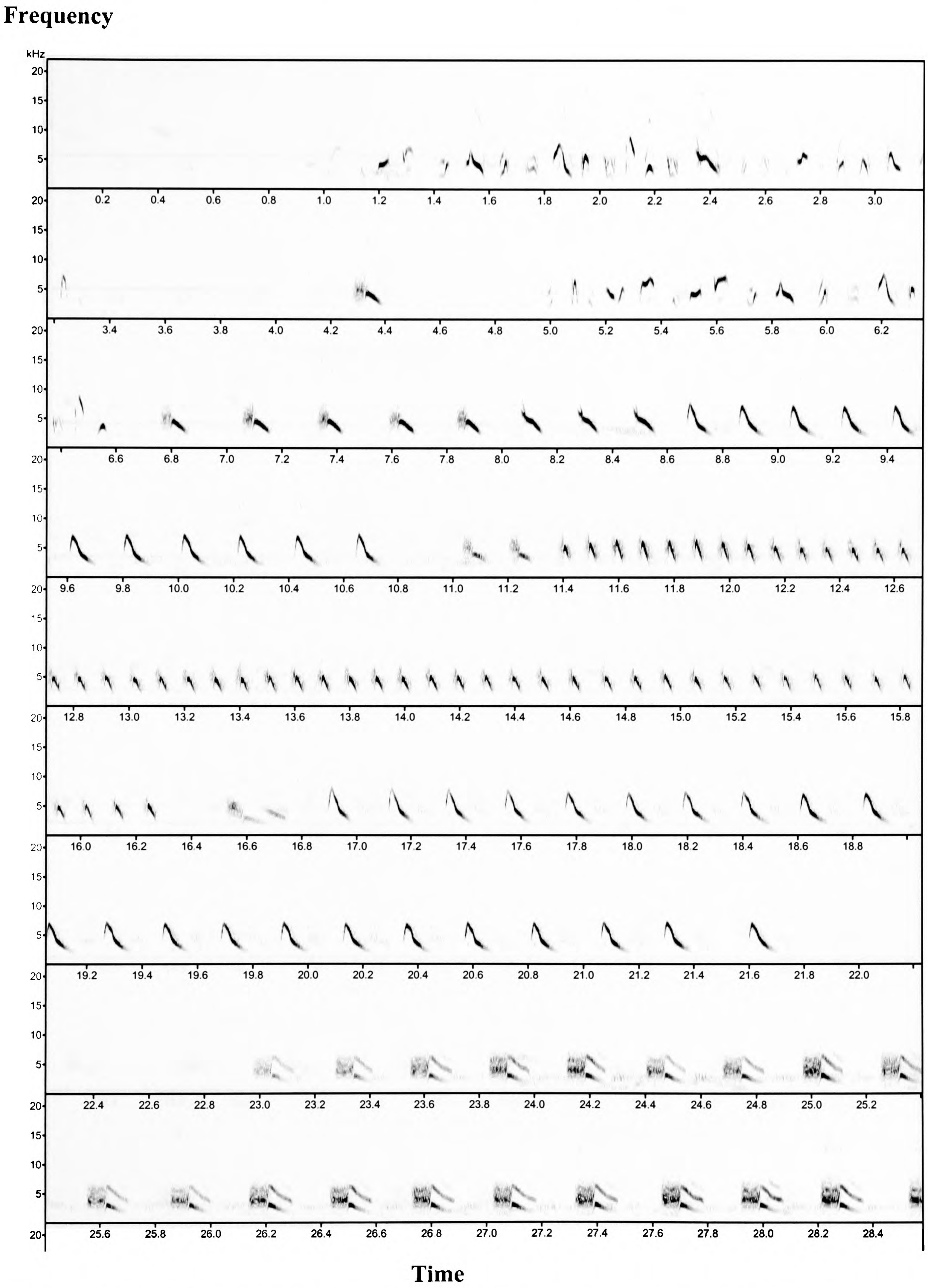
Carmelite Sunbird *Chalcomitra fuliginosa aurea* recorded in North Guitry, South Ivory Coast, by C. Chappuis.

Appendix 4. 37 - Sonogram showing a complex song



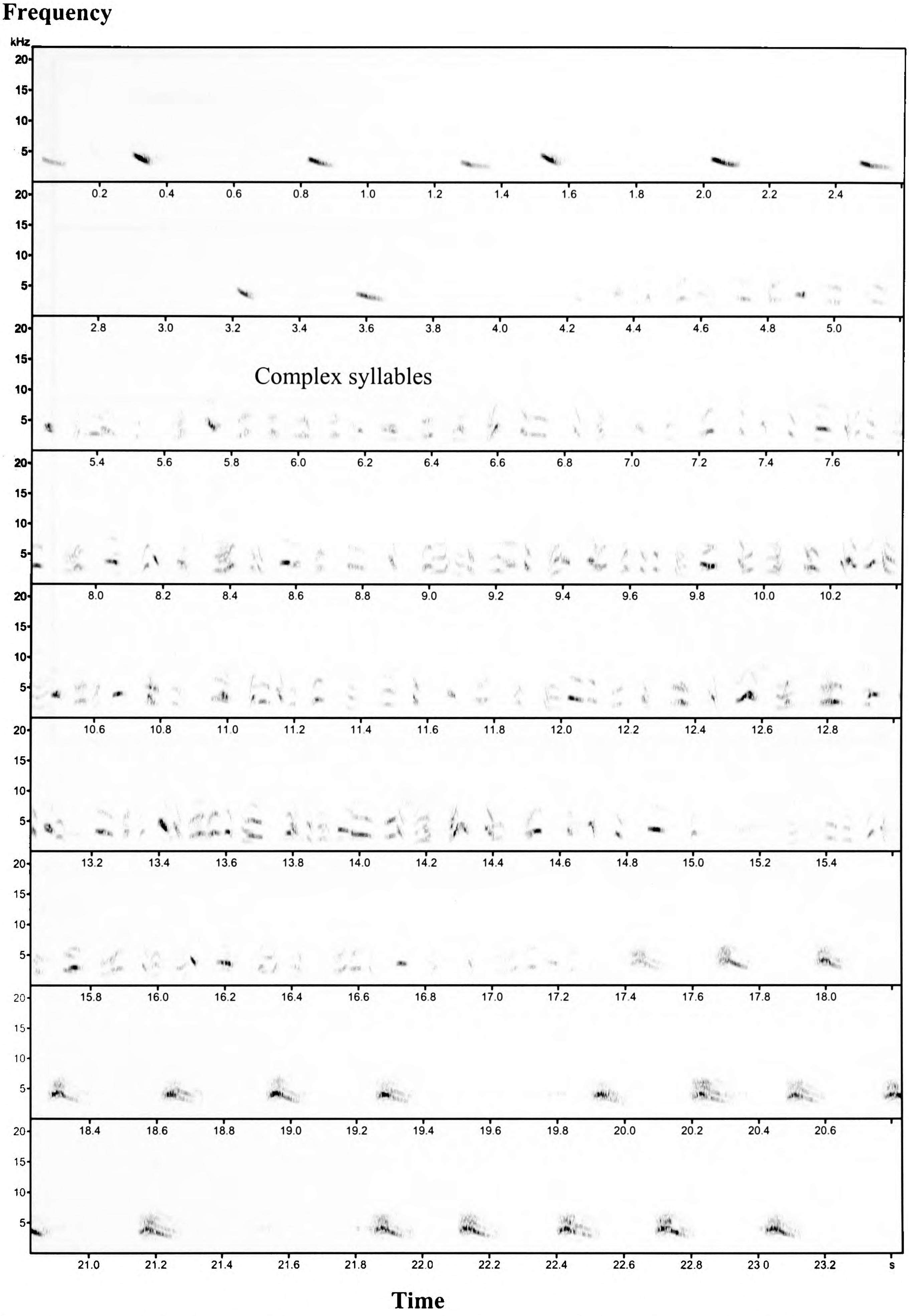
Green-throated Sunbird *Chalcomitra rubescens crossensis* recorded on the top of Mt Manengouba, South West Cameroon by C. Chappuis.

Appendix 4. 26 - Sonogram showing a complex series of calls



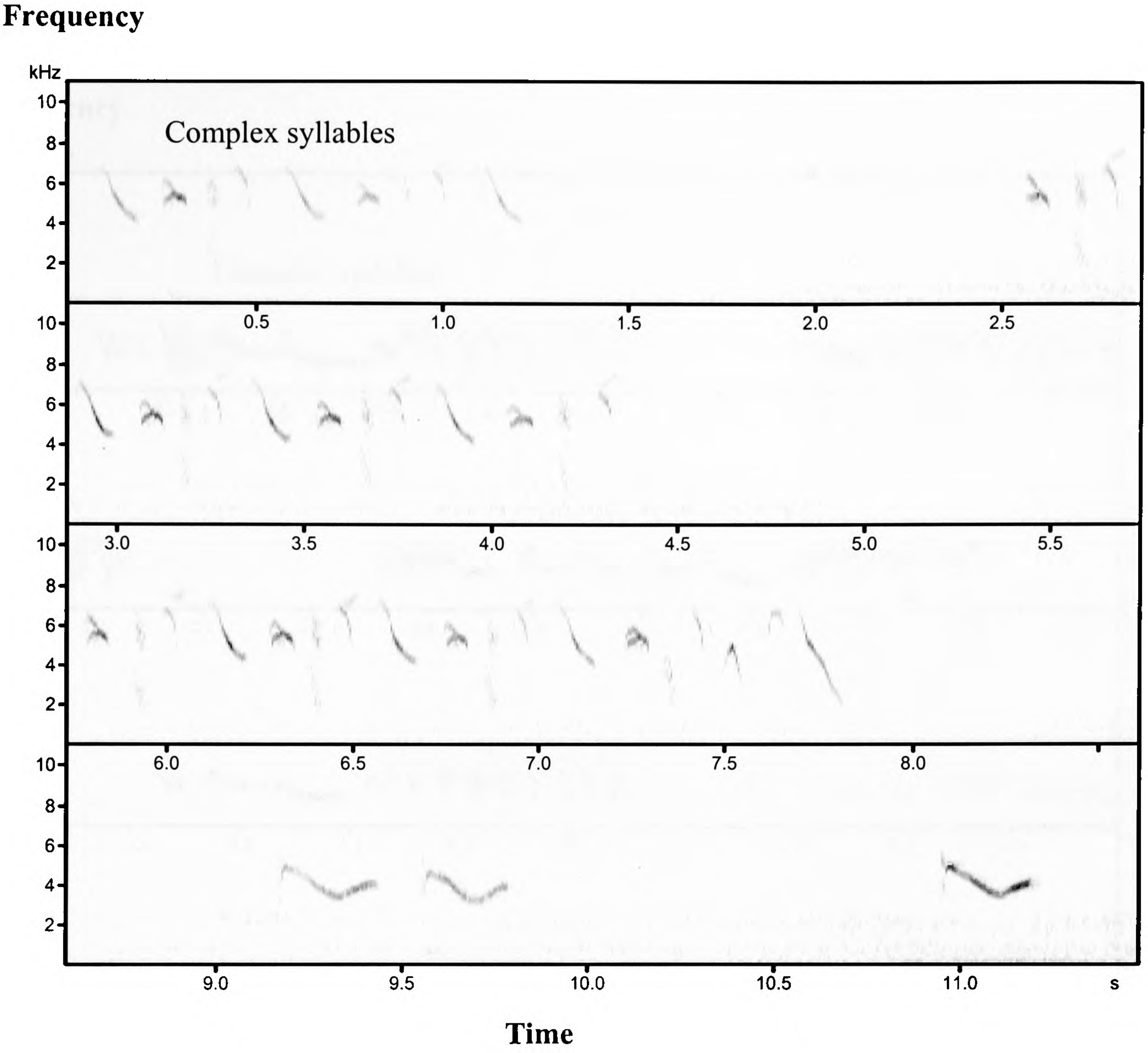
Green-throated Sunbird *Chalcomitra rubescens stangerii* recorded in Bioko, Equatorial Guinea, by C. Chappuis.

Appendix 4. 48 - Sonogram showing a complex song



Scarlet-chested Sunbird *Chalcomitra senegalensis cruentata* recorded in South West Chad by C. Chappuis.

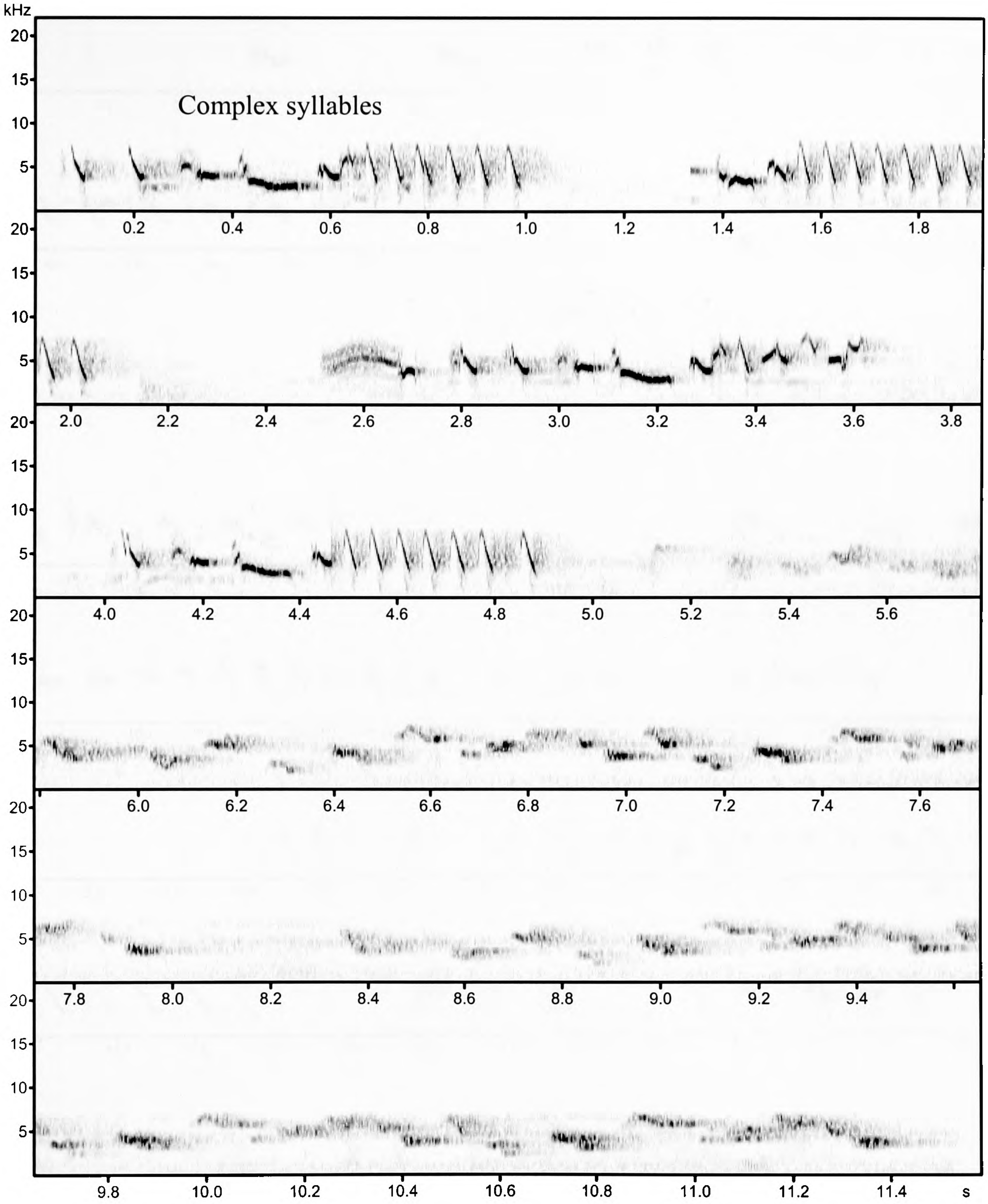
Appendix 4. 50 - Sonogram showing a Complex song



Socotra Sunbird *Chalcomitra balfouri* recorded at H. Playeau, Yemen by D. Pearson.

Appendix 4. 53 - Sonogram showing a complex song

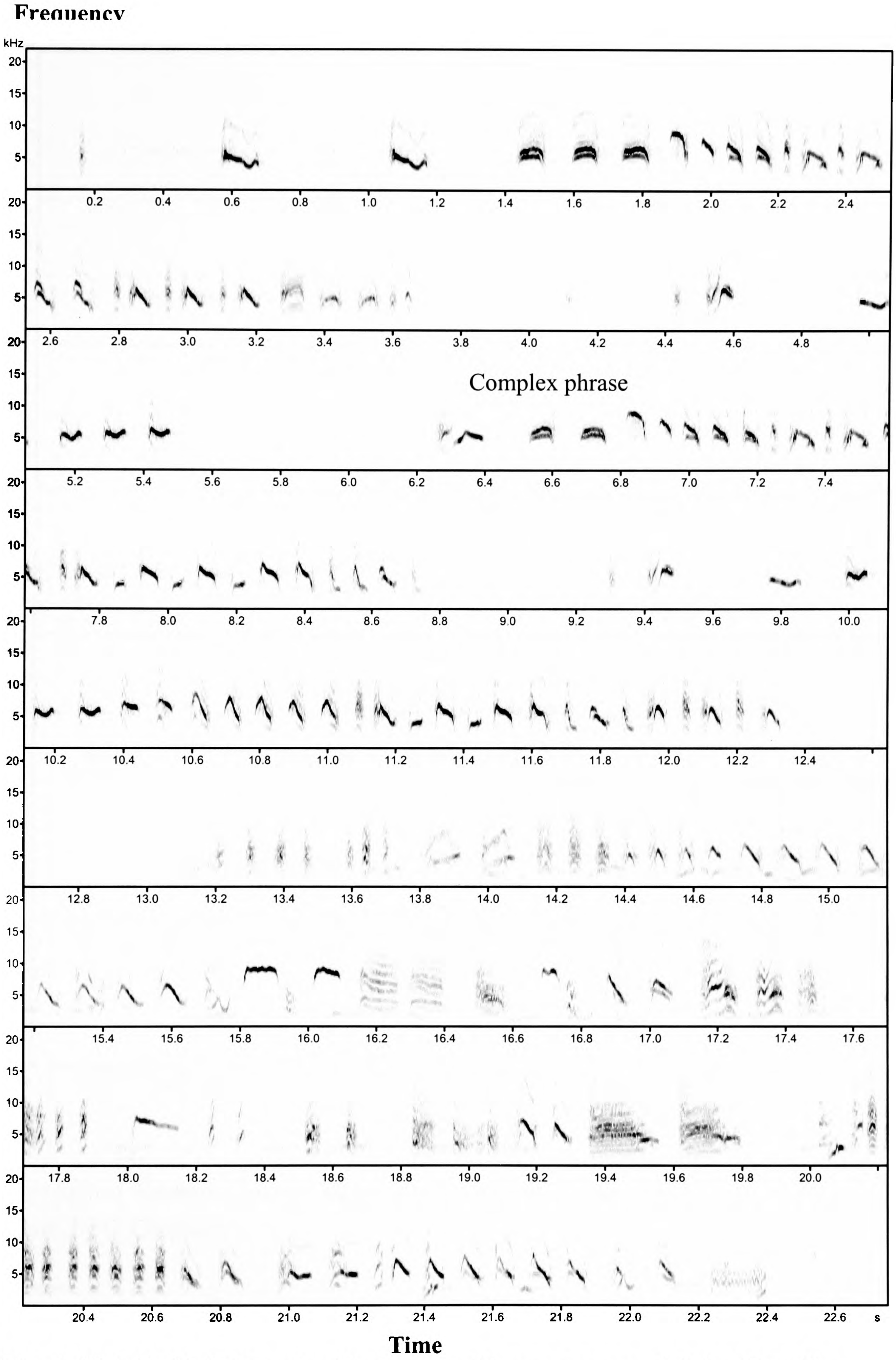
Frequency



Time

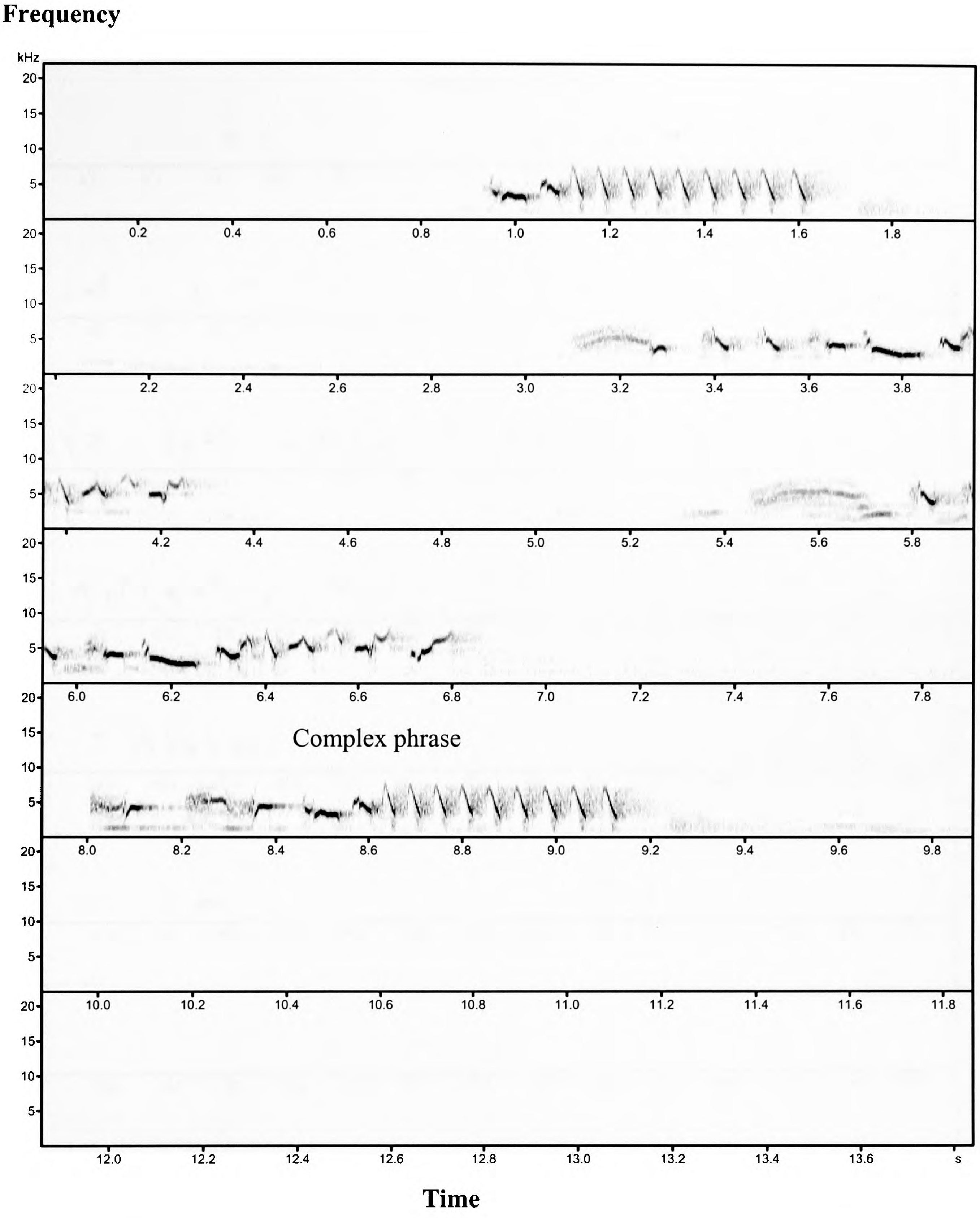
Greater Double-Collared Sunbird *Cinnyris afer saliens* recorded in Zululand, South Africa, by L. Macaulay.

Appendix 4. 60 - Sonogram showing a complex song



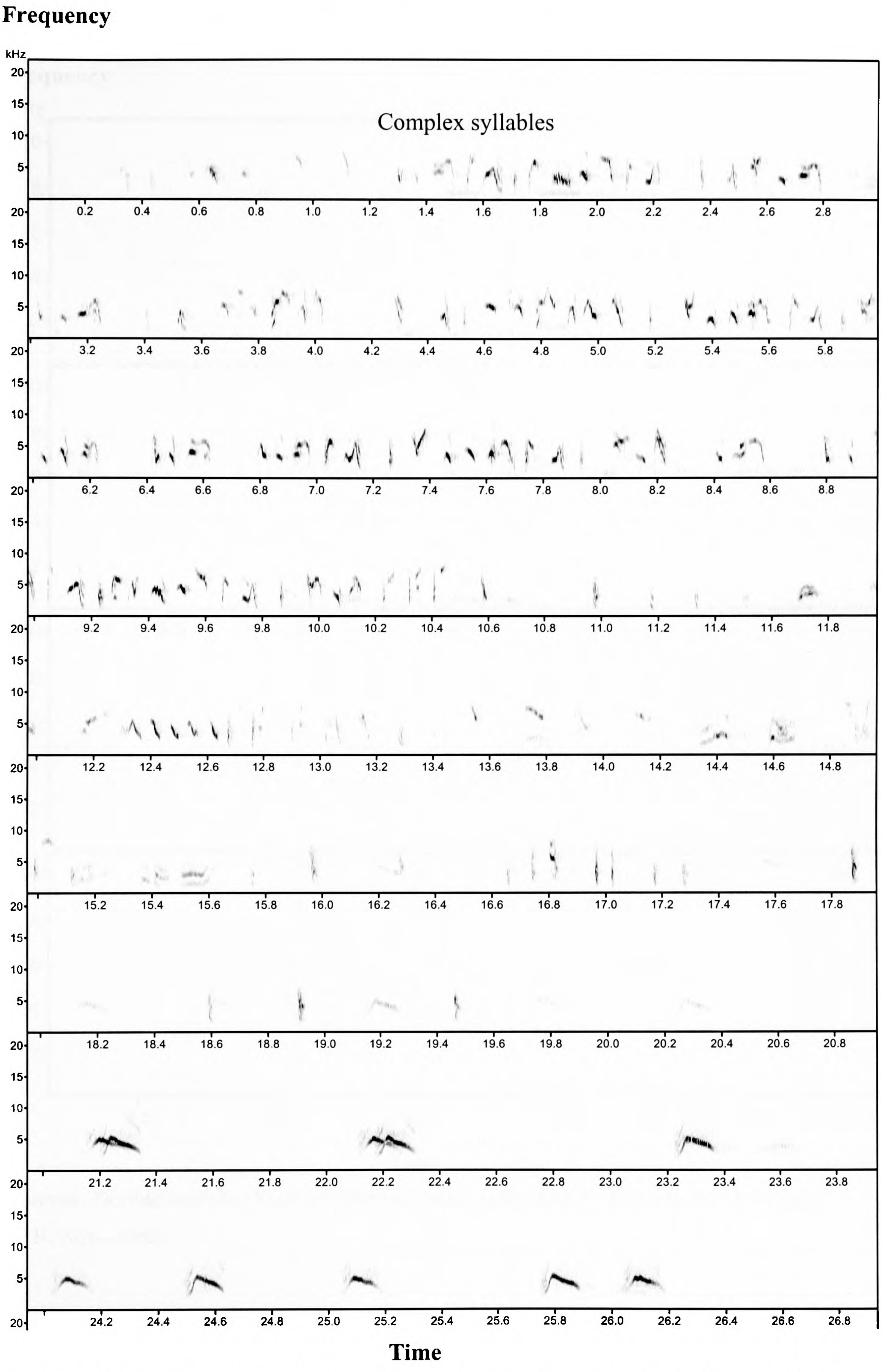
Olive-bellied Sunbird *Cinnyris chloropygius chloropygius* recorded in Libreville, Gabon, by C. Chappuis.

Appendix 4. 59 - Sonogram showing a complex song



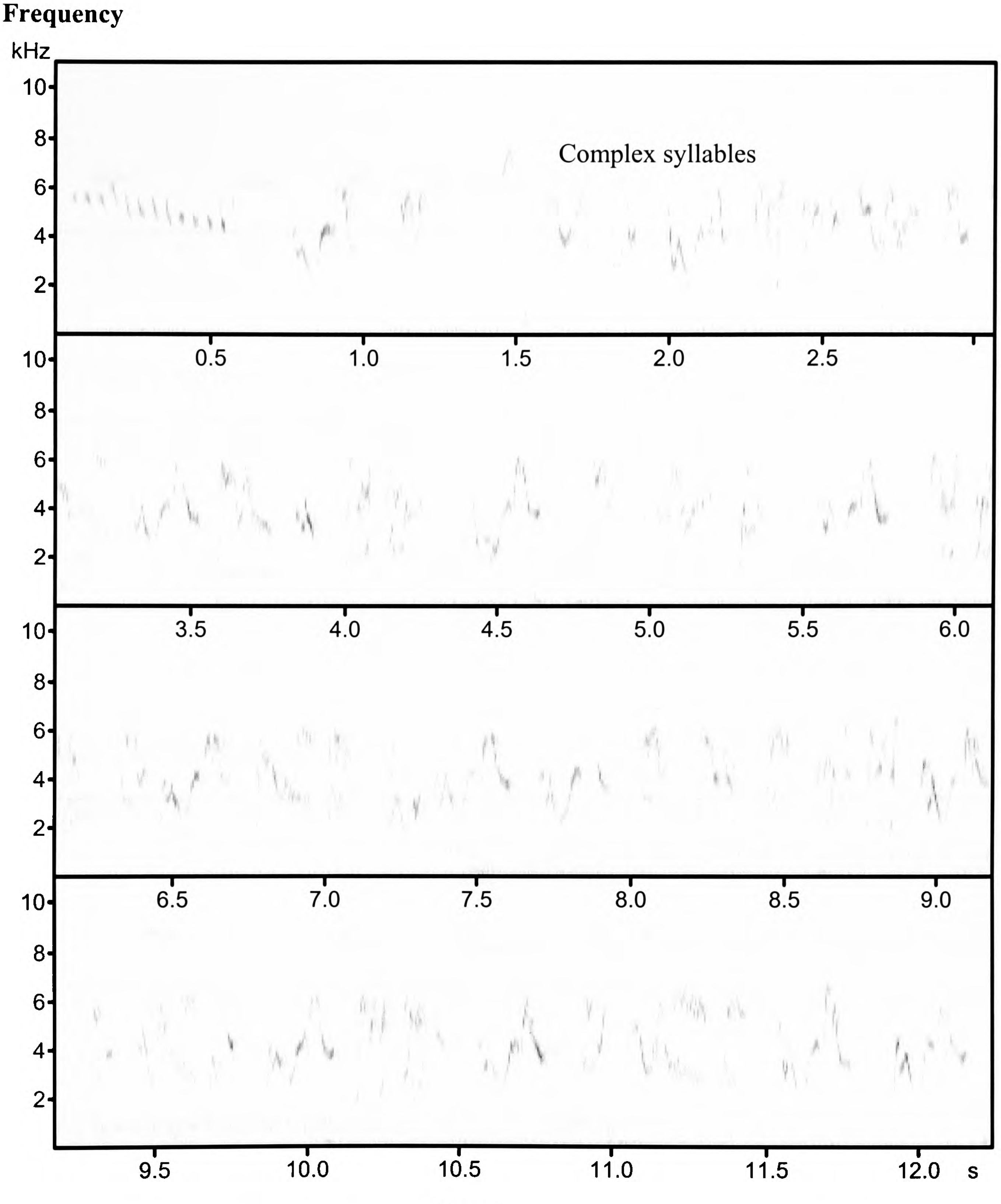
Olive-bellied Sunbird *Cinnyris chloropygius chloropygius* recorded in Libreville, Gabon, by C. Chappuis.

Appendix 4. 64 -Sonogram showing a complex song



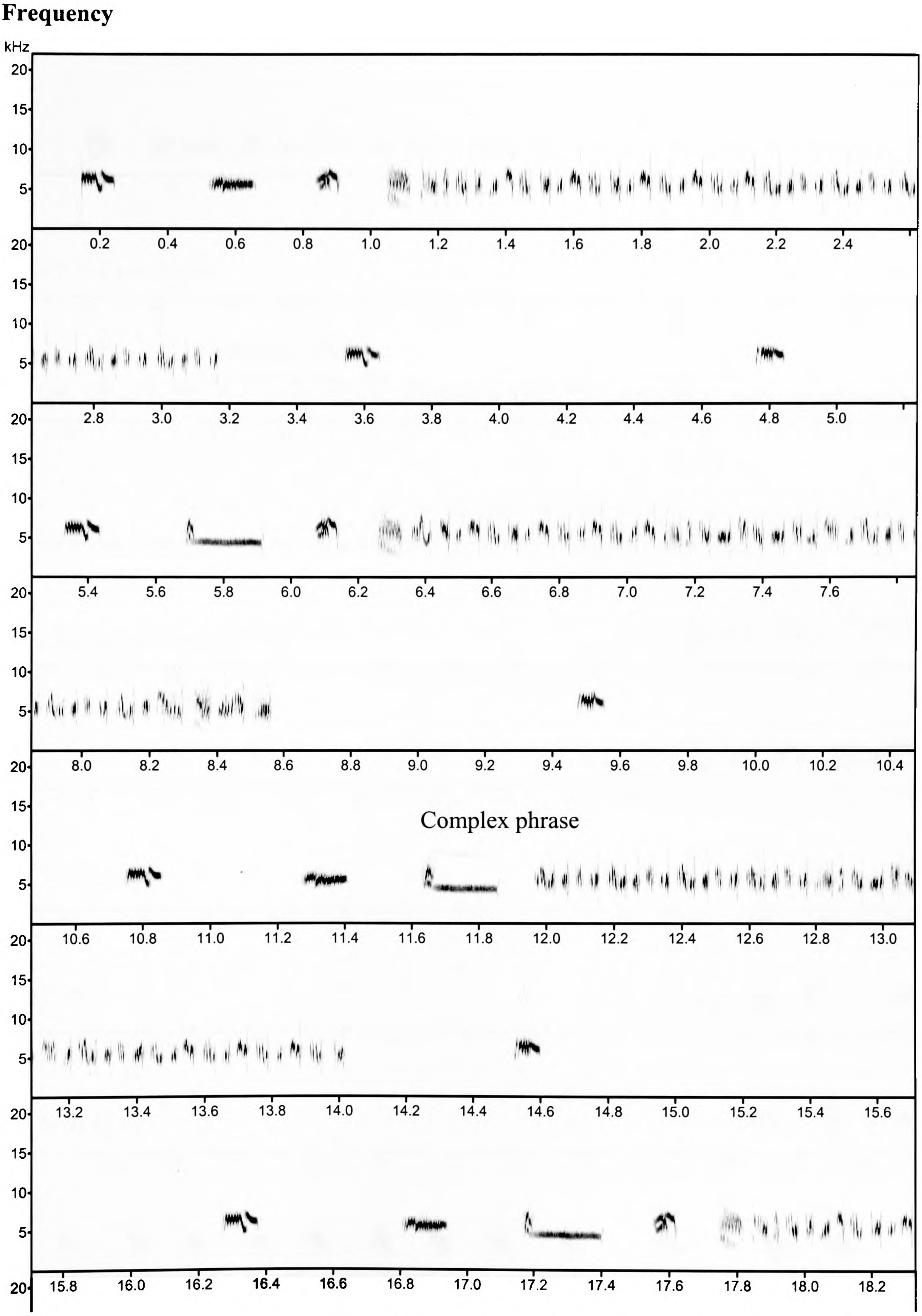
Loveridge's Sunbird *Cinnyris loveridgei* recorded in the Uluguru Mountains, Tanzania, by R. Stjernstedt.

Appendix 4. 66 - Sonogram showing a complex song



Miombo Double-collared Sunbird *Cinnyris manoensis manoensis* recorded in Malawi by R. Stjernstedt.

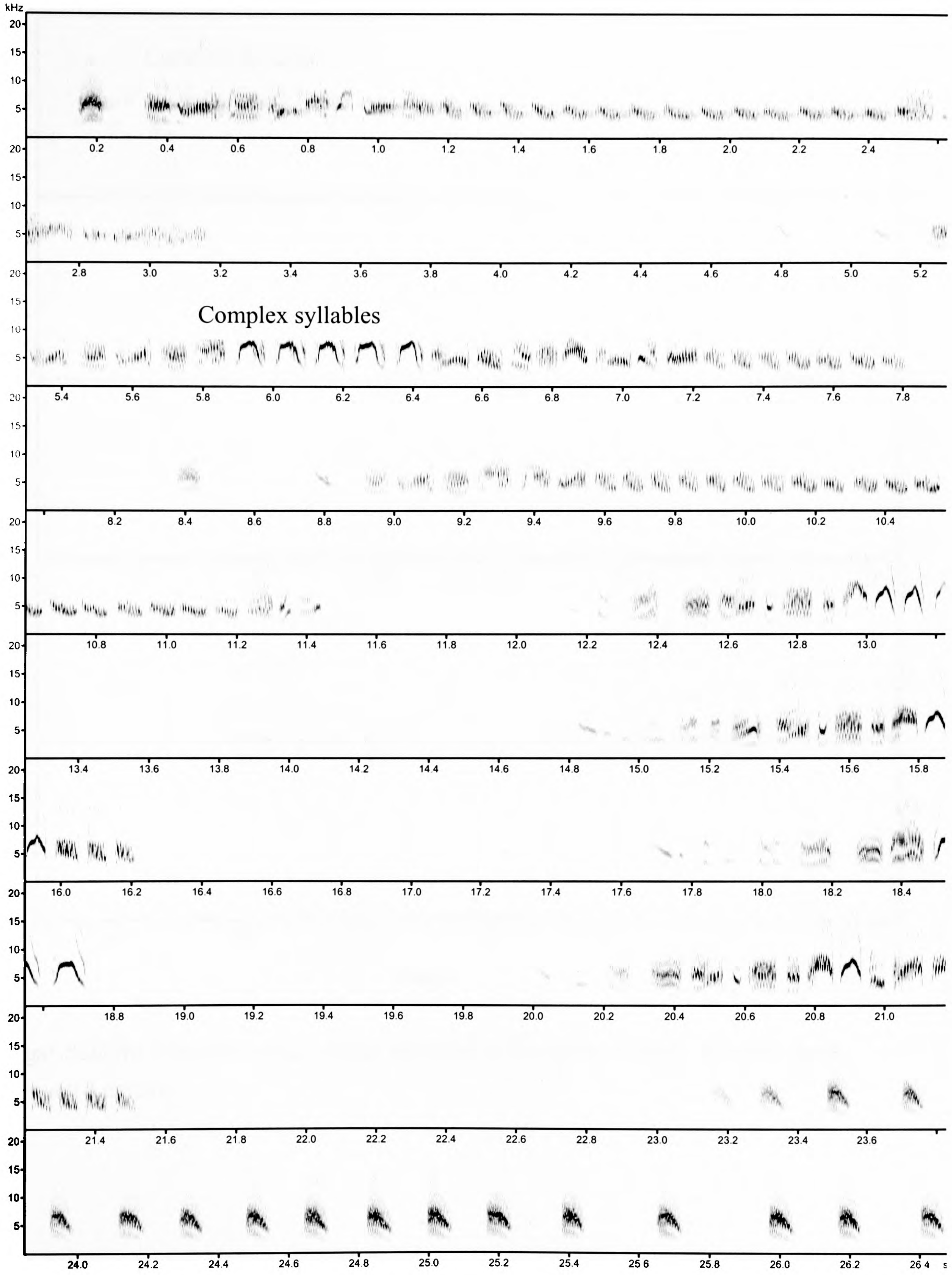
Appendix 4. 68 Sonogram showing a complex song



Eastern Double Collared Sunbird *Cinnyris mediocris mediocris* recorded in the Aberdare Mountains, Kenya, by C. Chappuis.

Appendix 4. 77 - Sonogram showing a complex song

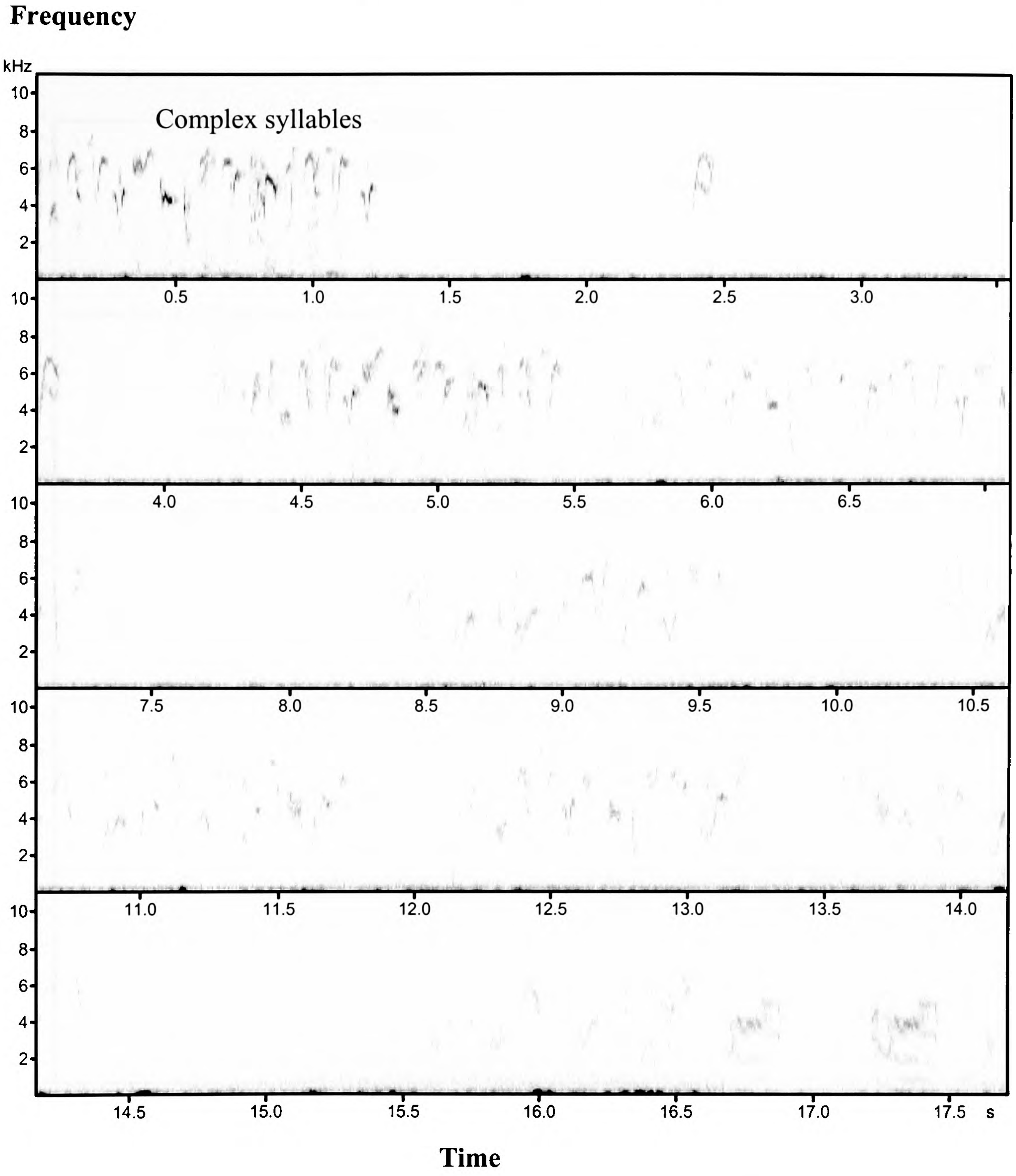
Frequency



Time

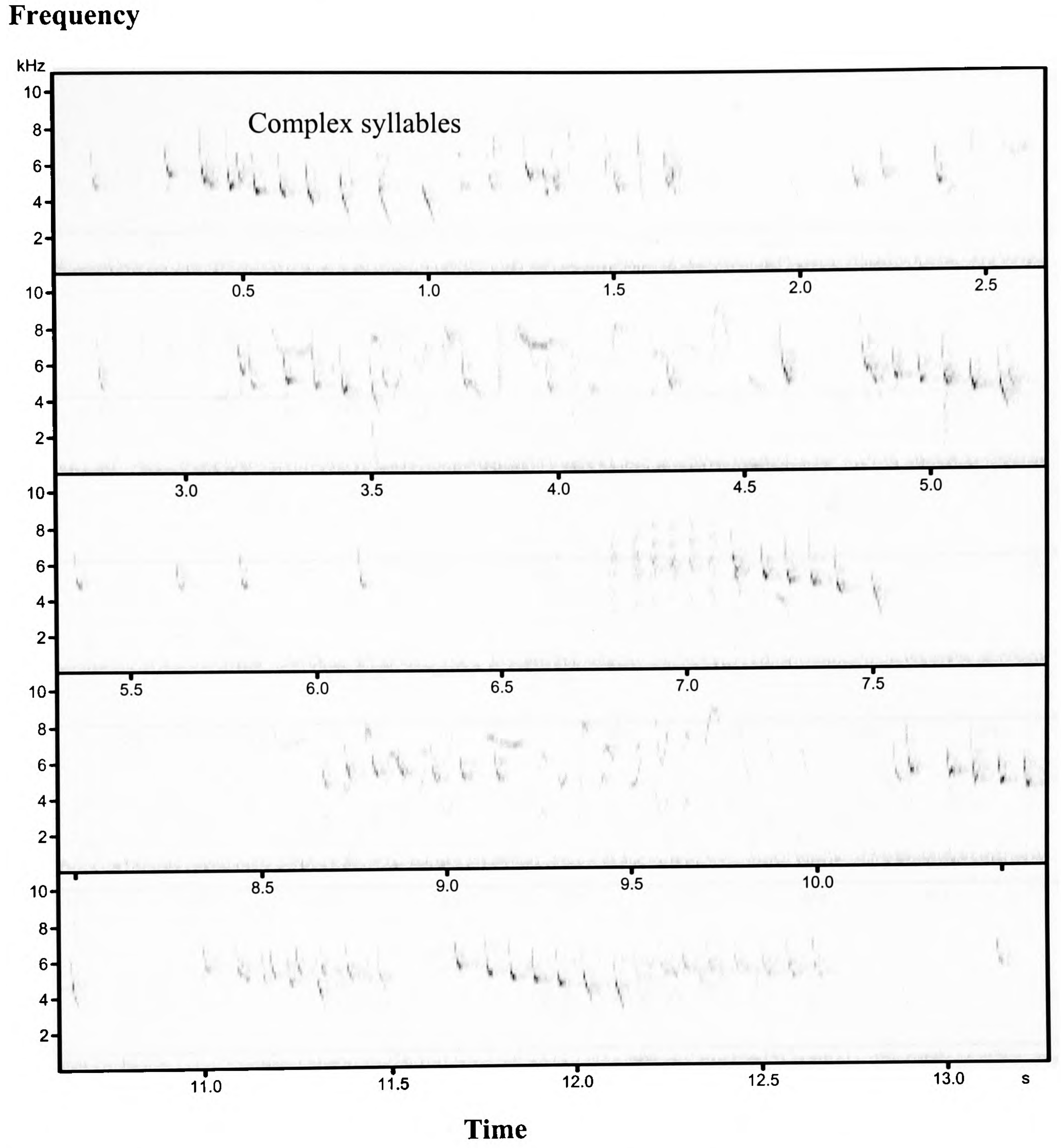
Northern Double-Collared Sunbird *Cinnyris preussi preussi* recorded on Mt Cameroon by C. Chappuis.

Appendix 4. 90 - Sonogram showing a complex song



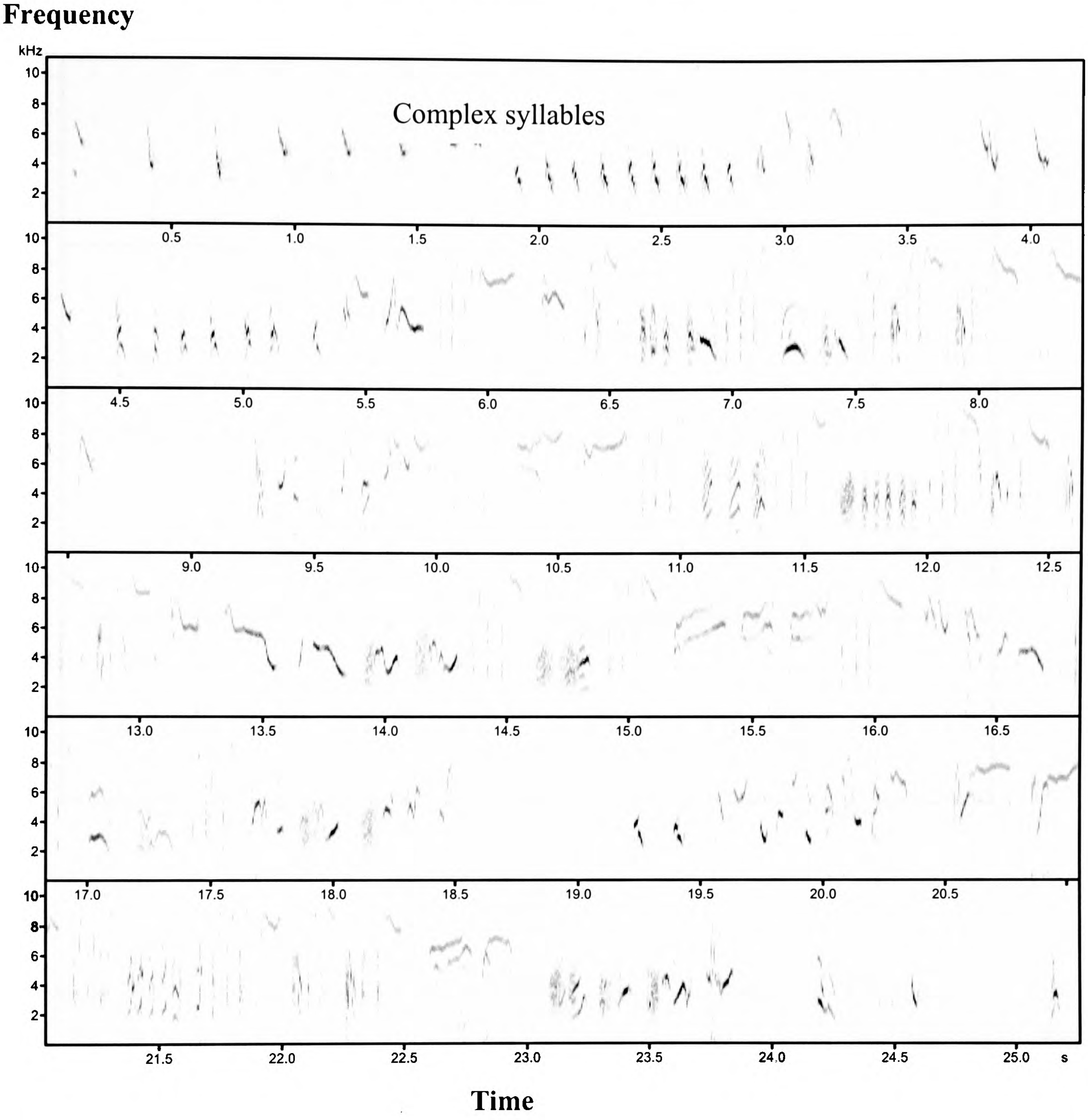
Regal Sunbird *Cinnyris regius regius* recorded in Nyungwe Forest, Rwanda, by F. Dowsett-Lemaire.

Appendix 4. 91 - Sonogram showing a complex song



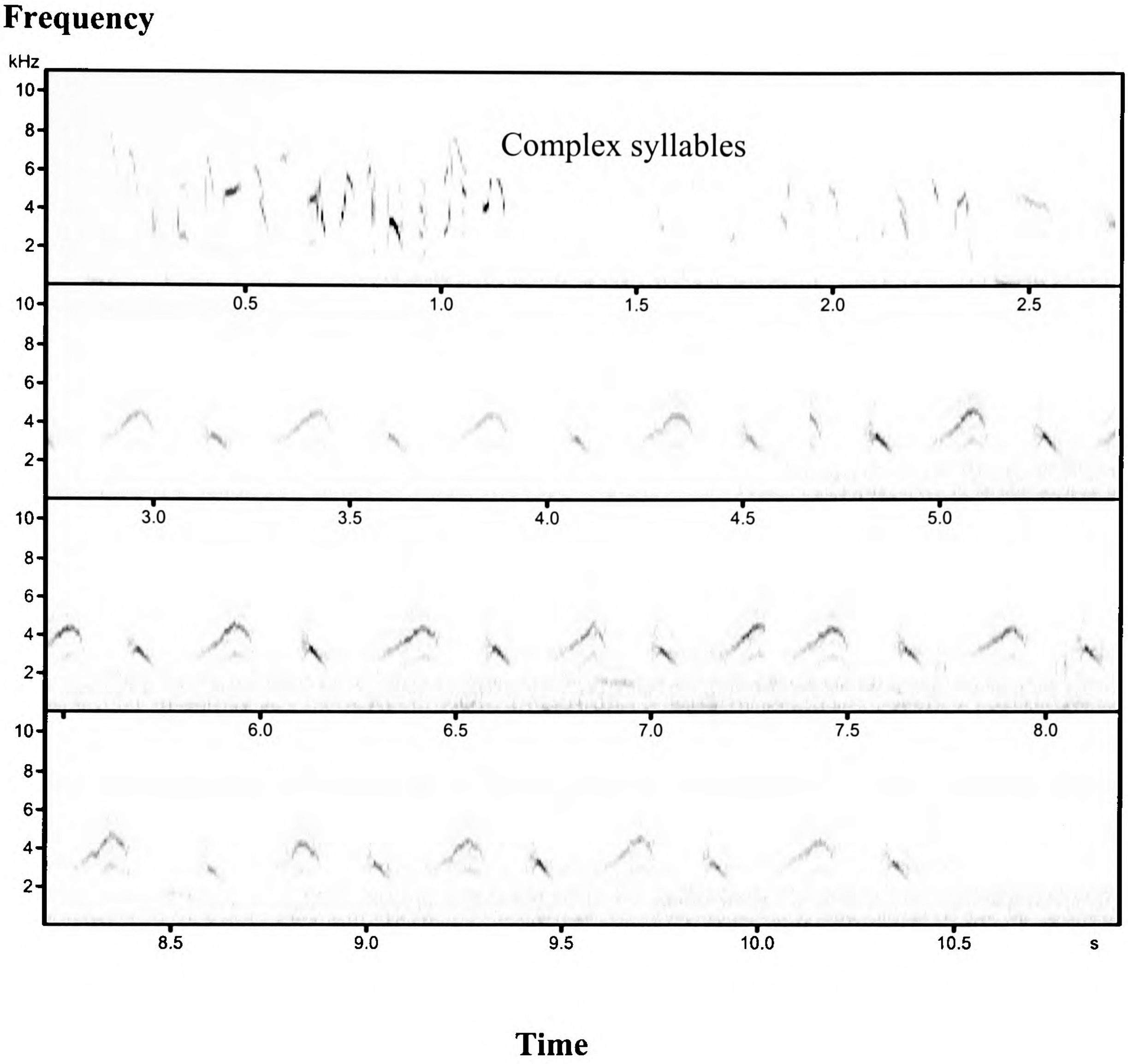
Purple-banded Sunbird *Cinnyris bifasciatus microrhynchus* recorded in South Africa by L. Gillard.

Appendix 4. 101 -Sonogram showing a Complex song



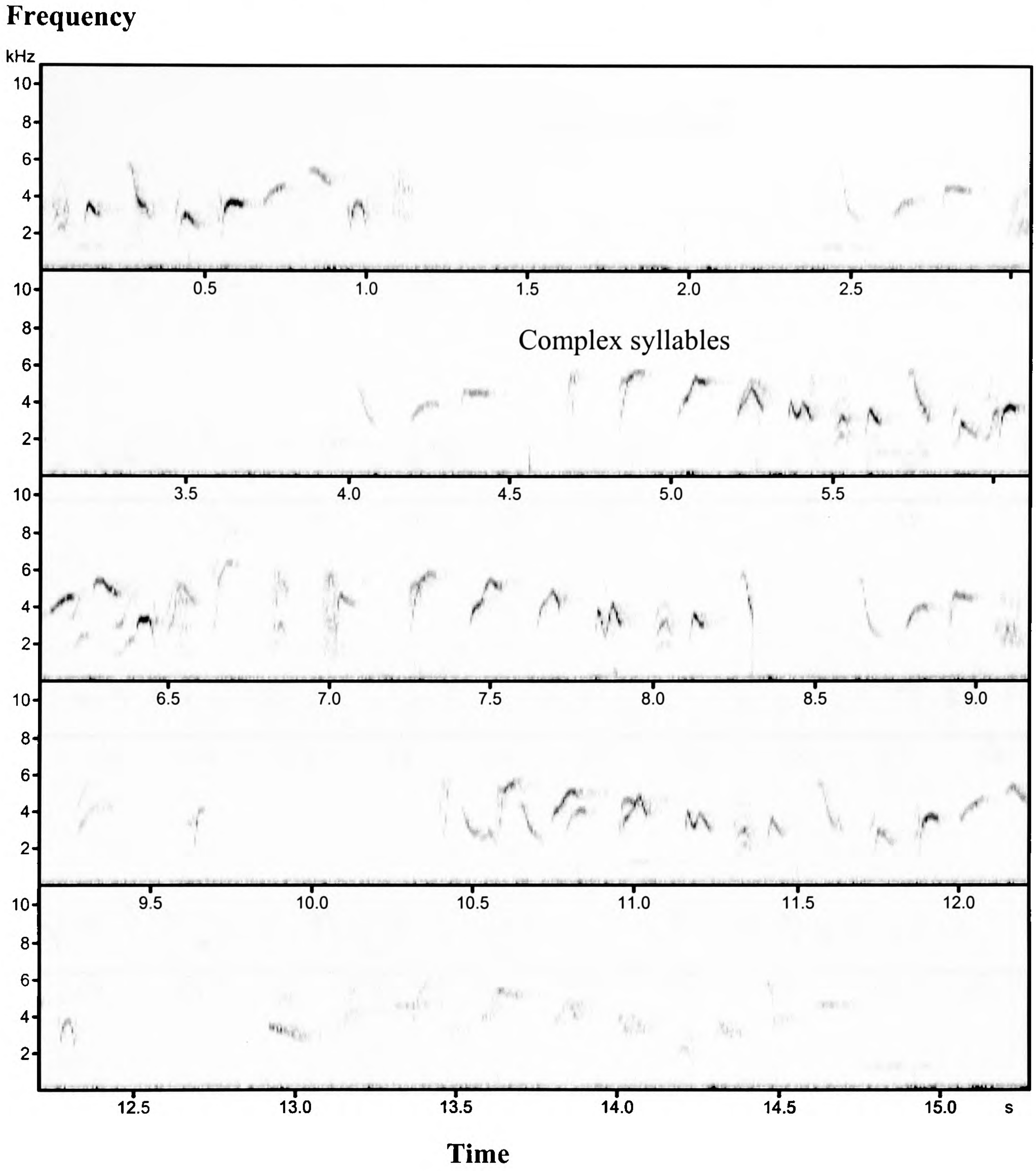
Mariqua Sunbird *Cinnyris mariquensis mariquensis* recorded in South Africa by L. Gillard.

Appendix 4. 112 - Sonogram showing a complex song



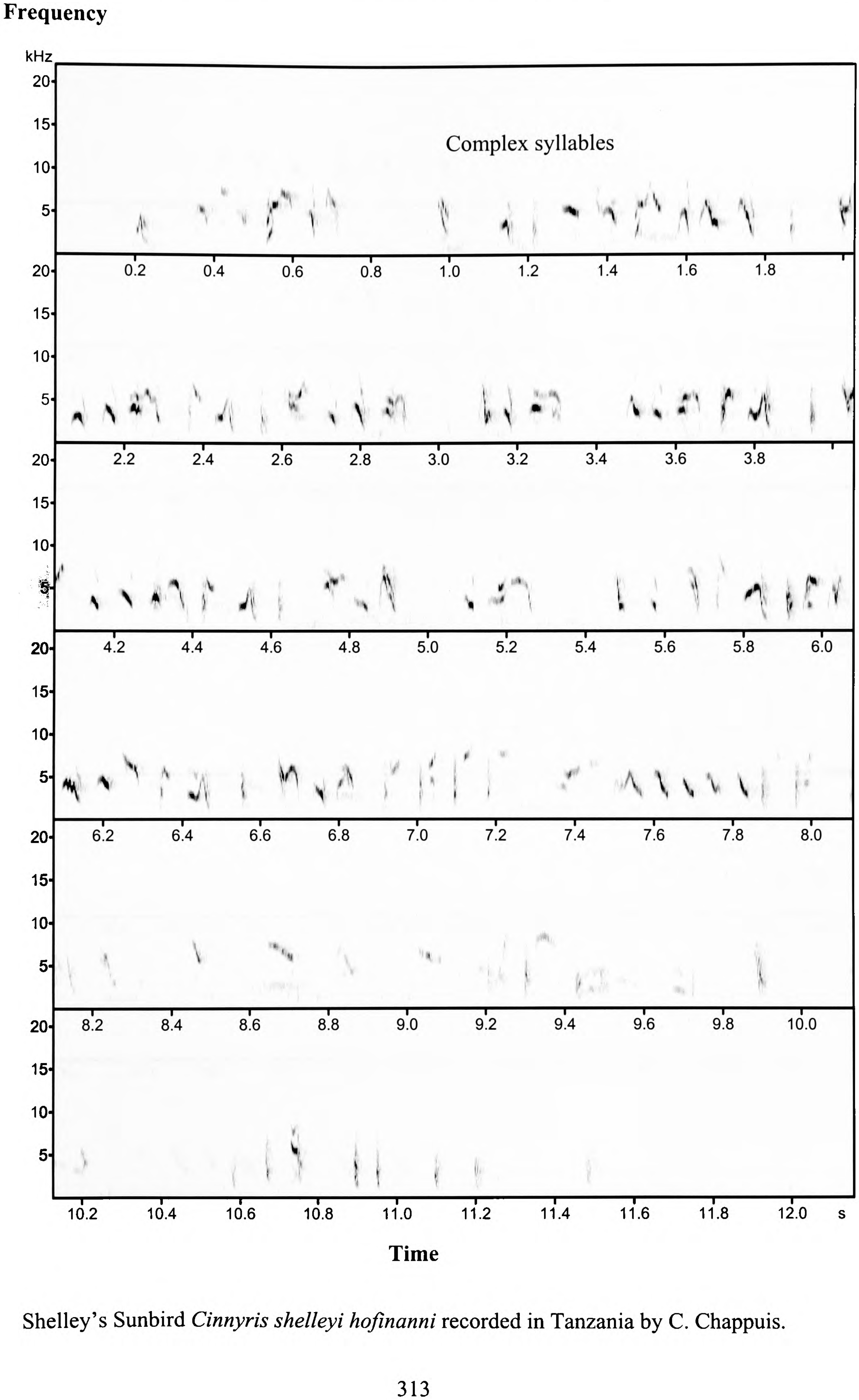
Palestine Sunbird *Cinnyris oseus oseus* recorded in Tel Aviv, Israel, by D. Hollom.

Appendix 4. 113 - Sonogram showing a complex song



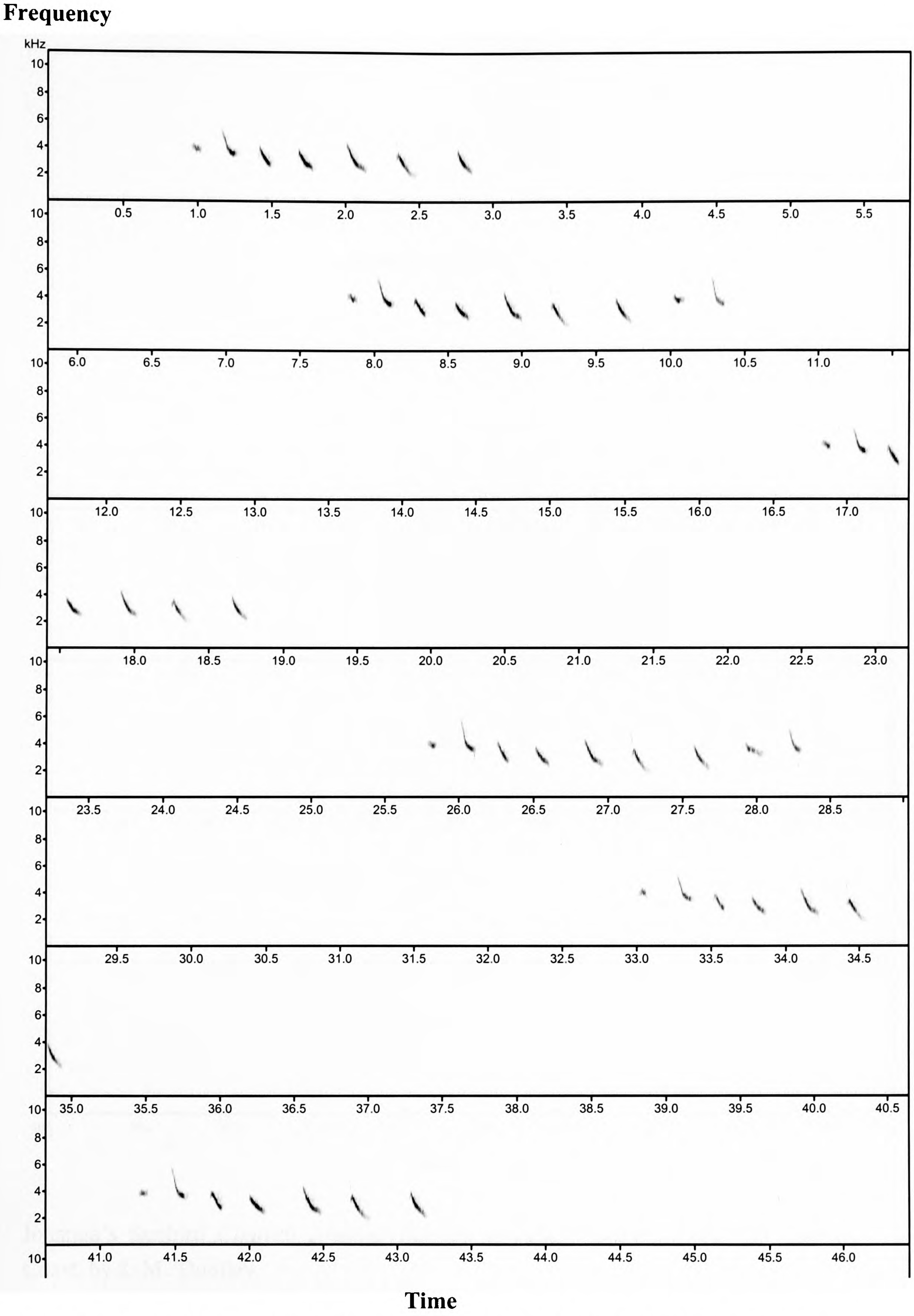
Kenya Violet-breasted Sunbird *Cinnyris chalcomelas* recorded in Sokoke Forest, Kenya, by R. McVicker.

Appendix 4. 119 - Sonogram showing a complex song



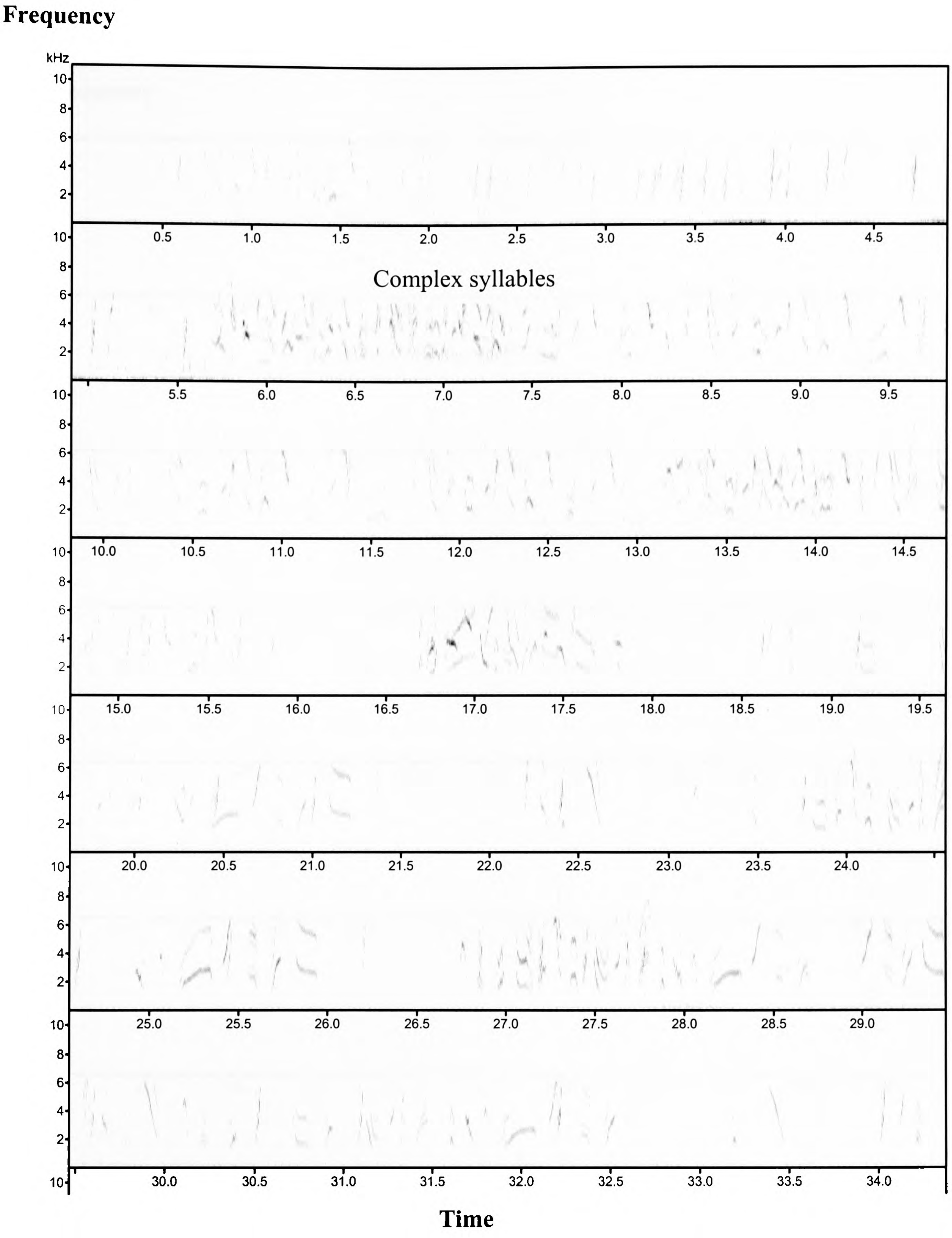
Shelley's Sunbird *Cinnyris shelleyi hofinanni* recorded in Tanzania by C. Chappuis.

Appendix 4. 120 - Sonogram showing call notes



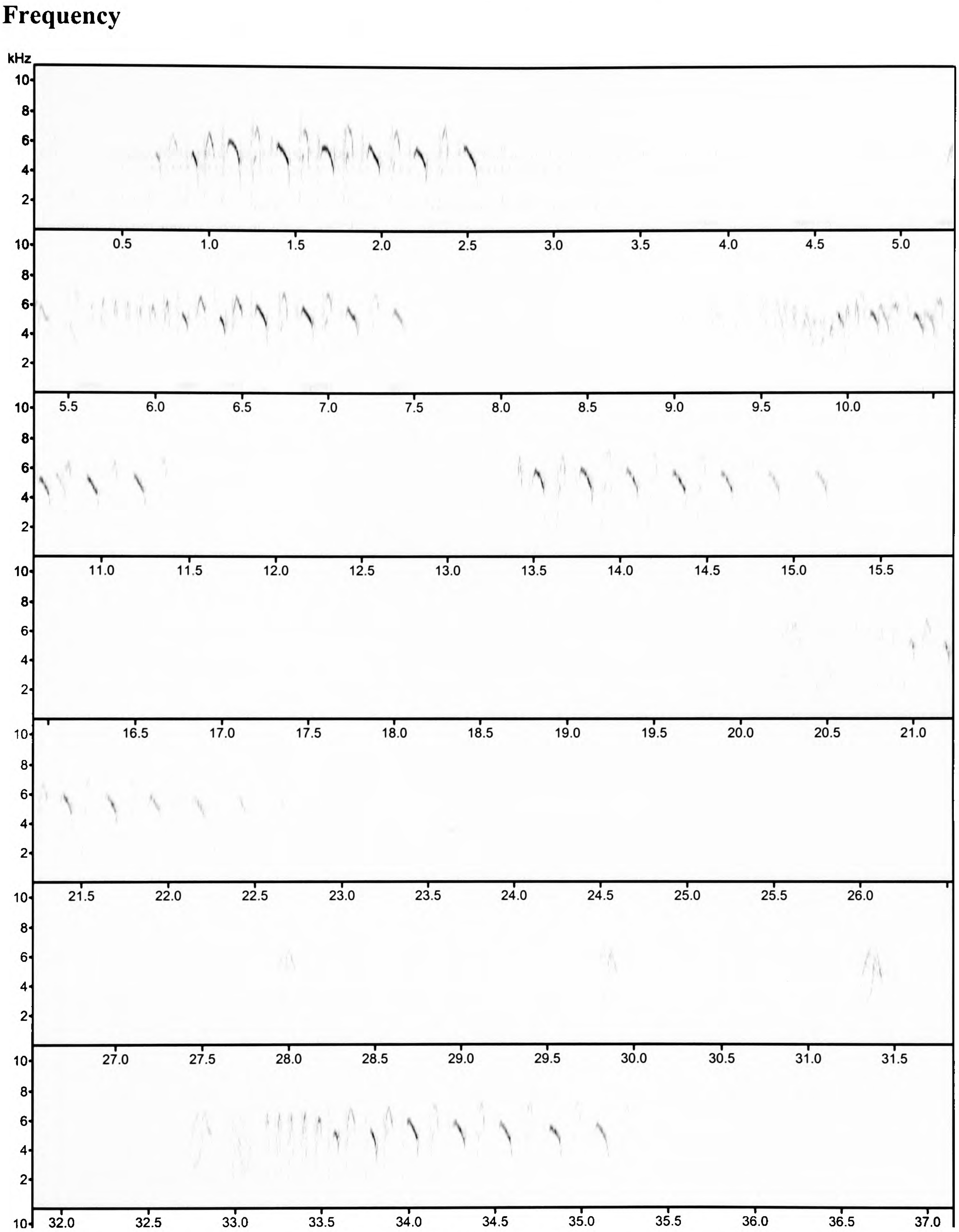
Splendid Sunbird *Cinnyris coccinigaster* recorded in the Shai Hills Nature Reserve, South Ghana, by C. R. Watson.

Appendix 4. 125 - Sonogram showing a complex song



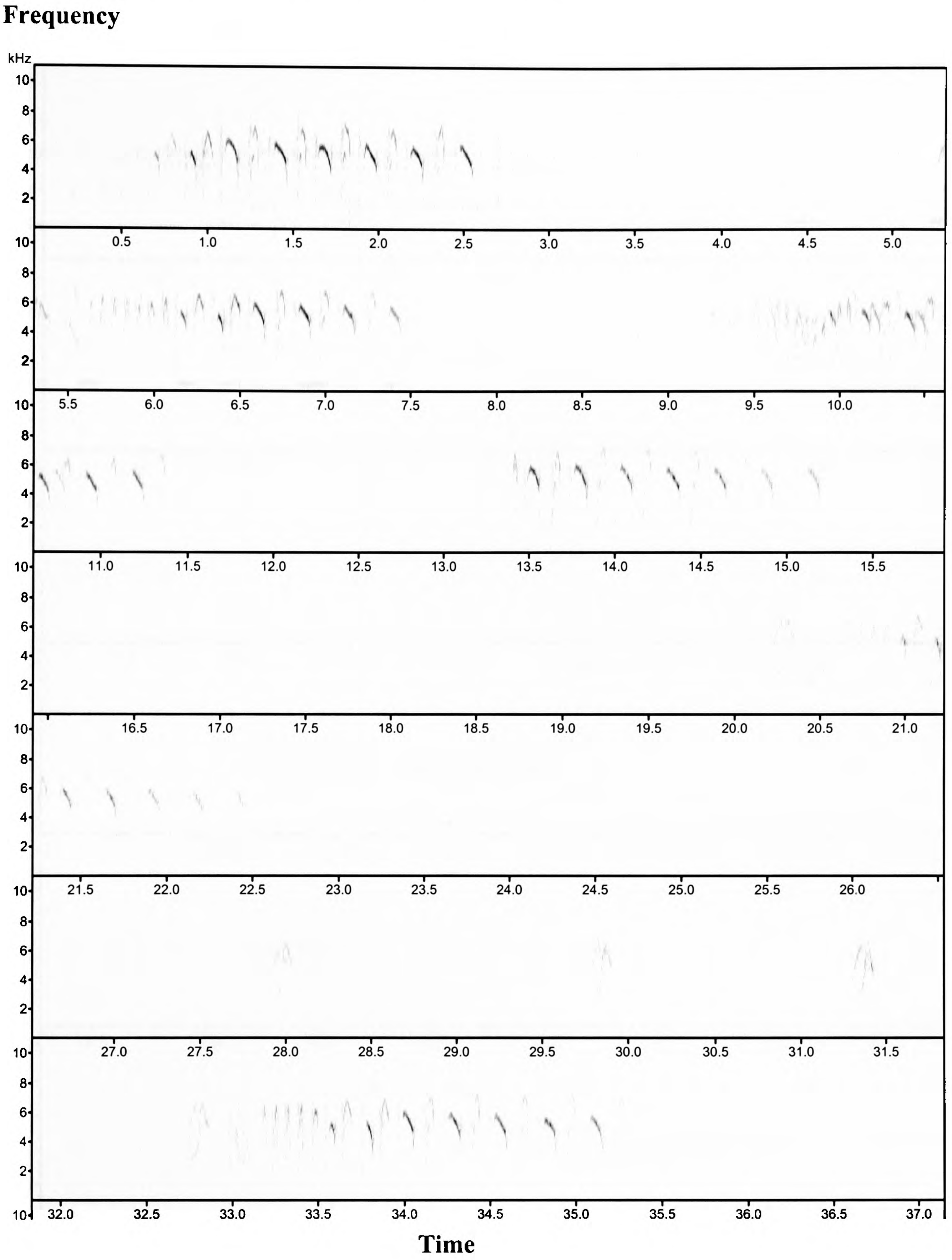
Johanna's Sunbird *Cinnyris johanna fasciata* recorded Ayame, South East Ivory Coast, by J.-M. Thiollay.

Appendix 4. 131 - Sonogram showing a complex song



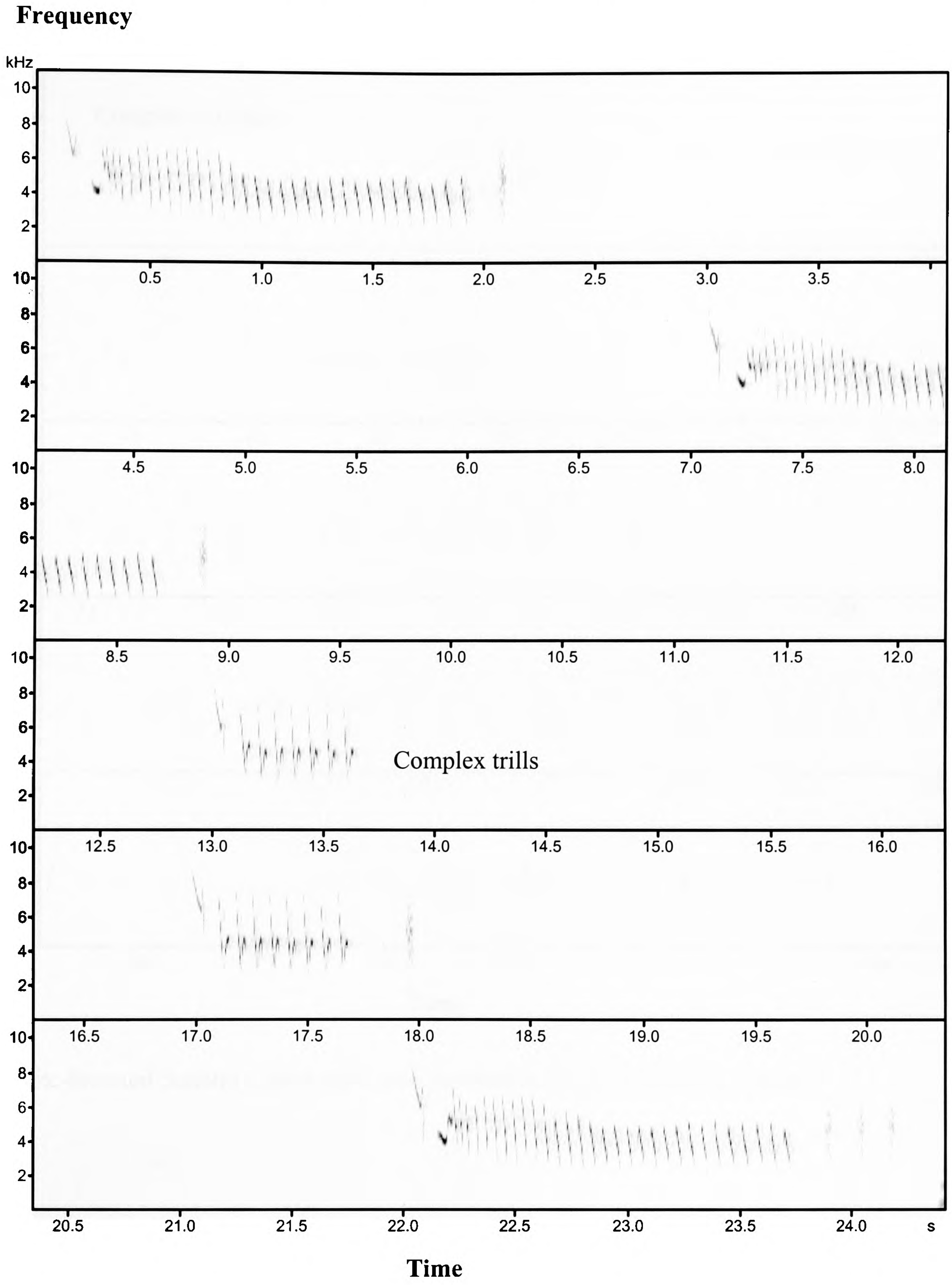
Superb Sunbird *Cinnyris superbus superbus* recorded in Yauonde Cameroon by Chappuis, C.

Appendix 4. 131 - Sonogram showing a complex song



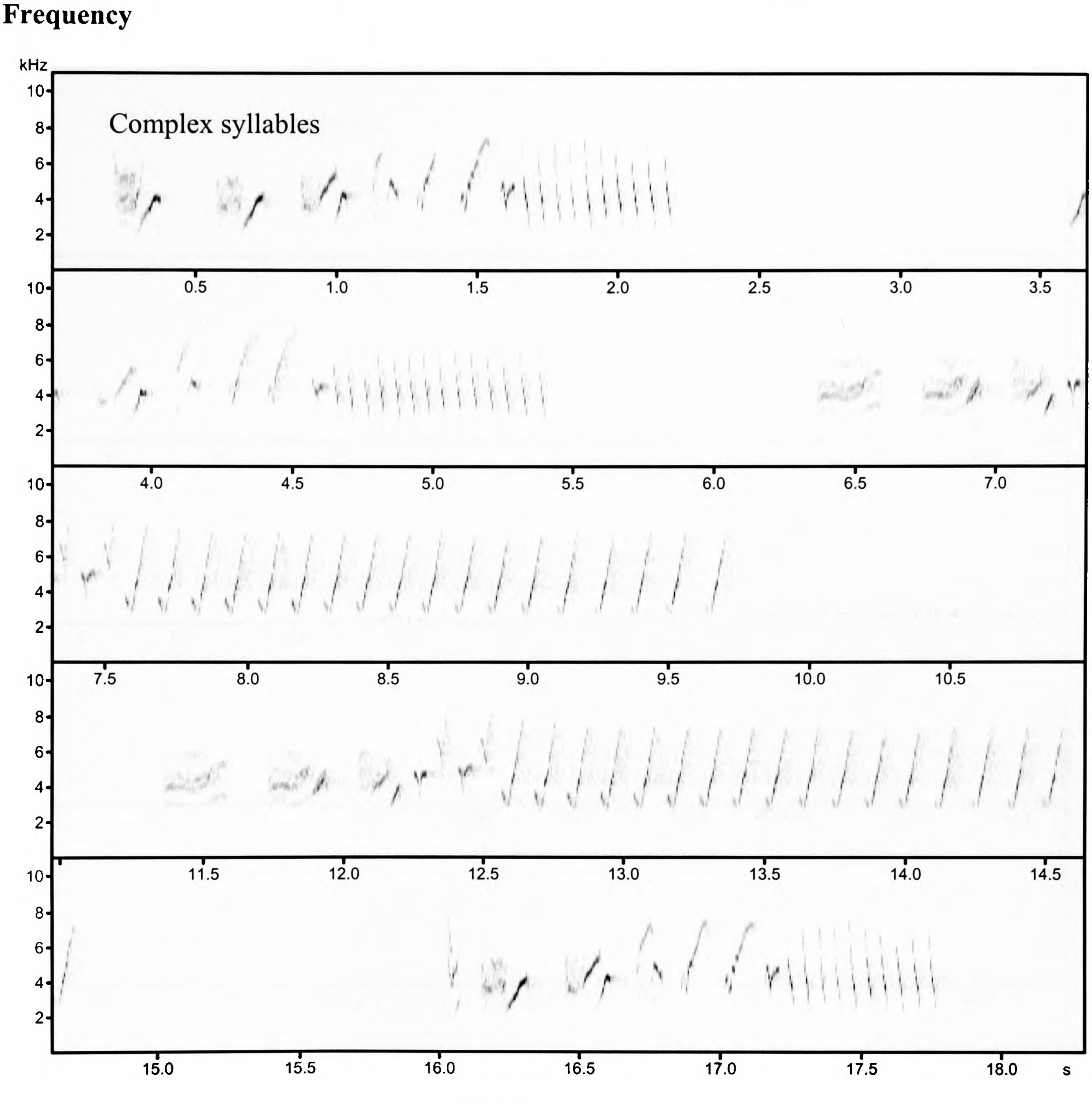
Superb Sunbird *Cinnyris superbus superbus* recorded in Yaoundé, Cameroon, by C. Chappuis.

Appendix 4. 133 - Sonogram showing complex song



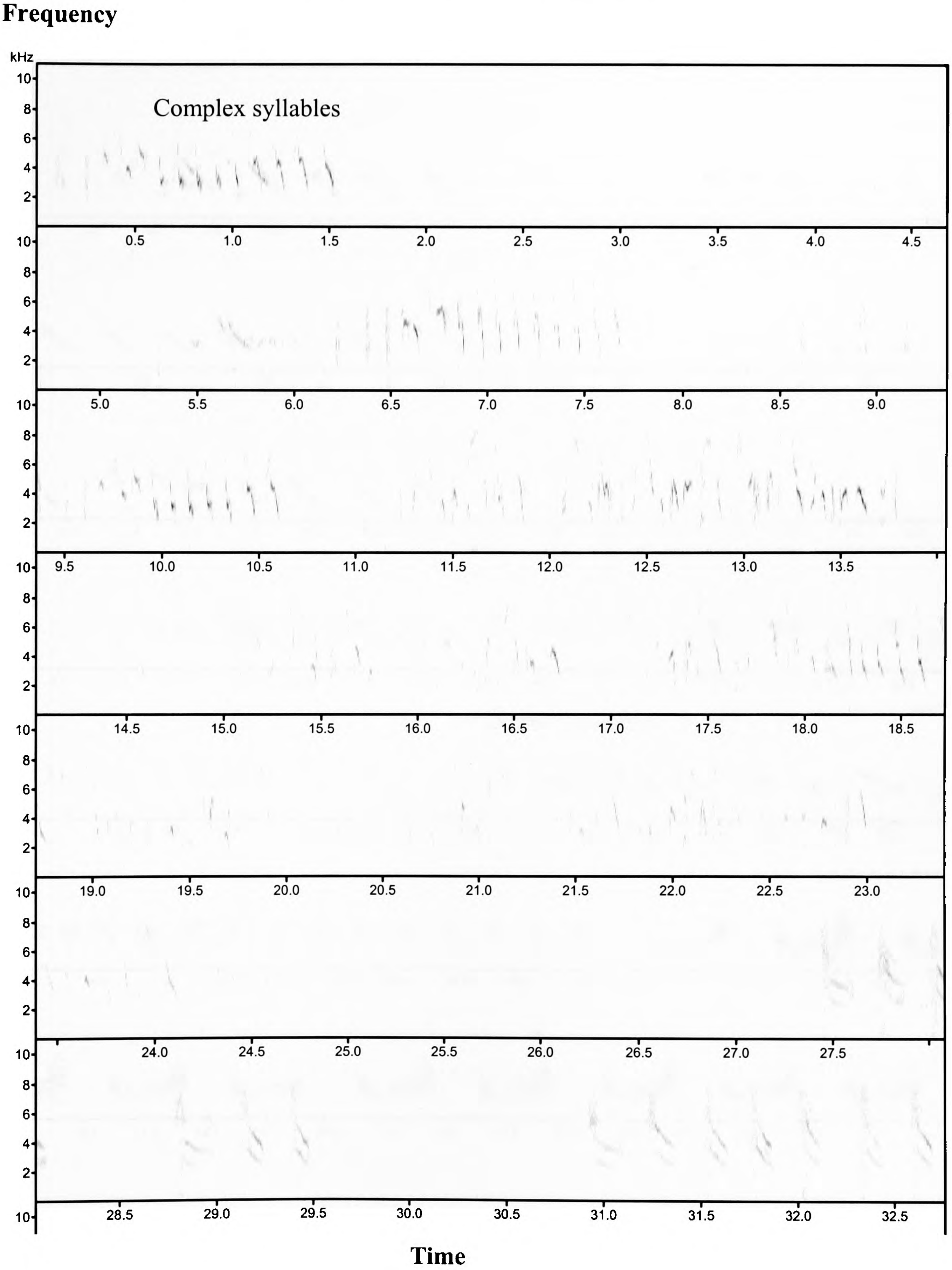
Dusky Sunbird *Cinnyris fuscus fuscus* recorded in Cape Province, South Africa, by L. Gillard.

Appendix 4. 138 - Sonogram showing a complex song



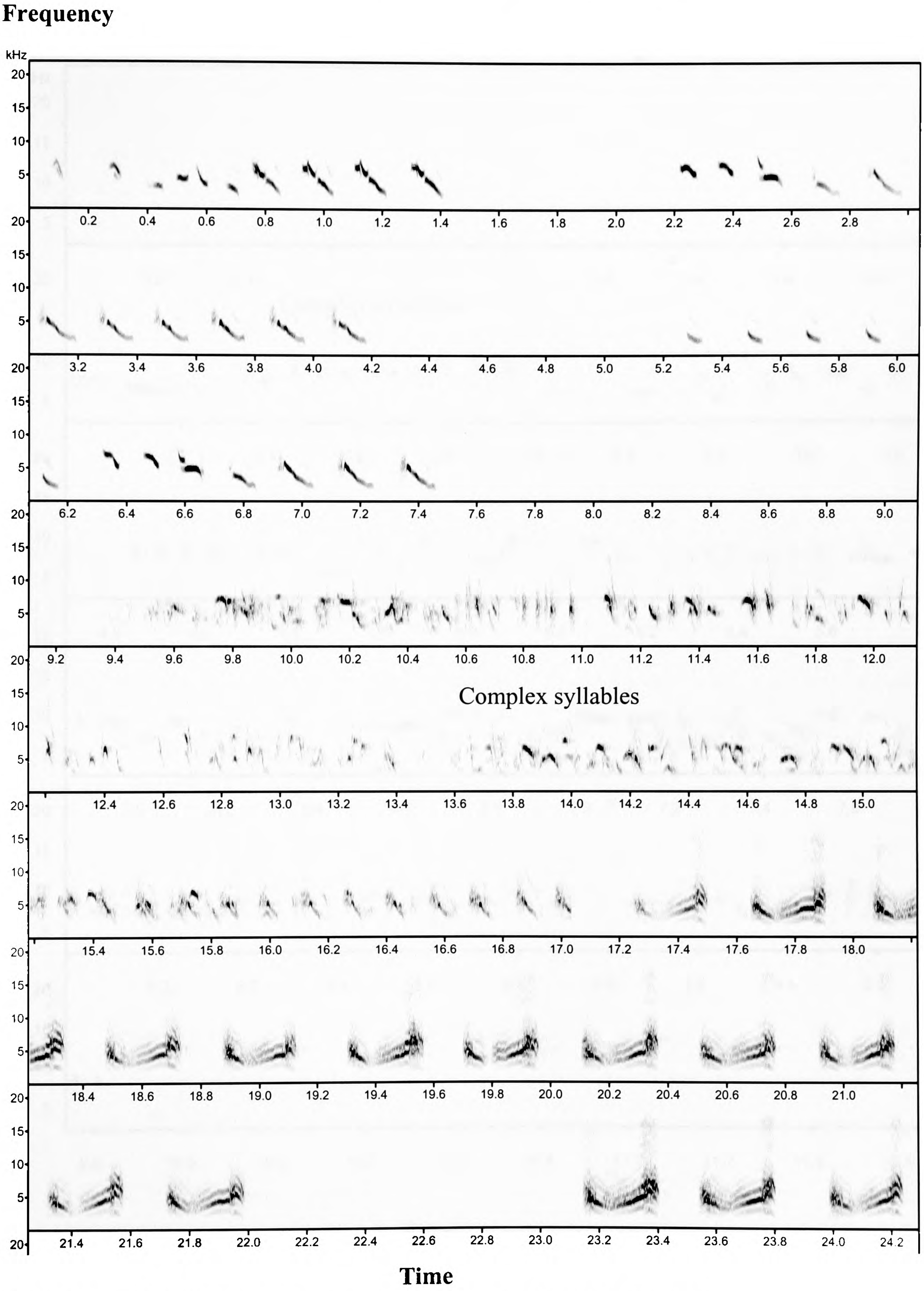
White-breasted Sunbird *Cinnyris talatala* recorded in South Africa by L. Gillard.

Appendix 4. 145 - Sonogram showing a complex song



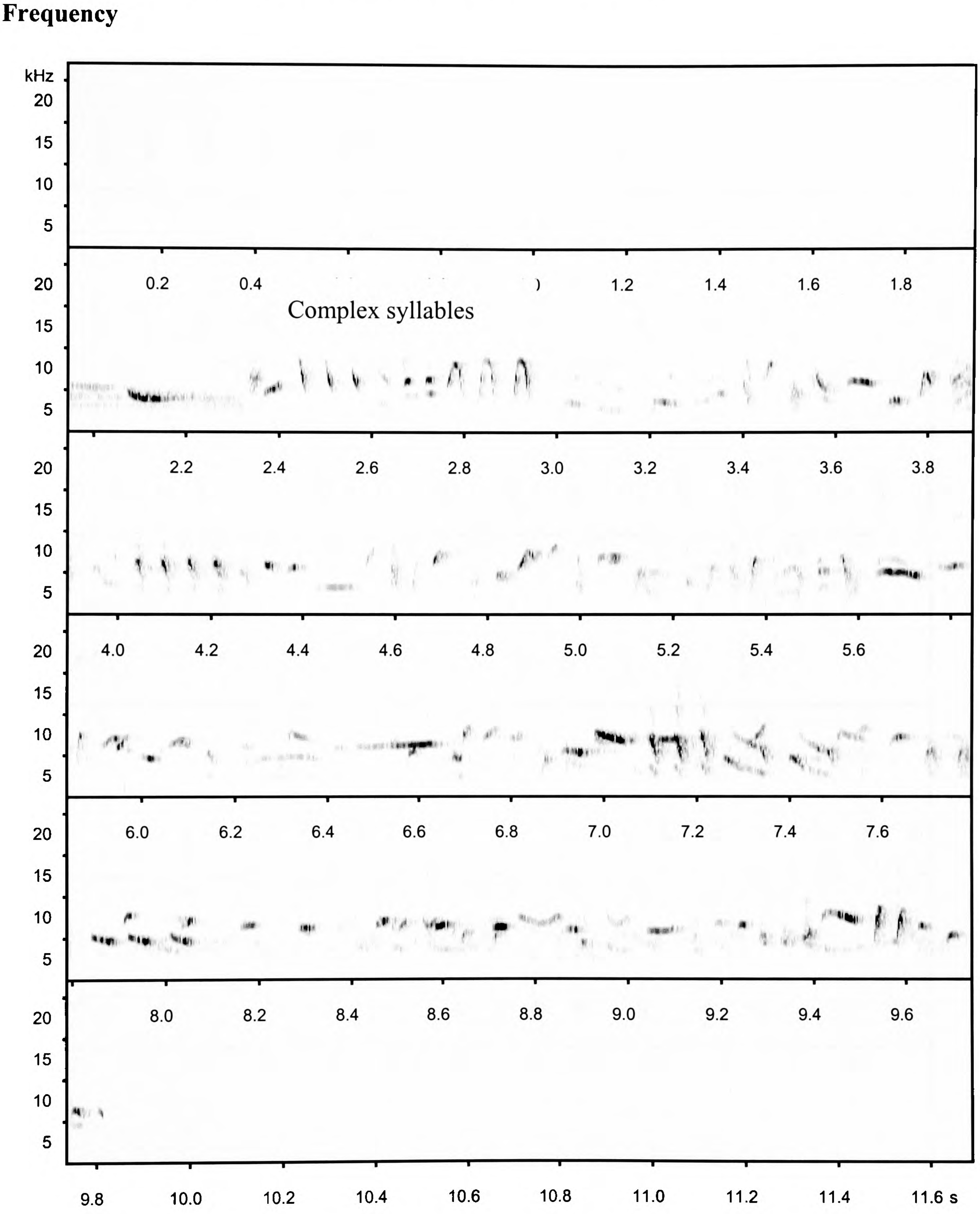
Variable Sunbird *Cinnyris venustus falkensteini* recorded in the Zambesi Valley, Zambia, by R. Stjernstedt.

Appendix 4. 151 - Sonogram showing a complex song



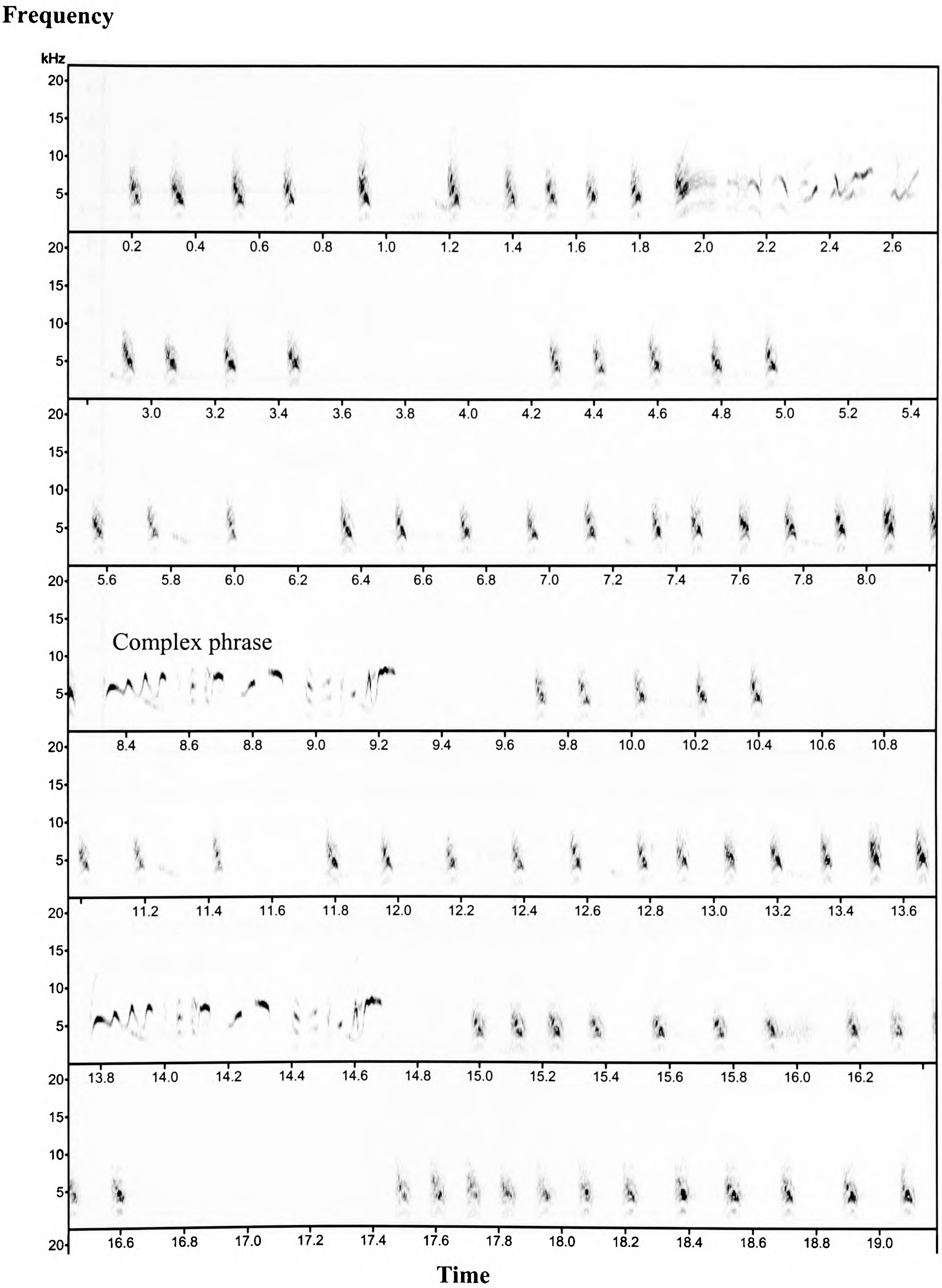
Variable Sunbird *Cinnyris venustus venustus* recorded in Ndali, Benin, by C. Chappuis.

Appendix 4. 159 - Sonogram showing a complex song



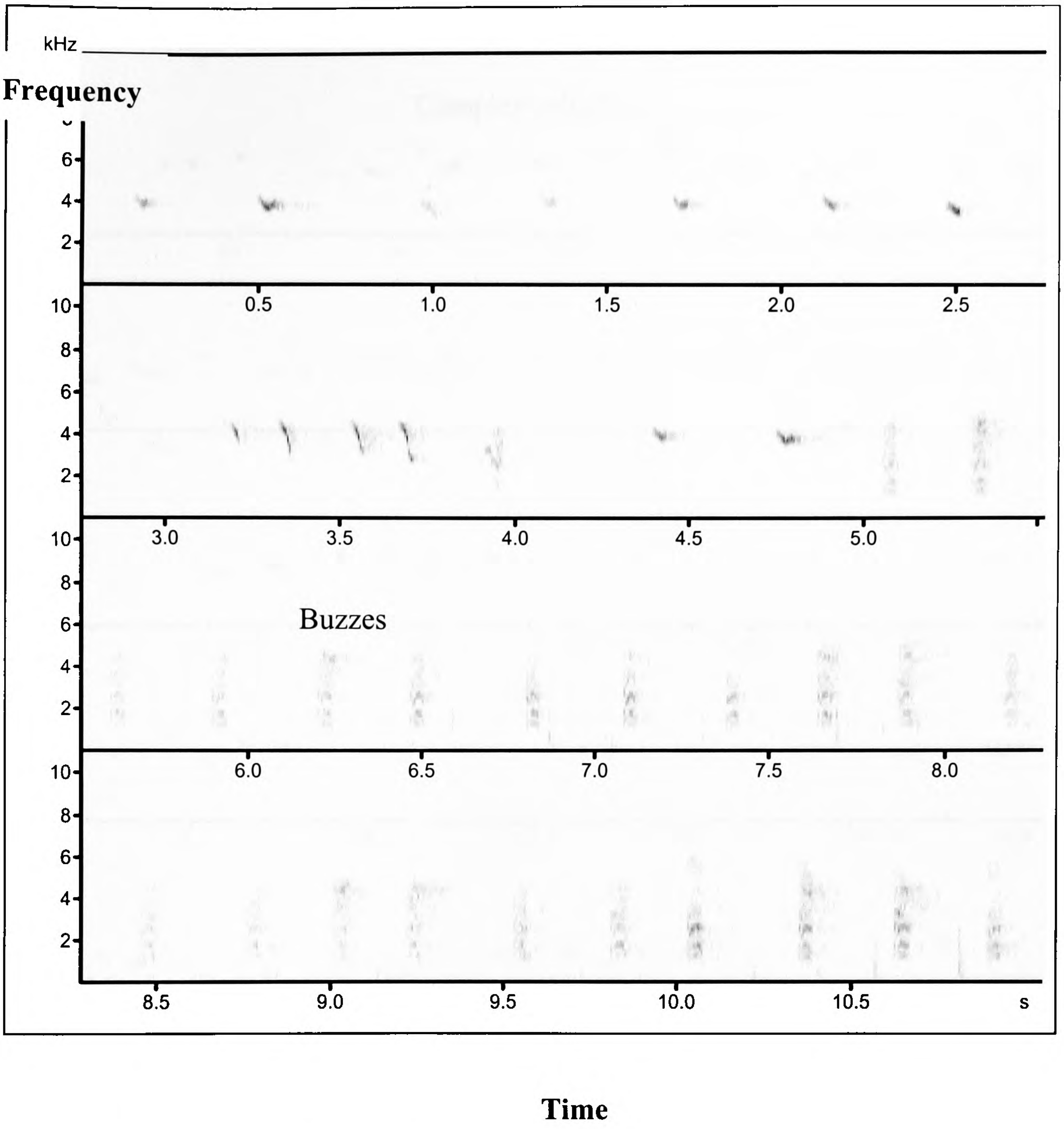
Ursula's Sunbird *Cinnyris ursulae* recorded on Mt Cameroon by C. Chappuis.

Appendix 4. 162 - Sonogram showing a complex song



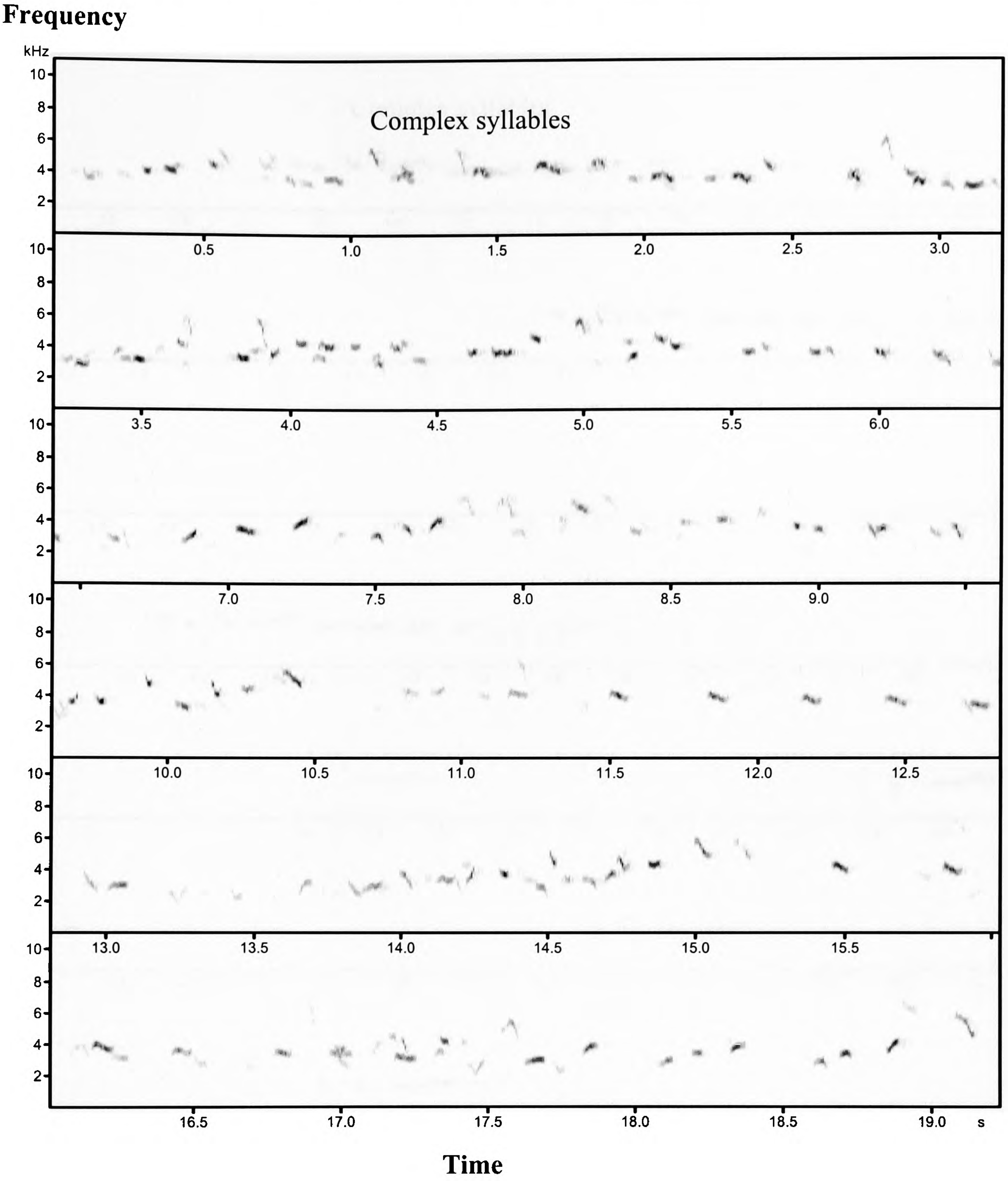
Copper Sunbird *Cinnyris cupreus cupreus* recorded in Ghana by D. Moyer.

Appendix 4. 172 - Sonogram showing buzz calls



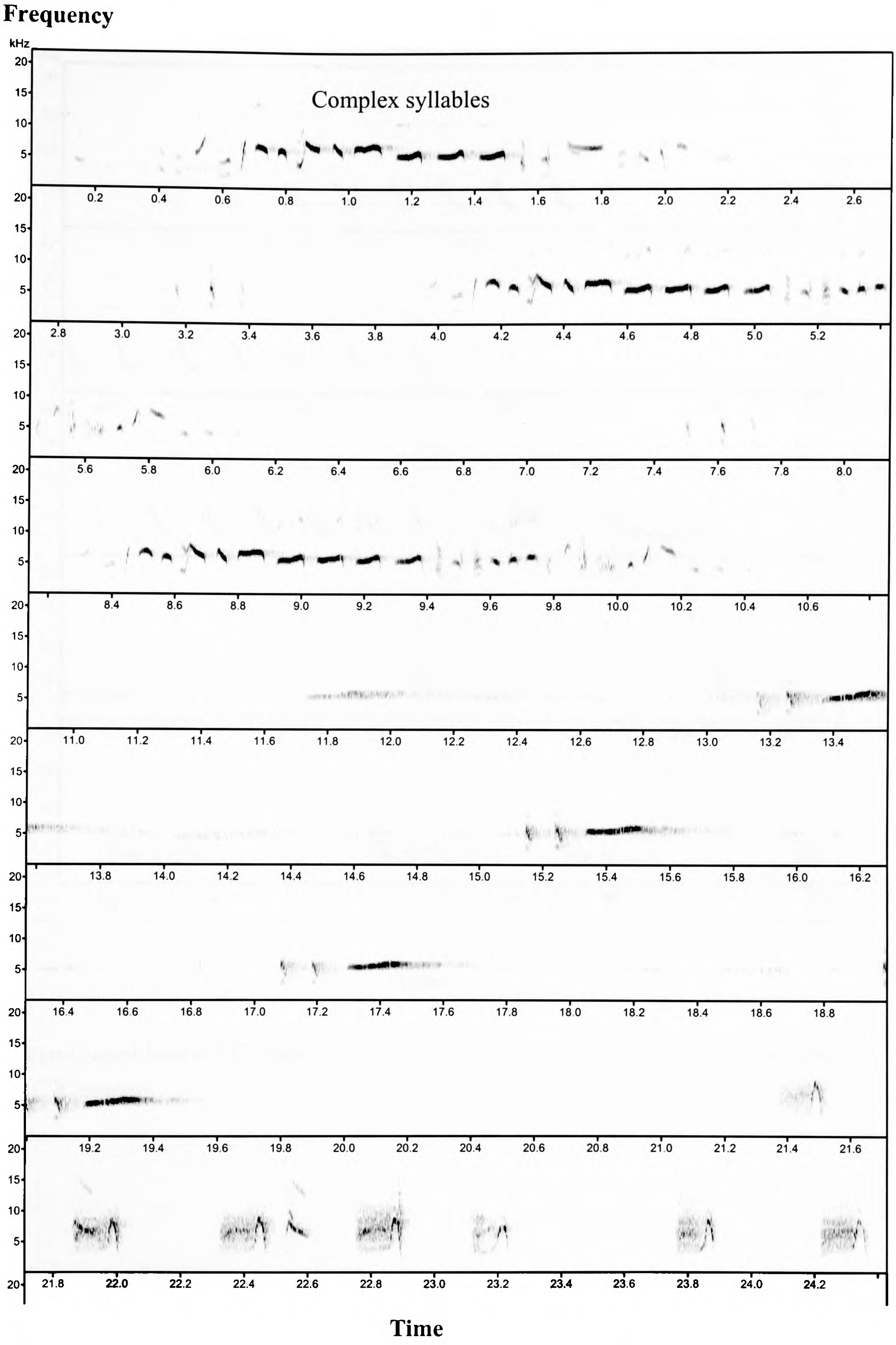
Western Olive Sunbird *Cyanomitra obscura sclateri* recorded in Vumba, Zimbabwe, by R. Stjernstedt.

Appendix 4. 178 - Sonogram showing a complex song



Eastern Olive Sunbird *Cyanomitra olivacea olivacea* recorded in South Zululand, South Africa, by L. Gillard.

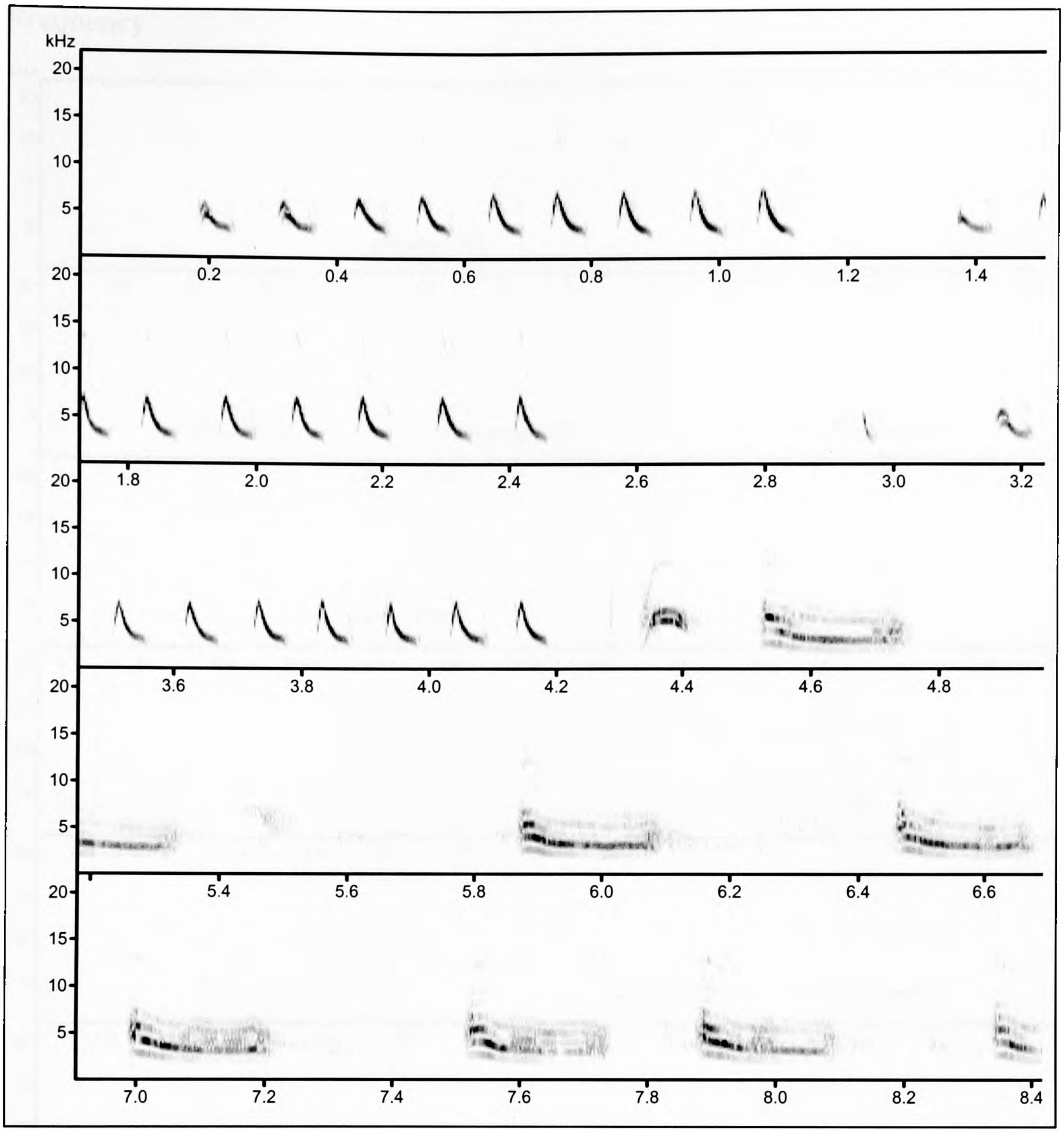
Appendix 4. 180 - Sonogram showing a complex song



Cameroon Sunbird *Cyanomitra oritis oritis* recorded on Mt Cameroon by C. Chappuis.

Appendix 4. 187 - Sonogram showing a simple song with harmonics

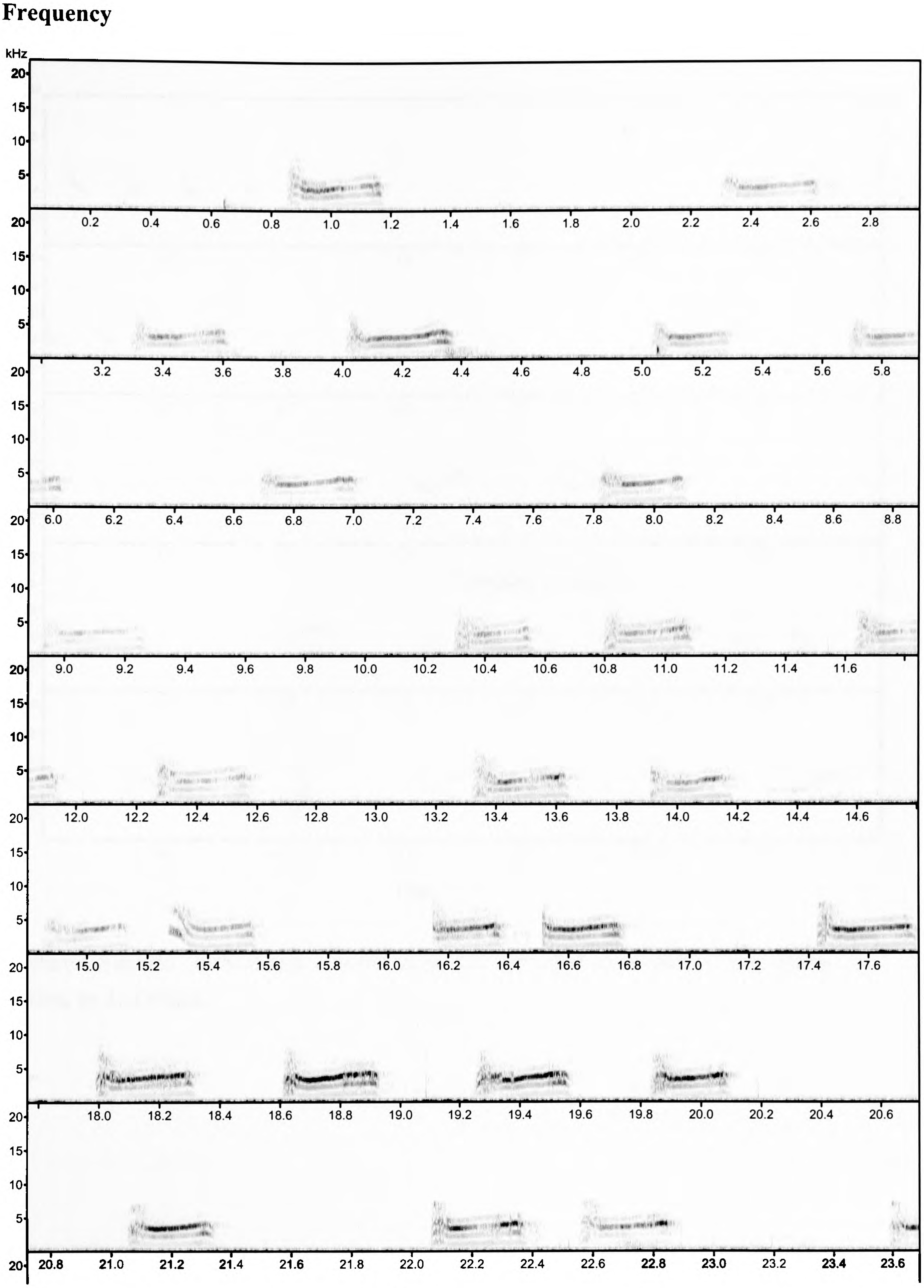
Frequency



Time

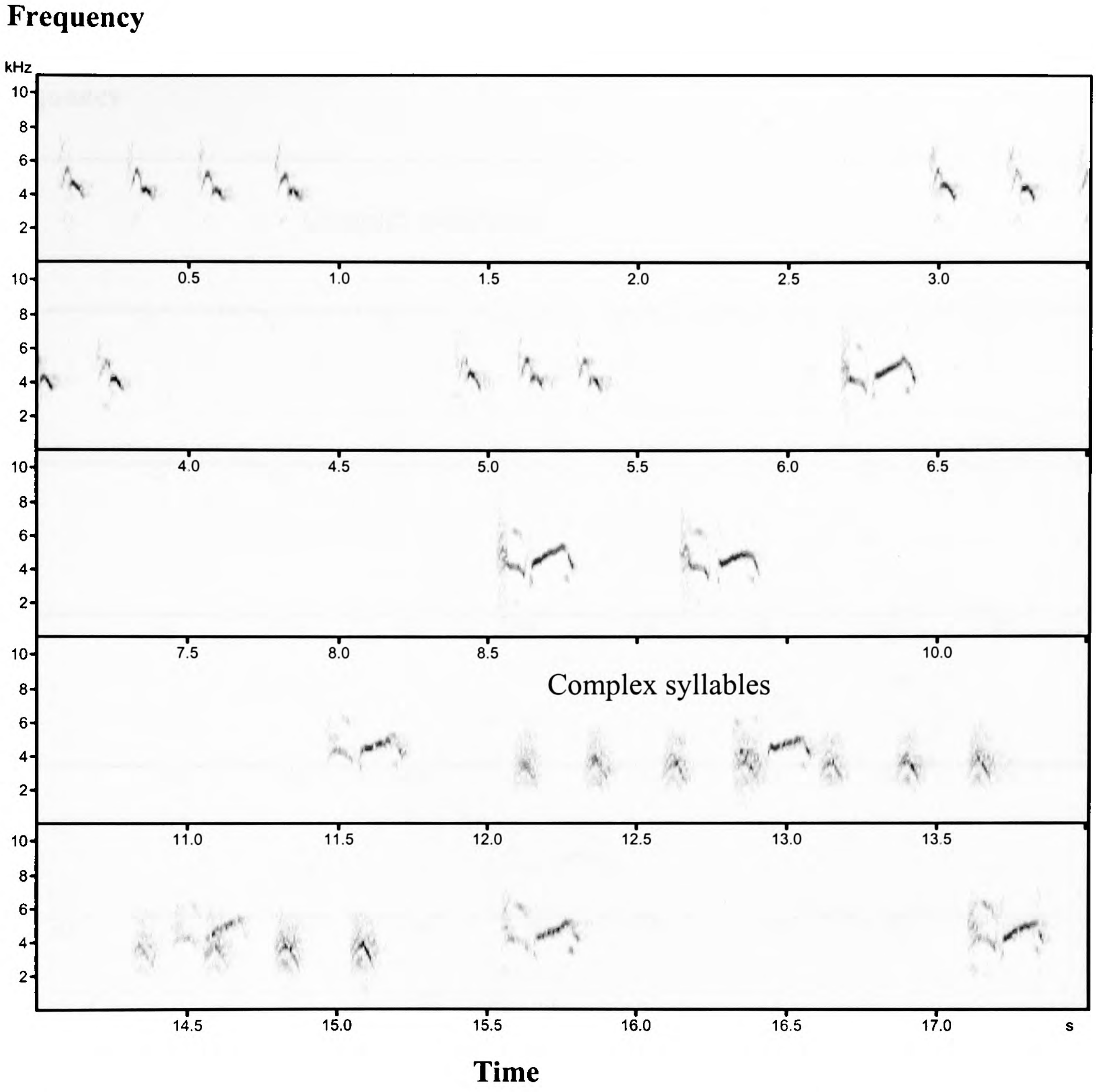
Green-headed Sunbird *Cyanomitra verticalis boehndorffi* recorded on Mt Cameroon, by C. Chappuis.

Appendix 4. 188 - Sonogram showing simple song with harmonics



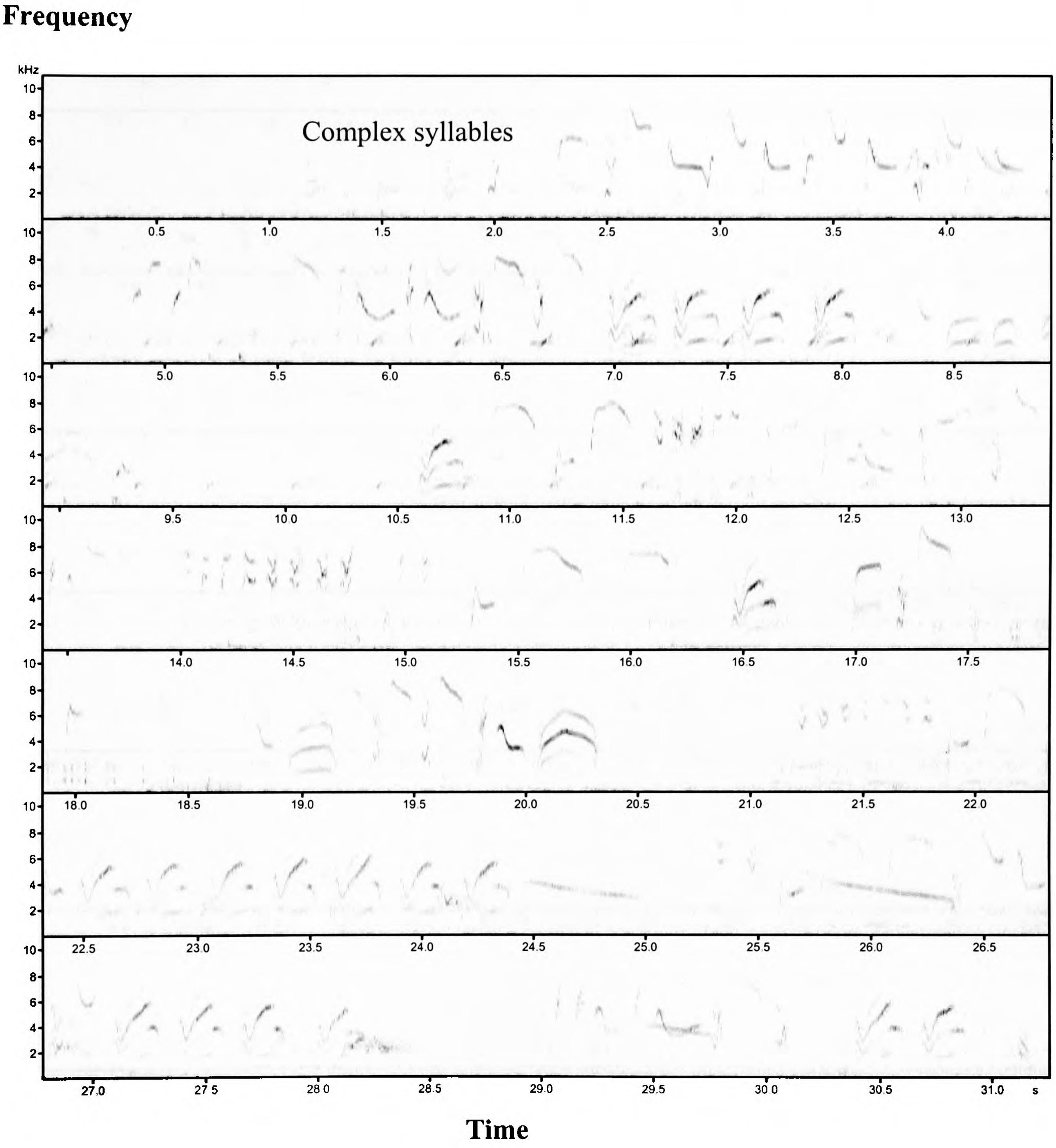
Green-headed Sunbird *Cyanomitra verticalis verticalis* recorded at Legon Hill, Ghana by L. Grimes.

Appendix 4. 197 - Sonogram showing a complex song



Collared Sunbird *Anthodiaeta collaris zuluensis* recorded in Eastern Cape, South Africa, by L. Gillard.

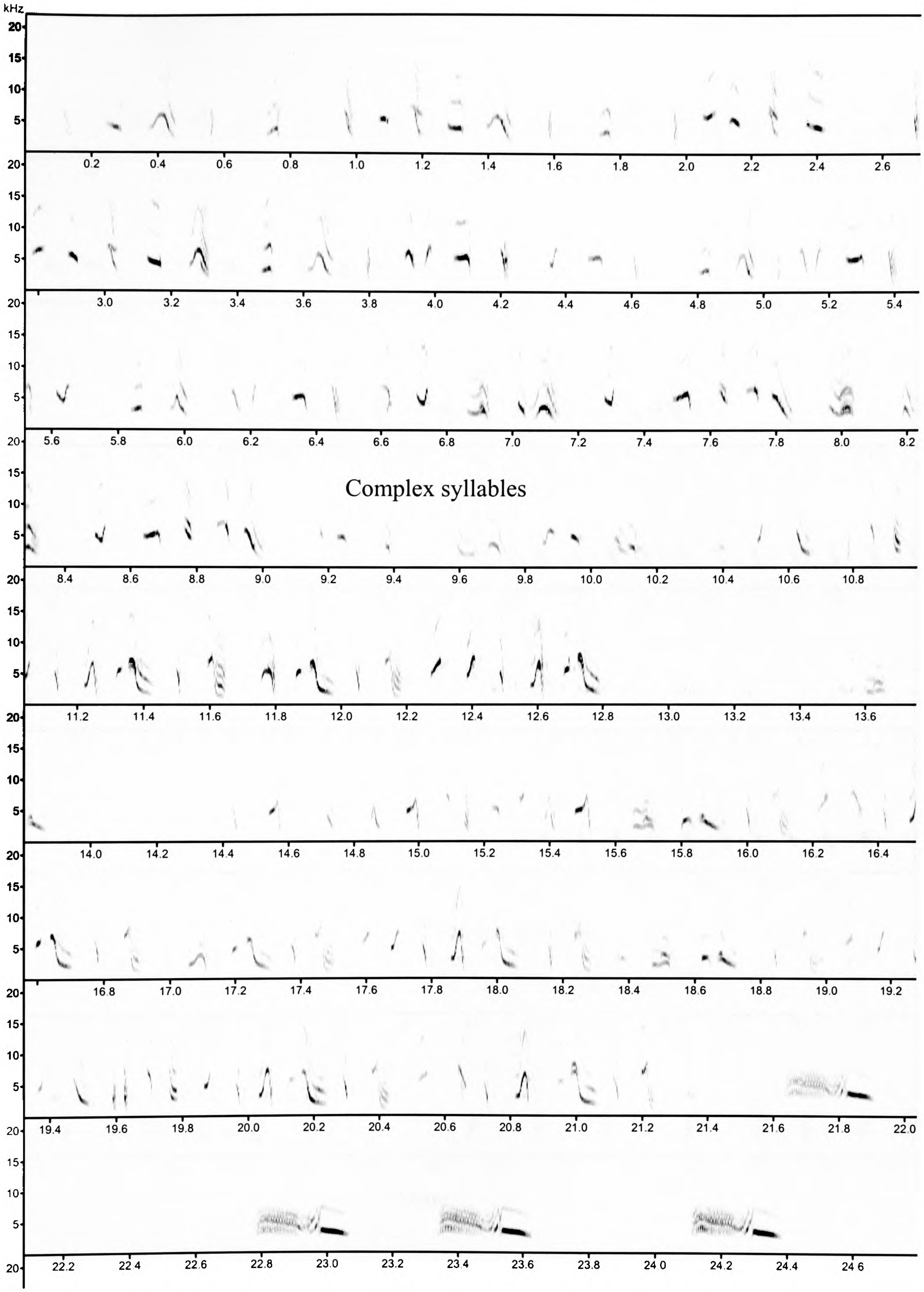
Appendix 4. 203 - Sonogram showing a complex song



Amani Sunbird *Anthodiaeta pallidigaster* recorded in the Usambara Mountains, Tanzania, by L. Keith.

Appendix 4. 218 - Sonogram showing a complex song

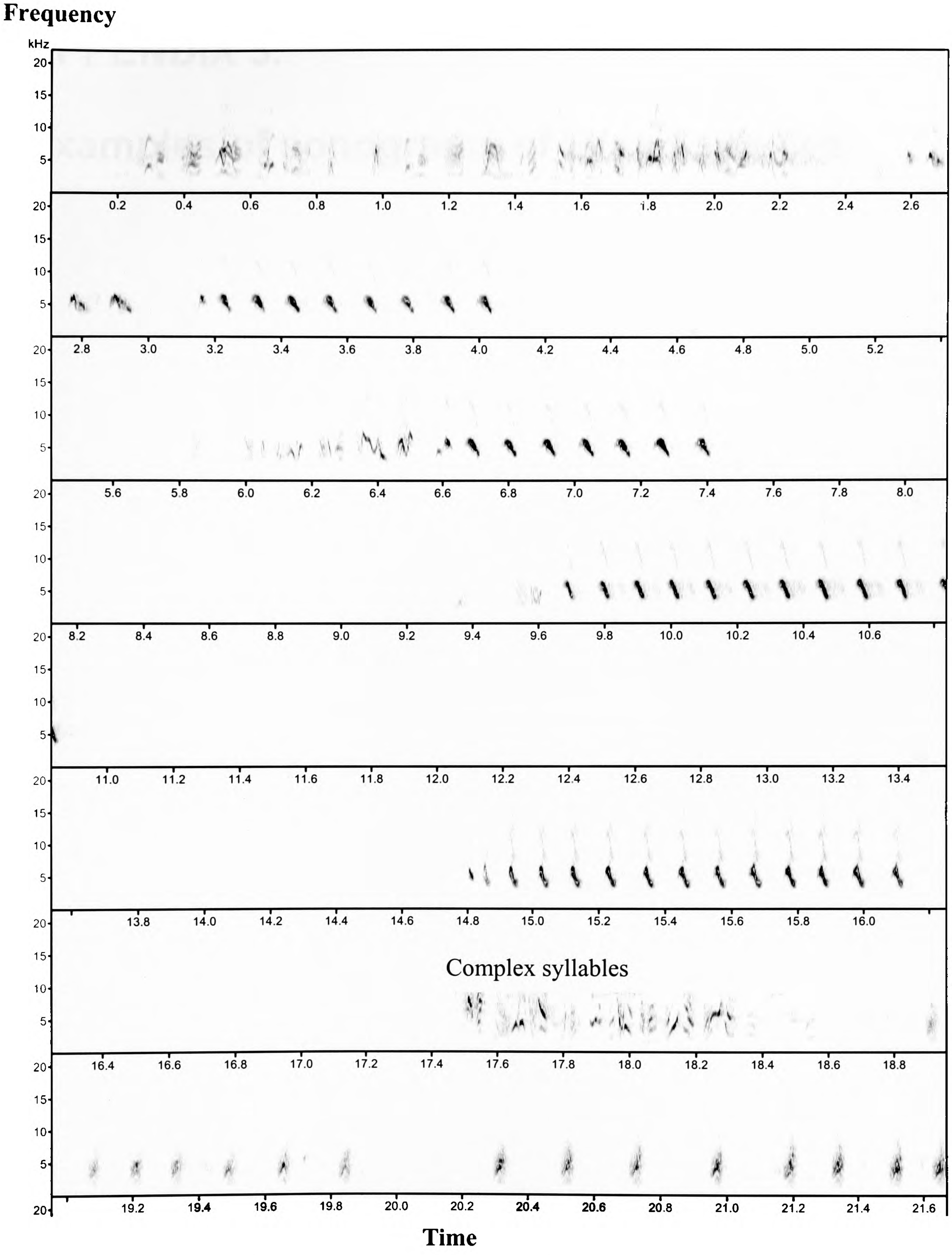
Frequency



Time

Bronze Sunbird *Nectarinia kilimensis kilimensis* recorded in Kericho, West Kenya, by C. Chappuis.

Appendix 4. 225- Sonogram showing a complex song

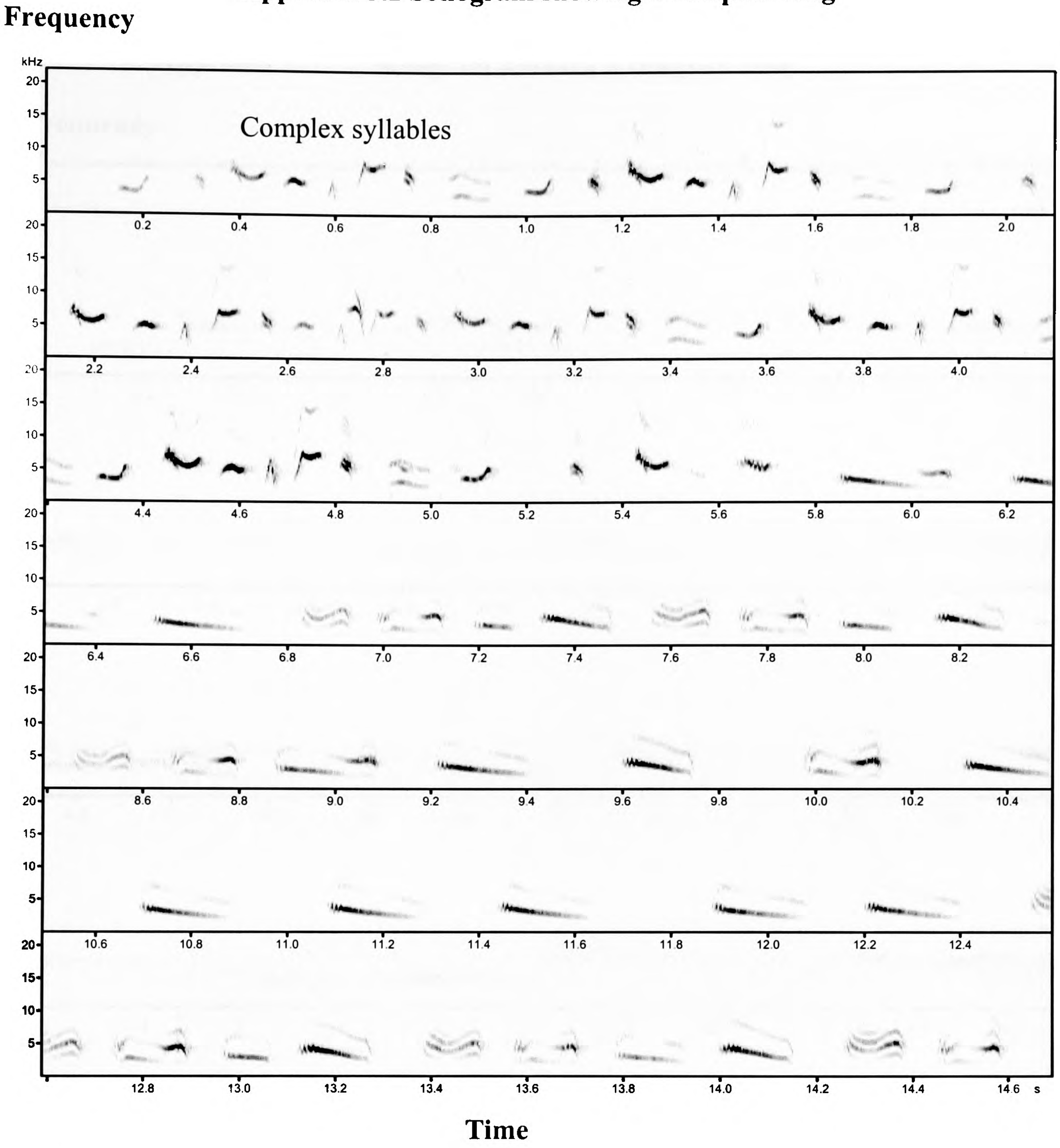


Golden-winged Sunbird *Drepanorhynchus reichenowi reichenowi* recorded on Mt Kenya, Central Kenya by C. Chappuis.

APPENDIX 5.

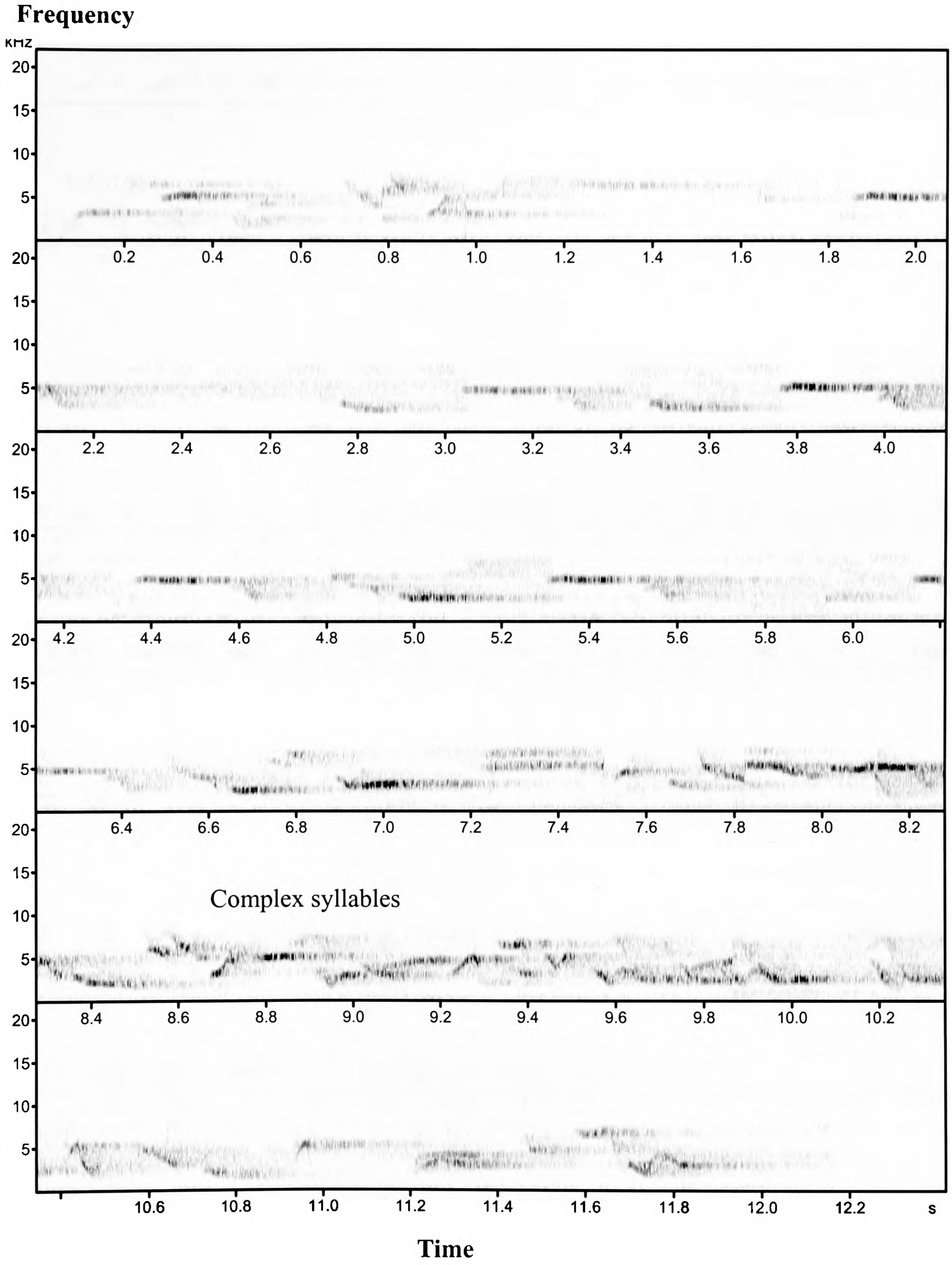
Examples of sonograms of island species

Appendix 5.2 Sonogram showing a complex song



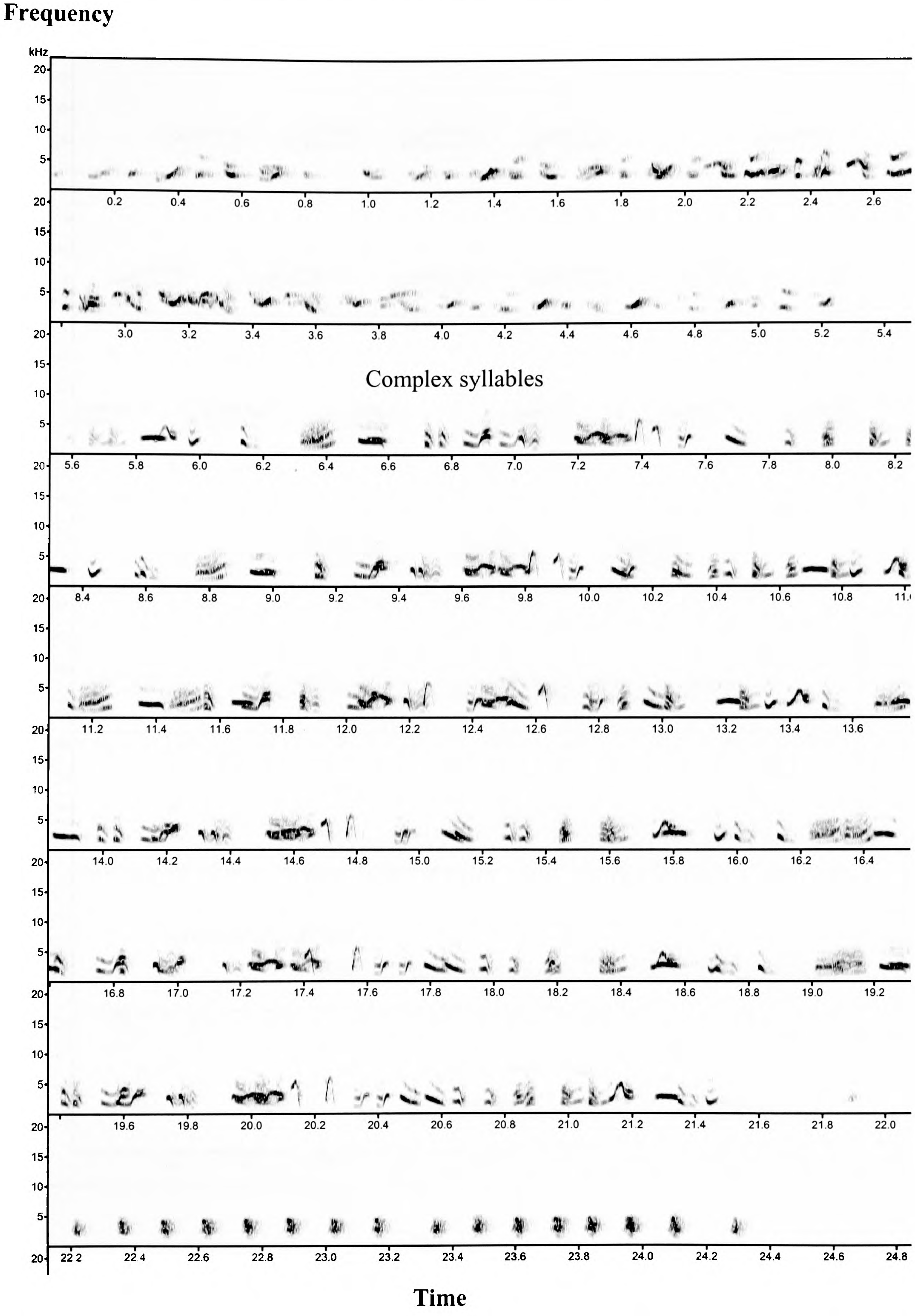
Principe Sunbird *Anabathmis hartlaubii* recorded on Principe by C. Chappuis.

Appendix 5. 11 – Sonogram showing a complex song



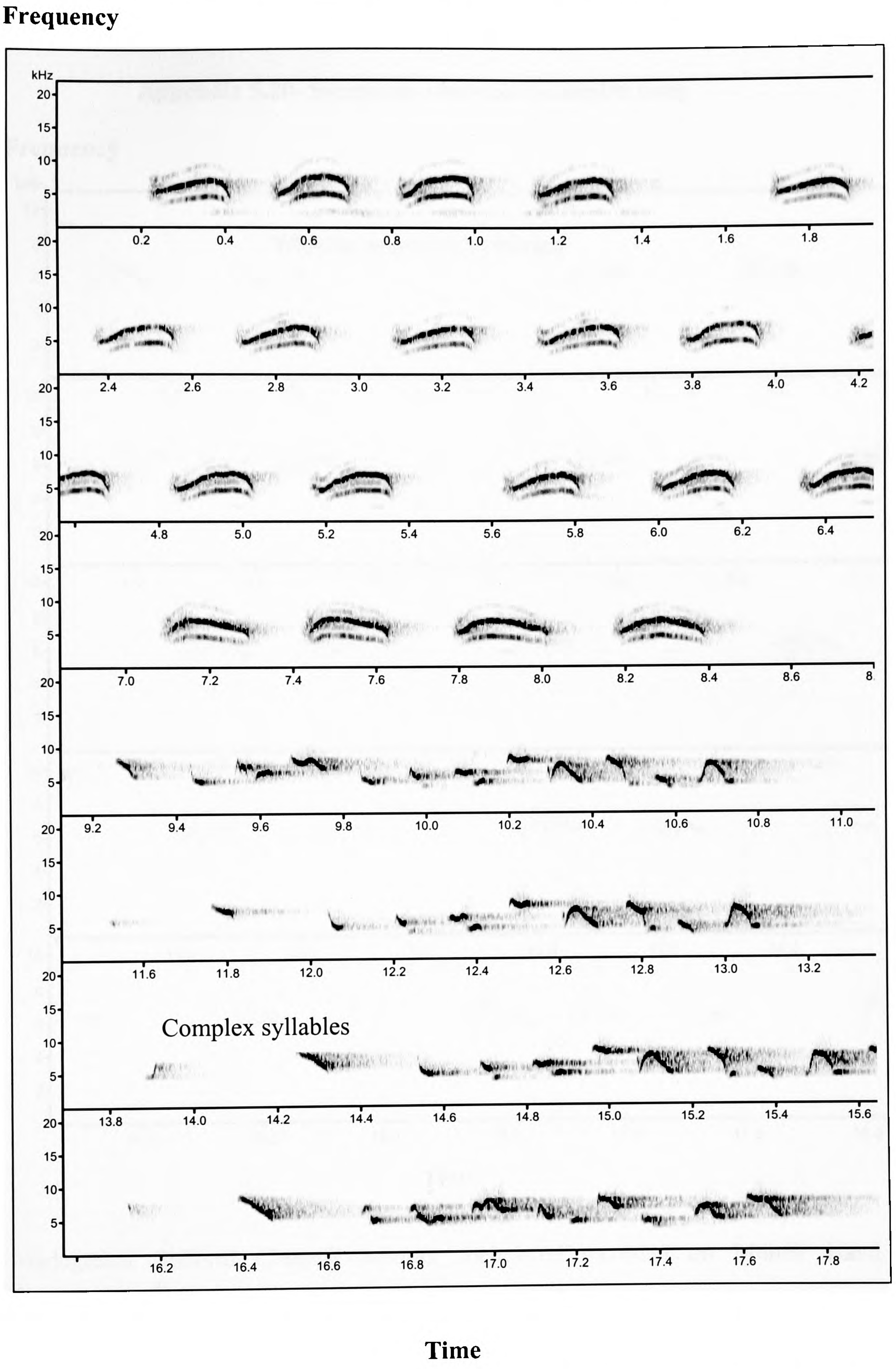
Sao Tome Sunbird *Dreptes thomensis* recorded on Sao Tome by C. Chappuis.

Appendix 5. 14 - Sonogram showing a complex song



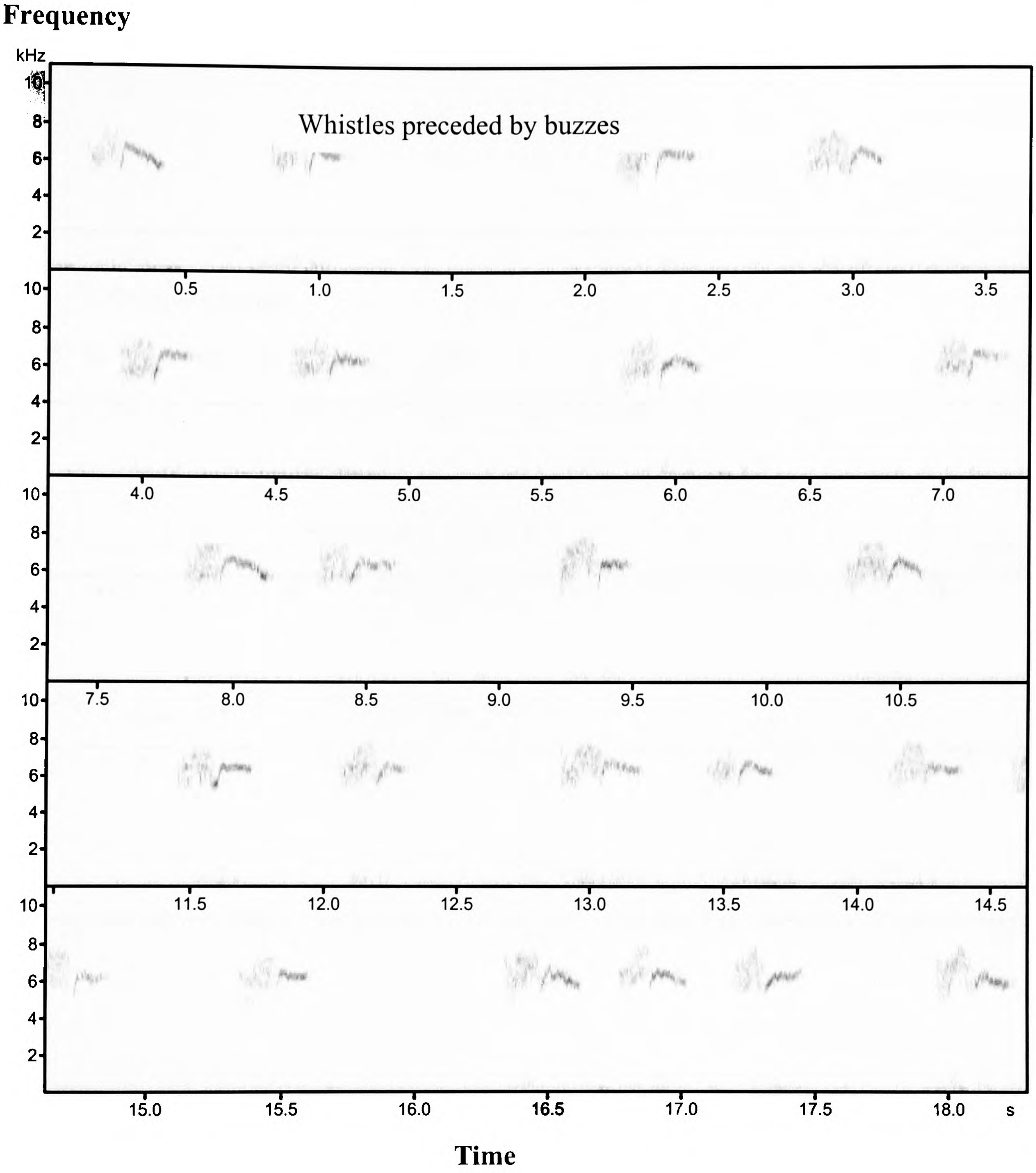
Seychelles Sunbird *Cinnyris dussumieri* recorded on Grand Comoro island, Seychelles, by H. G. La Convalescence.

Appendix 5. 17 - Sonogram showing a complex song



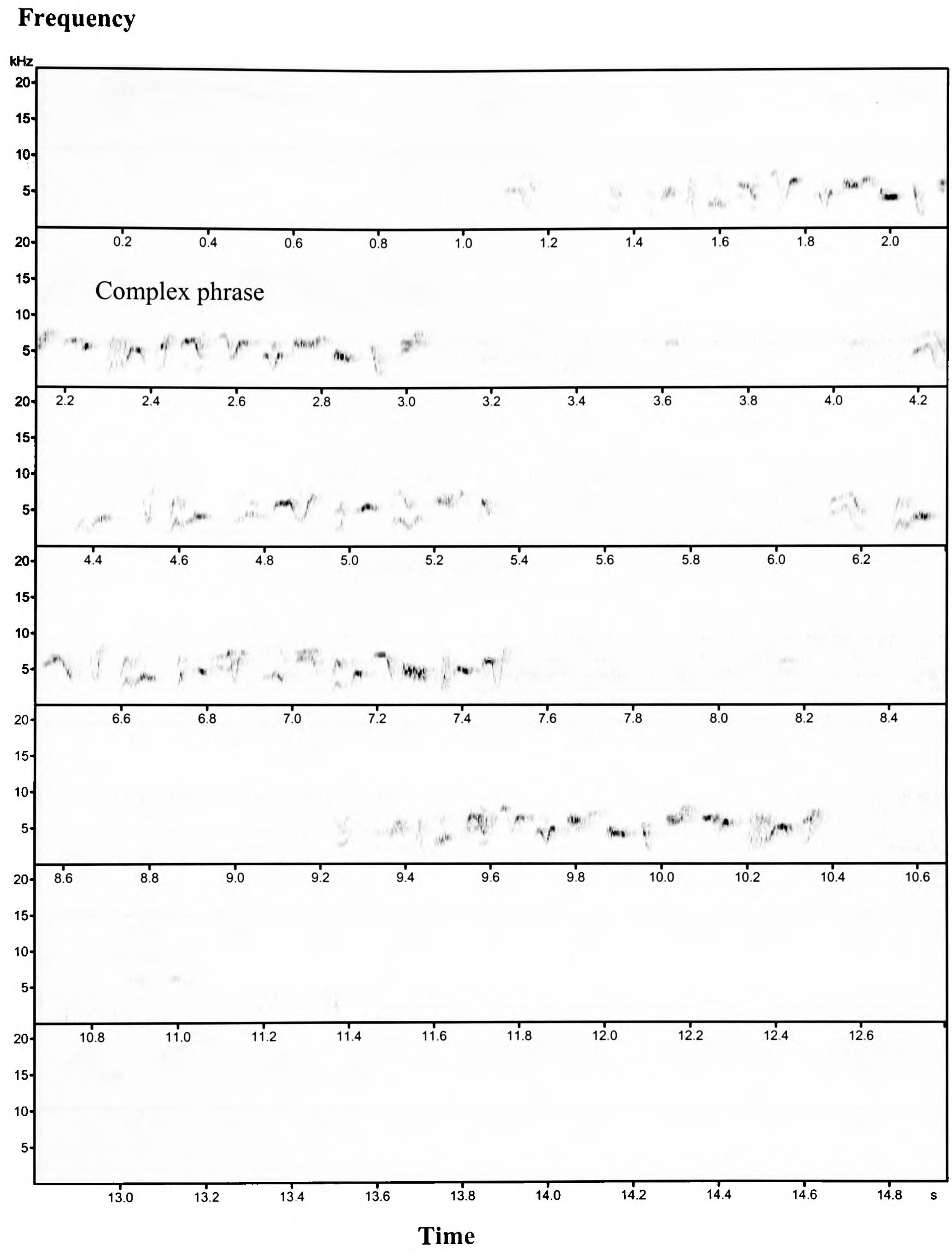
Madagascar Sunbird *Cinnyris notatus moebii* recorded in the Comoro Islands by H. G. La Convalescence.

Appendix 5.20- Sonogram showing a complex song



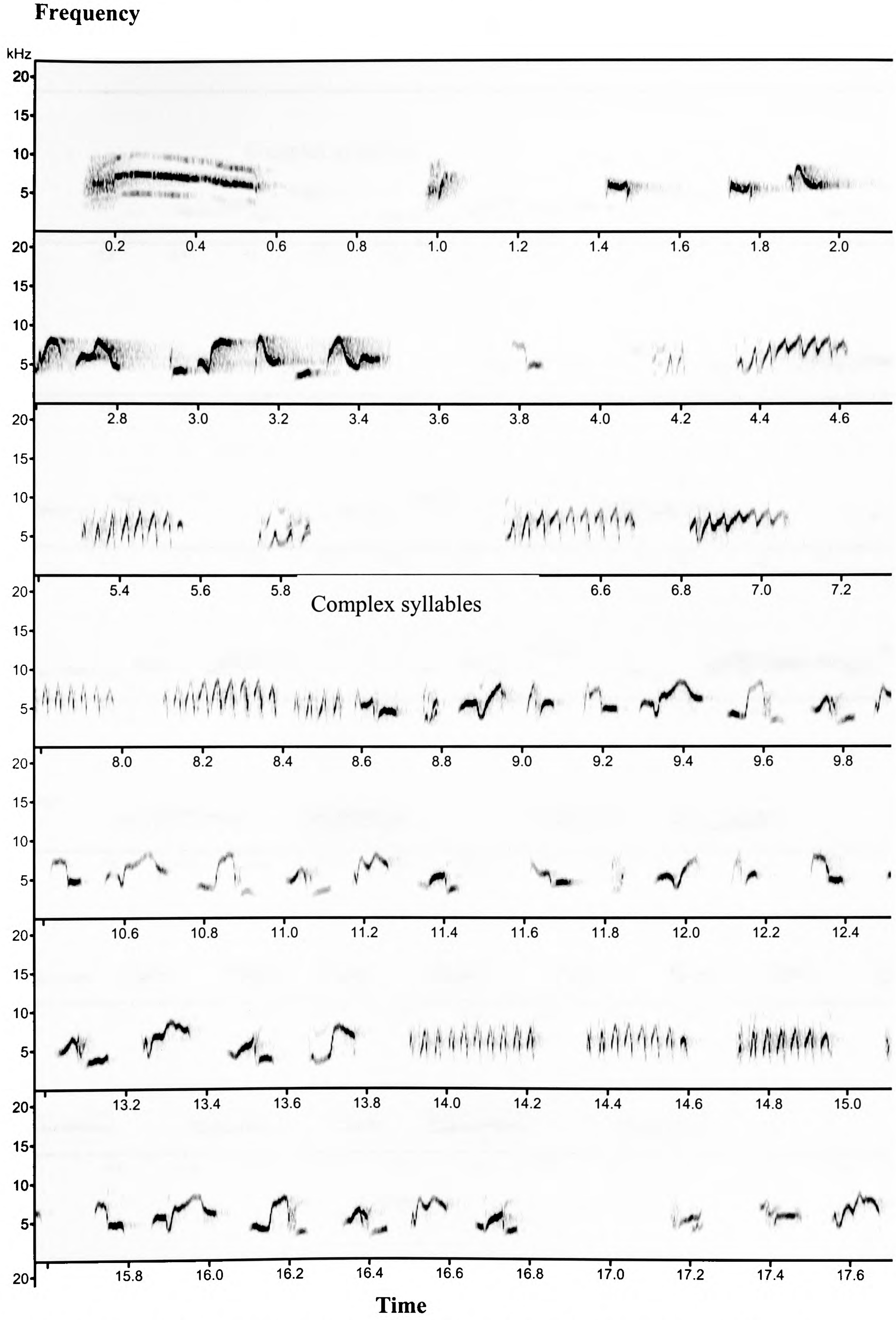
Madagascar Sunbird *Cinnyris notatus voeltzkowi* recorded on Moheli Isand, Comoros, by F. Dowsett-Lemaire.

Appendix 5. 25 - Sonogram showing a complex song



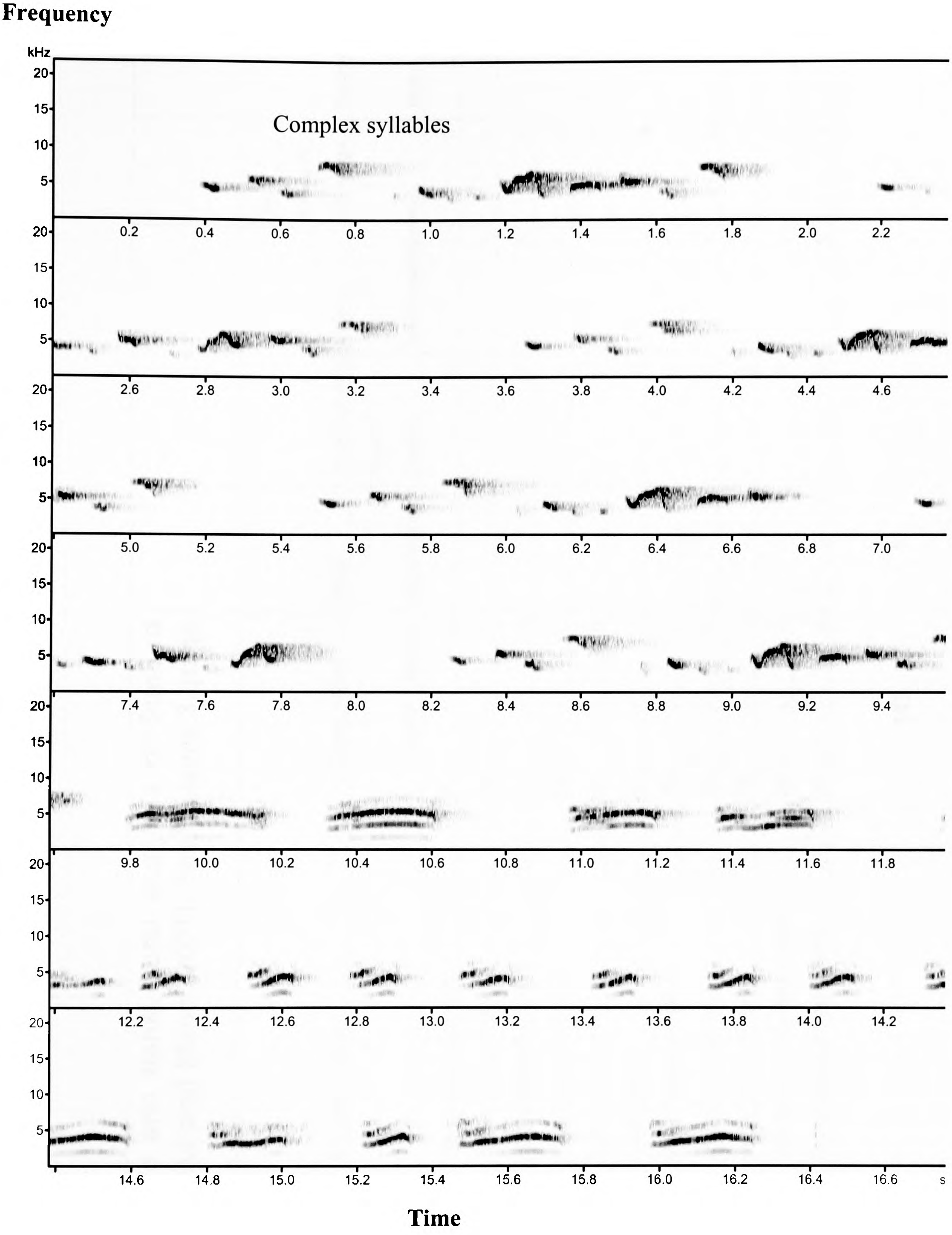
Souimanga Sunbird *Cinnyris souimanga souimanga* recorded in Marojejy, Madagascar, by F. Hawkins.

Appendix 5. 29 Sonogram showing a complex song



Humblot's Sunbird *Cinnyris humbloti humbloti* recorded in the Comoro Islands by H. G. La Convalescence.

Appendix 5. 30 - Sonogram showing a complex song



Mayotte Sunbird *Cinnyris conquerellii* recorded in Mayotte by S. Harrap.

APPENDIX 6 Taxonomic and behavioural analyses of Sunbird data extracted from Cheke and Mann (2001). See chapter 3, page 57 for explanation.

Ref.no.	Scientific name	Common name	Sp.n.	Nest shape		Nest	Plumage differences		Non-breeding Plumage.	Pectoral tufts	
				Porch	Beard	Suspension	Sexes similar	Male brighter/+col.		Male	Female
1	*Chalcoparia singalensis*	Ruby-cheeked Sunbird	47	1	0	1	0	1	0	0	0
2	*Deleornis fraseri*	Scarlet-tufted Sunbird	48	0	0	0	1	0	0	1	0
3	*Deleornis axillaris*	Grey-headed Sunbird	49	0	0	0	1	0	0	1	0
4	*Anthreptes reichenowi*	Plain-backed Sunbird	**50**	1	0	1	0	1	0	1	?
5	*Anthreptes anchietae*	Anchieta's Sunbird	51	0	0	1	0	1	0	1	?
6	*Anthreptes simplex*	Plain Sunbird	52	0	0	1	0	1	0	0	0
7	*Anthreptes malacensis*	Plain-throated Sunbird	53	0	0	1	0	1	0	1	1
8	*Anthreptes rhodolaema*	Red-throated Sunbird	54	0	0	1	0	1	0	0	0
9	*Anthreptes gabonicus*	Mouse-brown Sunbird	55	1	0	1	0	1	0	0	0
10	*Anthreptes longuemarei*	Western Violet-backed Sunbird	56	1	0	1	0	1	0	1	1
11	*Anthreptes orientalis*	Kenya Violet-backed Sunbird	57	1	0	1	0	1	0	0	0

12	*Anthreptes neglectus*	Uluguru Violet-backed Sunbird	58	0	0	1	1	1	0	1	?
13	*Anthreptes aurantium*	Violet-tailed Sunbird	59	1	0	1	1	1	0	1	1
14	*Anthreptes seimundi*	Little Green Sunbird	60	0	0	1	1	0	0	0	0
15	*Anthreptes rectirostris*	Green Sunbird	61	0	0	1	0	1	0	1	?
16	*Anthreptes rubritorques*	Banded Sunbird	62	0	0	1	1	1	0	1	?
17	*Anthodiaeta collaris*	Collared Sunbird	**63**	1	0	1	0	1	0	1	?
18	*Anthodiaeta platura*	Pygmy Sunbird	64	1	0	0	0	1	1	0	?
19	*Anthodiaeta metallica*	Nile Valley Sunbird	65	1	0	0	0	1	1	0	?
20	*Anthodiaeta pallidigaster*	Amani Sunbird	66	1	0	1	0	1	0	1	?
21	*Hypogramma hypogrammicum*	Purple-naped Sunbird	67	0	0	1	1	1	0	0	0
22	*Anabathmis reichenbachii*	Reichenbach's Sunbird	**68**	1	0	1	1	0	0	1	1
23	*Anabathmis hartlaubii*	Principe Sunbird	69	1	0	1	1	1	0	0	0
24	*Anabathmis newtoni*	Newton's Sunbird	70	1	1	1	1	1	0	0	0
25	*Dreptes thomensis*	Sao Tomé Sunbird	**71**	1	1	1	1	0	0	0	0
26	*Anthobaphes violacea*	Orange-breasted Sunbird	72	0	0	0	0	1	0	1	?
27	*Cyanomitra verticalis*	Green-headed Sunbird	**73**	0	0	1	0	1	0	1	0
28	*Cyanomitra bannermani*	Banneman's Sunbird	74	1	0	1	0	1	0	1	?
29	*Cyanomitra cyanolaema*	Blue-throated Brown Sunbird	75	1	0	1	0	1	0	1	?
30	*Cyanomitra oritis*	Cameroon Sunbird	76	1	0	1	1	1	0	1	0
31	*Cyanomitra alinae*	Blue-headed Sunbird	77	0	0	1	1	1	0	1	0
32	*Cyanomitra olivacea*	Eastern Olive Sunbird	78	1	1	1	1	0	0	1	1

33	*Cyanomitra obscura*	Western Olive Sunbird	79	1	0	1	1	1	0	1	0
34	*Cyanomitra veroxii*	Mouse-coloured Sunbird	80	1	1	1	1	1	0	1	1
35	*Chalcomitra adelberti*	Buff-throated Sunbird	**81**	1	0	1	0	1	0	0	0
36	*Chalcomitra fuliginosa*	Carmelite Sunbird	82	1	1	1	0	1	0	1	?
37	*Chalcomitra rubescens*	Green-throated Sunbird	83	1	0	1	0	1	1	0	0
38	*Chalcomitra amethystina*	Amethyst Sunbird	84	1	0	1	0	1	?	1	1
39	*Chalcomitra senegalensis*	Scarlet-chested Sunbird	85	1	0	1	0	1	0	?	?
40	*Chalcomitra hunteri*	Hunter's Sunbird	86	1	1	1	0	1	0	?	?
41	*Chalcomitra balfouri*	Socotra Sunbird	87	0	0	1	1	0	0	1	0
42	*Leptocoma zeylonica*	Purple-rumped Sunbird	**88**	1	0	1	0	1	0	0	0
43	*Leptocoma minima*	Crimson-backed Sunbird	89	1	0	1	0	1	1	1	?
44	*Leptocoma sperata*	Purple-throated Sunbird	90	?	?	1	0	1	0	0	0
45	*Leptocoma sericea*	Black Sunbird	91	1	0	1	0	1	0	0	0
46	*Leptocoma calcostetha*	Copper-throated Sunbird	92	0	0	1	0	1	0	1	1
47	*Nectarinia bocagei*	Bocage's Sunbird	**93**	0	0	0	0	1	1	?	?
48	*Nectarinia purpureiventris*	Purple-breasted Sunbird	94	1	1	1	0	1	1	?	?
49	*Nectarinia tacazze*	Tacazze Sunbird	95	0	1	1	0	1	1	?	?
50	*Nectarinia kilimensis*	Bronze Sunbird	96	1	0	1	0	1	0	?	?
51	*Nectarinia famosa*	Malachite Sunbird	97	1	0	0	0	1	1	1	?
52	*Nectarinia johnstoni*	Red-tufted Sunbird	98	0	0	1	0	1	1	1	1
53	*Drepanorhynchus reichenowi*	Golden-winged Sunbird	99	1	0	1	0	1	1	0	0

54	*Cinnyris chloropygius*	Olive-bellied Sunbird	**100**	1	1	1	0	1	0	1	?
55	*Cinnyris minullus*	Tiny Sunbird	101	1	0	1	0	1	0	1	?
56	*Cinnyris manoensis*	Miombo Double-collared Sunbird	102	0	0	1	0	1	0	1	?
57	*Cinnyris chalybeus*	Southern Double-collared Sunbird	103	1	0	1	0	1	1	1	?
58	*Cinnyris neergaardi*	Neergaard's Sunbird	104	0	0	1	0	1	0	1	?
59	*Cinnyris stuhlmanni*	Stuhlmann's Double-collared Sunbird	105	1	0	1	0	1	1	1	?
60	*Cinnyris prigoginei*	Prigogine's Double-collared Sunbird	106	0	0	0	0	1	1	1	?
61	*Cinnyris ludovicensis*	Montane Double-collared Sunbird	107	0	0	1	0	1	0	1	?
62	*Cinnyris reichenowi (preussi)*	Northern Double-collared Sunbird	108	1	0	1	0	1	0	1	?
63	*Cinnyris afer*	Greater Double-collared Sunbird	109	1	0	1	0	1	0	?	?
64	*Cinnyris regius*	Regal Sunbird	110	0	0	1	0	1	0	0	0
65	*Cinnyris rockefelleri*	Rockefeller's Sunbird	111	0	0	0	0	1	0	1	1
66	*Cinnyris mediocris*	Eastern Double-collared Sunbird	112	1	0	1	0	1	0	1	?
67	*Cinnyris moreaui*	Moreau's Sunbird	113	0	0	1	0	1	0	1	?
68	*Cinnyris loveridgei*	Loveridge's Sunbird	114	1	0	1	0	1	0	1	?
69	*Cinnyris pulchellus*	Beautiful Sunbird	115	1?.	1?.	1	0	1	1	?	?
70	*Cinnyris mariquensis*	Mariqua Sunbird	**116**	1	0	1	0	1	0	?	?
71	*Cinnyris shelleyi*	Shelley's Sunbird	117	0	0	1	0	1	1	?	?
72	*Cinnyris congensis*	Congo Sunbird	118	?	?	1	0	1	0	?	?
73	*Cinnyris erythroceria*	Red-chested Sunbird	119	1?.	0	1	0	1	0	?	?

74	*Cinnyris nectarinoides*	Black-bellied Sunbird	120	1	1	0	0	1	1	1	?
75	*Cinnyris bifasciatus*	Purple-banded Sunbird	121	0	1	1	0	1	1	?	?
76	*Cinnyris tsavoensis*	Tsavo Purple-banded Sunbird	122	0	1	1	0	1	0	?	?
77	*Cinnyris chalcomelas*	Kenya Violet-breasted Sunbird	123	0	0	0	0	1	1	?	?
78	*Cinnyris pembae*	Pemba Sunbird	124	0	0	1	0	1	0	?	?
79	*Cinnyris bouvieri*	Orange-tufted Sunbird	125	0	0	1	0	1	0	1	?
80	*Cinnyris osea*	Palestine Sunbird	126	1	1	1	0	1	1	1	?
81	*Cinnyris habessinicus*	Shining Sunbird	127	1	0	1	0	1	0	1	?
82	*Cinnyris coccinigaster*	Splendid Sunbird	**128**	1	0	1	0	1	0	1	?
83	*Cinnyris johannae*	Johanna's Sunbird	129	0	1	1	0	1	0	1	?
84	*Cinnyris superbus*	Superb Sunbird	130	1	1	1	0	1	0	0	0
85	*Cinnyris rufipennis*	Rufous-winged Sunbird	131	?	?	1	0	1	1	1	?
86	*Cinnyris oustaleti*	Oustalet's Sunbird	**132**	?	?	0	0	1	1	1	?
87	*Cinnyris talatala*	White-breasted Sunbird	133	1?.	0	1	0	1	1	1	?
88	*Cinnyris venustus*	Variable Sunbird	134	0	1	1	0	1	1	1	?
89	*Cinnyris fuscus*	Dusky Sunbird	135	0	0	1	0	1	1	1	?
90	*Cinnyris ursulae*	Ursula's Sunbird	**136**	1	0	0	0	1	0	1	1
91	*Cinnyris batesi*	Bates's Sunbird	137	0	0	1	0	1	0	1	1
92	*Cinnyris cupreus*	Copper Sunbird	**138**	1	1	1	0	1	1	0	0
93	*Cinnyris asiaticus*	Purple Sunbird	139	1	0	1	0	1	1	1	?
94	*Cinnyris jugularis*	Olive-backed Sunbird	140	0	1	1	0	1	1	1	?
95	*Cinnyris buettikoferi*	Apricot-breasted Sunbird	141	0	0	0	0	1	0	1	?

96	*Cinnyris solaris*	Flame-breasted Sunbird	142	?	?	?	0	1	0	1	?
97	*Cinnyris souimanga*	Souimanga Sunbird	143	1	0	1	0	1	1	1	?
98	*Cinnyris notatus*	Madagascar Sunbird	144	1	0	1	0	1	1	0	0
99	*Cinnyris dussumieri*	Seychelles Sunbird	145	1	0	1	0	1	0	1	0
100	*Cinnyris humbloti*	Humblot's Sunbird	146	0	0	1	0	1	0	1	0
101	*Cinnyris comorensis*	Anjouan Sunbird	147	0	0	1	0	1	0	1	?
102	*Cinnyris coquerelii*	Mayotte Sunbird	148	0	0	1	0	1	0	1	?
103	*Cinnyris lotenius*	Long-billed Sunbird	149	1	0	1	0	1	1	1	?
104	*Aethopyga primigenius*	Grey-hooded Sunbird	**150**	0	0	0	0	1	0	0	0
105	*Aethopyga boltoni*	Apo Sunbird	151	0	0	1	0	1	0	1	?
106	*Aethopyga linaraborae*	Lina's Sunbird	152	0	0	0	0	1	0	1	0
107	*Aethopyga flagrans*	Flaming Sunbird	153	0	0	0	0	1	0	?	?
108	*Aethopyga pulcherrima*	Metallic-winged Sunbird	154	0	0	1	0	1	0	?	?
109	*Aethopyga duyvenbodei*	Elegant Sunbird	155	0	0	0	0	1	0	?	?
110	*Aethopyga shelleyi*	Lovely Sunbird	156	0	1	1	0	1	0	?	?
111	*Aethopyga gouldiae*	Gould's Sunbird	157	0	0	1	0	1	0	?	?
112	*Aethopyga nipalensis*	Green-tailed Sunbird	158	0	0	1	0	1	0	?	?
113	*Aethopyga eximia*	White-flanked Sunbird	159	0	0	0	0	1	0	1	1
114	*Aethopyga christinae*	Fork-tailed Sunbird	160	0	0	1	0	1	0	?	?
115	*Aethopyga saturata*	Black-throated Sunbird	161	1	0	1	0	1	0	?	?
116	*Aethopyga vigorsii*	Western Crimson Sunbird	162	1	0	1	0	1	0	?	?
117	*Aethopyga siparaja*	Crimson Sunbird	163	1	0	1	0	1	1	?	?

118	*Aethopyga mystacalis*	Javan Sunbird (Scarlet Sunbird)	164	0	0	0	0	1	0	?	?
119	*Aethopyga temmincki*	Temminck's Sunbird	165	1	0	1	0	1	0	?	?
120	*Aethopyga ignicauda*	Fire-tailed Sunbird	166	0	0	1	0	1	1	?	?
121	*Arachnothera longirostra*	Little Spiderhunter	**167**	0	0	1	1	0	0	1	0
122	*Arachnothera crassirostris*	Thick-billed Spiderhunter	168	0	0	?	1	0	0	1	0
123	*Arachnothera robusta*	Long-billed Spiderhunter	169	0	0	1	1	0	0	1	0
124	*Arachnothera flavigaster*	Spectacled Spiderhunter	170	0	0	1	1	0	0	0	0
125	*Arachnothera chrysogenys*	Yellow-eared Spiderhunter	171	0	0	1	1	0	0	1	0
126	*Arachnothera clarae*	Naked-faced Spiderhunter	172	0	0	?	1	0	0	0	0
127	*Arachnothera modesta (affinis)*	Grey-breasted Spiderhunter	173	0	0	?	1	0	0	0	0
128	*Arachnothera affinis*	Streaky-breasted Spiderhunter	174	0	0	1	1	0	0	0	0
129	*Arachnothera magna*	Streaked Spiderhunter	175	0	0	1	1	0	0	0	0
130	*Arachnothera juliae*	Whitehead's Spiderhunter	176	0	0	?	1	0	0	0	0
		* 0 Unknown.									
		* 1 Described and or present.									
		*1? Unconfrimed									
		*? Undescribed, no information & no records									

APPENDIX 7 Habitat analyses for Flowerpeckers as described in chapter 3, page 56.

	Common name	Coastal Mangrove	Scrub land	Bushes Grasses	Wood land	Woodland Savanna	Gallery forest	Secondary growth	Secondary forest	Primary forest	Montane Forest	Forest edge	Upland moorlands
1	Olive-backed Flowerpecker	0	0	0	0	0	0	1	0	1	0	1	0
2	Yellow-breasted Flowerpecker	0	1	0	0	0	0	0	1	1	0	1	0
3	Crimson-breasted Flowerpecker	1	1	0	0	0	0	1	1	1	1	0	0
4	Yellow-rumped Flowerpecker	0	0	0	0	0	0	0	1	1	0	1	0
5	Scarlet-breasted Flowerpecker	0	0	0	0	0	0	0	1	1	0	1	0
6	Golden-rumped Flowerpecker	0	0	0	1	0	0	0	0	1	0	0	0

7	Thick-billed Flowerpecker	1?	0	0	1	0	1?	1	0	1	0	1	0
8	Whiskered Flowerpecker	0	0	0	0	0	0	1	0	1	0	1	0
9	White-throated Flowerpecker	0	0	0	0	0	0	0	0	1	0	0	0
10	Olive-capped Flowerpecker	0	0	0	0	0	0	0	0	1	0	0	0
11	Bicolored Flowerpecker	0	0	0	0	0	0	1	0	1	0	1	0
12	Cebu Flowerpecker	0	0	0	0	0	0	0	0	1	0	0	0
13	Red-striped Flowerpecker	0	0	0	0	0	0	0	0	1	0	1	0
14	Scarlet-collared Flowerpecker	0	0	0	0	0	0	0	0	1	0	1	0
15	Orange-bellied Flowerpecker	1	1	0	0	0	0	1	0	1	1	1	0
16	Buzzing Flowerpecker	0	0	0	0	0	0	0	0	1	0	1	0

17	Pale-billed Flowerpecker	1	0	0	0	0	0	0	0	1	0	1	0
18	Plain Flowerpecker	0	0	0	0	0	0	1	0	1	1	1	0
19	Pygmy Flowerpecker	0	0	0	0	0	0	1	0	1	0	1	0
20	Crimson-crowned Flowerpecker	1	0	0	0	0	0	0	0	0	1	1	0
21	Ashy Flowerpecker	1	0	0	0	0	0	0	0	1	0	1	0
22	Olive-crowned Flowerpecker	0	0	0	0	0	0	1	0	1	0	0	0
23	Red-banded Flowerpecker	0	0	0	0	1	0	1	0	1	0	1	0
24	Midget Flowerpecker	1?	1?	1?	1?	1?	1?	1?	1?	1?	1?	1?	1?
25	Mottled Flowerpecker	0	0	0	0	0	0	1	0	1	1	1	0
26	Black-fronted Flowerpecker	1	1	0	1	0	0	0	1	1	0	0	0

27	Red-chested Flowerpecker	0	0	0	1	0	0	0	1	1	0	0	0
28	Fire-breasted Flowerpecker	0	0	0	0	0	0	1	0	1	1	0	0
29	Black-sided Flowerpecker	0	0	0	0	0	0	0	0	0	1	0	0
30	Grey-sided Flowerpecker	0	1	0	0	0	0	0	1	1	1	1	0
31	Blood-breasted Flowerpecker	0	0	0	1	0	0	0	1	1	1	0	0
32	Mistletoebird	1	1	1	1	1	1	1	0	1	1?	1	0
33	Scarlet-backed Flowerpecker	0	0	0	0	0	0	1	0	1	0	1	0
34	Scarlet-headed Flowerpecker	1	0	1	1	0	0	0	0	0	0	0	0
	* 0 Unknown												
	*1 Descried or present												
	* 1? unsure												
	*? Undescrbed												

APPENDIX 8 Habitat analyses for Sunbirds and Spiderhunters as described in chapter 3, page 58.

Ref.no.	Species Name	Coastal mangrove	Scrub land	Bushes/ Grass lands	Wood lands	Savannah	Gallery forest	Secondary growth	Secondary forest	Primary forest	Montane Forest	Forest edge	Upland moorlands
1	Ruby-cheeked Sunbird	1	1	0	0	0	1	0	1	1	0	1	0
2	Scarlet-tufted Sunbird	0	0	0	0	0	1	0	1	1	0	1	0
3	Grey-headed Sunbird	0	0	0	0	0	0	0	1	1	0	1	0
4	Plain-backed Sunbird	0	0	1	0	1	1	0 1?		1	0	1	0
5	Anchieta's Sunbird	-	0	0	1	0	0	0	0	0	0	0	0
6	Plain Sunbird	1	1	0	0	0	0		1	1	0	0	0
7	Plain-throated Sunbird	1	1	0	1	0	1	0	0	1	0	1	0
8	Red-throated Sunbird	1	0	0	0	0	0	0	0	1	0	0	0

9 Mouse-brown Sunbird	1	0	0	0	1	1	0	0	0	0	0	0
10 Western Violet-backed Sunbird	1	1	0	1	1	1	0	0	0	0	0	0
11 Kenya Violet-backed Sunbird	0	0	1	1 1?		1	0	0	0	0	0	0
12 Uluguru Violet-backed Sunbird	1	0	1	1	0	1	0	0	1	1	1	0
13 Violet-tailed Sunbird	1	0	0	0	1	1	0	1	1	0	0	0
14 Little Green Sunbird	0	0	1	0	0	1	0	1	1	0	1	0
15 Green Sunbird	0	0	0	0	0	1	0	1	1 1?		0	0
16 Banded Sunbird	0	1		1	0	0	0	0	0	1	0	0
17 Collared Sunbird	1	0	1	0	1	1	0	1	1 1?		1	0

18 Pygmy Sunbird	0	1	0	1	1	0	0	0	0	0	0	0
19 Nile Valley Sunbird	0	1	1	0	0	0	0	0	0	0	0	0
20 Amani Sunbird	1	0	0	0	0	0	1	0	1	1	1	0
21 Purple-naped Sunbird	0	0	0	0	0	1	1	1	1	0	0	0
22 Reichenbach's Sunbird	1	0	0	0	0 1?.		0	0	0	0	1	0
23 Principe Sunbird	1	1	1	1	0	1	1	1	1	0	1 1?	
24 Newton's Sunbird	0	0	0	1	1	0	0	0	0	0	0	0
25 Sao Tomé Sunbird	0	1	0	0	0	0	0	1	0	1	0	0
26 Orange-breasted Sunbird	0	0	0	0	0	0	0	0	0 1?		0	0
27 Green-headed Sunbird	1	0	0	0	1	1	0	1	1	0	0	0
28 Bannerman's Sunbird	0	0	0	1	0	1	0	0	1	0	1	0

29 Blue-throated Brown Sunbird	1	0	0	1	0 1?		0	1	1	0	1	0
30 Cameroon Sunbird	0	0	0	0	0 1?		0	1	1	1	1	0
31 Blue-headed Sunbird	0	0	0	0	0	1	0	1	1	1	0	0
32 Eastern Olive Sunbird	1	0	0	1	0	0	0	1	1	0	0	0
33 Western Olive Sunbird	1	0	1	1	0	1	0	1	1	0	0	0
34 Mouse-coloured Sunbird	1	1	0	1	0	1	0	0	0	1	0	0
35 Buff-throated Sunbird	0	0	0	0	0	0	0	1	1	0	0	0
36 Carmelite Sunbird	1	0	0	0	1	0	0	0	0	0	0	0
37 Green-throated Sunbird	0	0	1	1	1	1	1	0	1	0	1	0
38 Amethyst Sunbird	0	0	0	1	1	1	0	0	0	0	1	0
39 Scarlet-chested Sunbird	1	1	1	1	1	0	0	0	0	0	0	0

40 Hunter's Sunbird		0	0	1	1	0	0	0	0	0	0	0	0
41 Socotra Sunbird	1?	1?		1	1?	1?	1?	1?	1?	1?	1?	1?	
42 Purple-rumped Sunbird		0	0	0	0	0	0	0	1	1	0	0	0
43 Crimson-backed Sunbird		0	0	0 1?		0	0	0	0	0	0	0	0
44 Purple-throated Sunbird		1	0	0	0	0	1	1	0	1	0	0	0
45 Black Sunbird		1	1	0	1	0	1	0	0	1	0	1	0
46 Copper-throated Sunbird		1	0	0	0	0	0	0	1	0	0	0	0
47 Bocage's Sunbird		0	0	0	1	0	0	0	0	0	0	1	0
48 Purple-breasted Sunbird		0	0	0	0	0	1	0	0	0	1	1	0
49 Tacazze Sunbird		0	0	1	0	0	0	0	0	1 1?		1	0
50 Bronze Sunbird		0	1	1	0	0	0	1	0	0	0	1	0

51 Malachite Sunbird	0	1	1	0	0	0	0	0	0	0	1	1
52 Red-tufted Sunbird	0	0	1	0	0	0	0	0	0	0	0	1
53 Golden-winged Sunbird	0	0	1	0	0	0	0	0	0	0	1	0
54 Olive-bellied Sunbird	1	1	0	0	1	1	0	1	1	1	1	0
55 Tiny Sunbird	0	0	0	0	1	0	0	1	1	0	1	0
56 Miombo Double-collared Sunbird	0	0	0	1	1	0	0	0	0	0	0	0
57 Southern Double-collared Sunbird	1	0	1	0	0	0	0	0	0	1	1	0
58 Neergaard's Sunbird	1	1	1	1	0	0	0	0	0	0	0	0
59 Stuhlmann's Double-collared Sunbird	0	0	0	0	0	0	0	0	0	1	1	0

60 Prigogine's Double-collared Sunbird	0	0	0	0	0	1	0	0	0 1?		0	0
61 Montane Double-collared Sunbird	0	1	1	0	0	1	1	0	0	1	1	0
62 Northern Double-collared Sunbird	0	0	0	0	0	1	0	1	0	1	1	0
63 Greater Double-collared Sunbird	1	1	0	1	0	0	0	0	0	0	1	0
64 Regal Sunbird	0	1	0	0	0	0	1	0	1	1	0	0
65 Rockefeller's Sunbird	0	0	1	0	0 1?		0	0	0	0	0	0
66 Eastern Double-collared Sunbird	0	0	1	0	0	0	0	0	0	1	0	0
67 Moreau's Sunbird	0	0	1	0	0	0	0	0	0	1	0	0
68 Loveridge's Sunbird	0	0	1	0	0	0	0	0	0	1	0	0

69 Beautiful Sunbird	0	0	1	0	1 1?.		0	0	0	0	0	0
70 Mariqua Sunbird	0	1	1	1	1	0	0	0	0	0	0	0
71 Shelley's Sunbird	0	1	0	1	0	0	0	0	0	0	0	0
72 Congo Sunbird	0	0	0	0	0	1	0	0	0	0	0	0
73 Red-chested Sunbird	0	0	1	0	1 1?		0	0	1	0	0	0
74 Black-bellied Sunbird	0	0	0	0	1 1?		0	0	0	0	0	0
75 Purple-banded Sunbird	1	0	1	1	1	1	0	0	1	0	0	0
76 Tsavo Purple-banded Sunbird	0	0	0	1	1 1?		0	0	0	0	0	0
77 Kenya Violet-breasted Sunbird	1	0	0	0	1	0	0	0	0	0	0	0
78 Pemba Sunbird	1	1	0	0	0	0	0	0	1	0	0	0

79 Orange-tufted Sunbird	0	1	1	1	1	0	0	0	0	0	1	0
80 Palestine Sunbird	0	0	1	0	1 1?		0	0	0	0	0	0
81 Shining Sunbird	0	0	1	0	0	0	0	0	0	1	0	0
82 Splendid Sunbird	1	1	0	0	1 1?		0	1	0	0	1	0
83 Johanna's Sunbird	0	0	0	0	0	0	0	1	1	0	0	0
84 Superb Sunbird	1	0	1	1	1	1	0	1	1	0	1	0
85 Rufous-winged Sunbird	0	0	0	0	0	0	0	0	0	1	1	0
86 Oustalet's Sunbird	0	1	0	1	0	0	1	0	0	0	0	0
87 White-breasted Sunbird	0	0	0	1	1	1	0	0	0	0	0	0
88 Variable Sunbird	1	1	1	1	1	1	0	0	1	0	1	0
89 Dusky Sunbird	1	1	1	0	0 1?		0	0	0	0	0	0

90 Ursula's Sunbird	0	0	0	0	0	0	0	1	1	0	1	0
91 Bates's Sunbird	0	0	0	0	0	0	1	0	1	0	1	0
92 Copper Sunbird	1	0	0	1	1 1?		0	0	0	0	0	0
93 Purple Sunbird	0	1	0	0	0	0	0	0	1	0	0	0
94 Olive-backed Sunbird	1	1	0	1	0	1	1	0	1	0	1	0
95 Apricot-breasted Sunbird	0	1	0	0	0	0	1	1	0	0	1	0
96 Flame-breasted Sunbird	0	1	1	1	0	0	0	1	0	0	1	0
97 Souimanga Sunbird	1	0	0	0	0	0	1	0	1	0	0	0
98 Madagascar Sunbird	1	0	0	1	0	0	0	1	1	0	0	0
99 Seychelles Sunbird	1	0	0	0	0	0	1	1	1	0	0	0
100 Humblot's Sunbird	0	1	0	0	0	0	0	0	1	0	0	0

101 Anjouan Sunbird	0	0	1	0	0	0	0	0	1	0	0	0
102 Mayotte Sunbird	0	0	1	0	0	0	0	0	0	0	1	0
103 Long-billed Sunbird	0	0	1	1	1	0	0	0	1	0	0	0
104 Grey-hooded Sunbird	0	0	0	0	0	0	0	0	1	0	1	0
105 Apo Sunbird	0	0	1	0	0	0	0	0	1	1	0	0
106 Lina's Sunbird	0	0	0	0	0	0	0	0	0	1	0	0
107 Flaming Sunbird	0	0	0	0	0	0	1	0	1	0	1	0
108 Metallic-winged Sunbird	0	0	0	0	0	0	1	0	0	1	1	0
109 Elegant Sunbird	0	1	0	1	0	0	0	0	0	0	0	0
110 Lovely Sunbird	0	1	0	0	0	0	1	0	1	0	1	0
111 Gould's Sunbird	0	1	0	0	0	0	0	0	1	0	0	0

112 Green-tailed Sunbird	0	1	0	1	0	0	0	0	1	0	0	0
113 White-flanked Sunbird	0	1	0	0	0	0	0	0	1	0	1	0
114 Fork-tailed Sunbird	0	0	0	0	0	0	0	0	1	0	1	0
115 Black-throated Sunbird	0	1	1	0	0 1?		1	0	1	0	1	0
116 Western Crimson Sunbird	0	0	1	0	0	0	0	0	1	0	0	0
117 Crimson Sunbird	1	1	1	1	0	1	1	1	0	0	1	0
118 Javan Sunbird (Scarlet Sunbird)	0	0	0	0	0	0	0	1	0	1	1	0
119 Temminck's Sunbird	0	0	0	0	0	0	0	0	0	1	0	0
120 Fire-tailed Sunbird	0	0	0	0	0	0	0	0	1	0	0	0
121 Little Spiderhunter	1	1	0	0	0	0	1	0	1	1	1	0

122 Thick-billed Spiderhunter	1	0	0	0	0	0	1	0	1	0	0	0
123 Long-billed Spiderhunter	0	0	0	0	0	0	1	0	1	0	0	0
124 Spectacled Spiderhunter	0	0	0	0	0	0	0	1	1	0	1	0
125 Yellow-eared Spiderhunter	1	0	0	0	0	0	0	1	1	0	1	0
126 Naked-faced Spiderhunter	0	1	0	0	0	0	0	0	1	0	1	0
127 Grey-breasted Spiderhunter	1	1	0	0	0	0	0	1	1	0	1	0
128 Streaky-breasted Spiderhunter	0	0	0	0	0	0	0	0	0	1	1	0
129 Streaked Spiderhunter	0	0	0	0	0	0	0	0	1	1	1	0
130 Whitehead's Spiderhunter	0	0	0	0	0	0	0	0	1	1	1	0

* 0 Unknown. *1?. Unsure

* 1 Described and or present.
*? Undescribed, no information & no records

APPENDIX 9. ANALYSIS OF CHARACTER SCORES AS DESCRIBED IN CHAPTER 4, PAGE 64.

Grouping	Freq kHz	Note duration	Note interval	Peak Ampl.	Bandw.	Entropy	Phrase duration	No. of notes in a phrase	Size of Repr't	Intro. rattle	Click	Squawk	Note %	Pause rate	Song duration	Rhythm of freq.
A	> 8.0	0.02-0.04	0.7-0.9	20.0-24.0	> 8.0	0.7-0.9	0-1	1-2	1	0	0	0	0-0.3	6-8	1-2	1
B	7.0-8.0	0.04-0.06	0.5-0.7	24.0-26.0	7.0-7.5	0.66-0.7	1-2	2-4	2-3	0	0	0	0.4-0.5	4-6	2-3	1-2
C	5.0-6.0	0.06-0.08	0.3-0.5	26.0-28.0	6.5-7.0	0.34-0.3	3.4	4-6	4-5	0	0	0	0.6-0.7	2-4	3-4	2-3
D	0-6.0	0.08-0.09	0.1-0.3	28.0-30.0	0-6.5	<0.3	4.5	6.8	5-6	1	1	1	>0.8	1-2	5-6	4-5

* A & B = Call vocalisation

* C = Simple song

* D = Complex song

*Repr't - Repertoire

APPENDIX 10. GROUP DATA MATRIX OF FLOWERPECKERS IN (NEXUS) FILE FORMAT FOR PAUP, AS DESCRIBED IN CHAPTER 3, PAGE 59 AND CHAPTER 4, PAGES 64 AND 79.

Ref no.	Species Name	Sub-species	Species No.	Ampl.	Bandw	Dur. Syll.	No. of notes in a phrase	Reper,t size	Rhythm. freq.	Freq (kHz)	Entropy	Note duration	Note intervals
1	Olive-backed Flowerpecker	3,1	3	B	A	B	A	C	B	B	B	C	B
2	Yellow-breasted Flowerpecker	4,1		B	A	B	A	C	A	B	B	C	B
3	Yellow-breasted Flowerpecker	4,3	4	B	A	B	A	C	A	B	B	C	B
4	Crimson-breasted Flowerpecker	5,2		B	A	B	A	C	B	A	A	B	B
5	Yellow-rumped Flowerpecker	7,#	7	B	A	A	B	C	B	A	A	B	B
6	Scarlet-breasted Flowerpecker	8,#	8	D	D	C	B	C	B	D	D	B	C

7	Golden-rumped Flowerpecker	9,1		D	B	B	B	C	B	B	B	C	C
8	Thick-billed Flowerpecker	10,1	10	C	C	C	D	D	B	C	C	C	B
9	Thick-billed Flowerpecker	10,11	10	C	C	C	D	C	B	C	C	B	B
9	Whiskered Flowerpecker	12,#	12	D	D	D	D	D	B	D	D	D	C
11	Yellow-vented Flowerpecker	13,2	13	D	B	C	B	C	B	C	B	C	C
12	White-throated Flowerpecker	15,#	15	C	B	C	D	C	B	B	C	B	C
13	Yellow-sided Flowerpecker	16,1	16	D	B	B	B	C	B	B	B	A	C
14	Olive-capped Flowerpecker	17,2	17	A	B	D	C	D	B	B	C	A	B
15	Flame-crowned Flowerpecker	18,1	18	C	B	B	B	C	A	B	B	E	C
16	Bicoloured Flowerpecker	19,2	19	D	C	C	B	C	B	C	C	C	C
17	Cebu Flowerpecker	20,#	20	C	B	B	C	B	C	B	B	D	B

18	Red-striped Flowerpecker	21,#	21	C	B	B	B	C	A	B	B	A	C
19	Scarlet-collared Flowerpecker	23,#	23	A	B	B	C	C	B	B	B	G	C
20	Orange-bellied Flowerpecker	24,6	24	A	C	B	B	B	B	C	C	C	C
21	Orange-bellied Flowerpecker	24,9	24	A	B	B	C	C	B	B	B	G	C
22	Orange-bellied Flowerpecker	24,17	24	A	C	C	B	B	B	B	C	C	C
23	Buzzing Flowerpecker	25,3	25	D	C	B	C	B	B	D	B	C	C
24	Buzzing Flowerpecker	25,5	25	D	C	B	C	B	B	D	B	C	C
25	Pale-billed Flowerpecker	26,1	26	D	C	B	C	B	B	D	B	C	C
36	Mottled Flowerpecker	37#	37	D	B	B	C	D	B	B	B	E	C
37	Black-fronted Flowerpecker	38,2	38	A	C	C	D	D	B	C	C	E	C
38	Red-chested Flowerpecker	39,1	39	B	C	C	D	C	C	C	B	C	C

39	Fire-breasted Flowerpecker	40,5	40	D	D	C	C	C	B	C	C	C	B
40	Fire-breasted Flowerpecker	40,7	40	D	D	C	C	C	B	C	B	C	B
41	Black-sided Flowerpecker	41#	41	D	C	C	D	C	B	C	B	C	C
42	Grey-sided Flowerpecker	42,1		A	B	B	C	B	B	B	D	D	C
43	Blood-breasted Flowerpecker	43,2	43	B	B	B	B	D	B	E	C	C	D
44	Blood-breasted Flowerpecker	43,4	43	A	C	C	B	C	B	D	C	A	C
45	Mistletoebird	44,2	44	B	A	C	C	C	B	B	C	A	C
46	Scarlet-backed Flowerpecker	45,3	45	B	C	C	C	B	B	D	B	C	C
47	Scarlet-headed Flowerpecker	46,2	46	D	B	C	B	C	A	D	C	B	C

* Ampl. – Amplitude

* Bandw – Bandwidth

* Dur. Syll. – Duration of syllable

* Reper't – Repertoire

APPENDIX 11. GROUP DATA MATRIX FOR SUNBIRDS AND SPIDERHUNTERS IN (NEXUS) FILE FORMAT FOR PAUP, AS DESCRIBED IN CHAPTER 3, PAGE 59 AND CHAPTER 4, PAGES 64 AND 79.

Common name	Ampl.	Bandw	Dur. Syll.	Size of rep.	Rhythm Freq.	Freq (kHz)	Entropy	Note duration	Note intervals	Phrase duration	No of notes in a phrase	Intro .Rattle	Click	Squawk	Note %	Pause rate	Song duration
Ruby-cheeked Sunbird	B	A	A	A	B	A	B	A	A	A	B	A	A	A	A	A	B
Ruby-cheeked Sunbird	B	A	A	B	A	A	B	A	A	B	A	A	A	A	A	B	B
Plain Sunbird	A	B	A	B	B	B	A	B	A	B	B	B	A	B	B	B	A
Plain-throated Sunbird	A	B	C	B	A	B	B	C	B	B	C	B	A	B	B	A	B
Plain-throated Sunbird	A	B	C	B	A	C	B	B	C	C	B	B	A	B	B	B	B
Purple-naped Sunbird	B	A	A	B	C	A	C	C	B	A	C	B	A	B	A	C	C
Purple-rumped Sunbird	B	B	A	C	C	A	C	C	B	B	C	A	A	B	B	B	C
Purple-rumped Sunbird	A	B	C	C	C	B	B	B	C	C	B	A	A	B	B	B	B
Crimson-backed Sunbird	C	B	C	C	D	B	C	D	C	B	C	A	A	B	B	D	C
Purple-throated Sunbird	A	B	C	B	B	B	A	A	A	C	B	A	A	B	B	B	A
Purple-throated Sunbird	B	A	C	A	B	A	B	A	B	B	C	A	A	B	A	B	B
Black Sunbird	A	A	B	C	B	A	A	B	B	B	C	A	A	B	A	B	A
Black Sunbird	B	B	A	C	A	B	B	A	A	C	C	A	A	B	B	A	B
Black Sunbird	A	A	B	B	C	A	B	A	A	B	C	A	A	B	A	B	B
Black Sunbird	B	A	A	A	B	A	C	B	A	C	B	A	A	B	A	B	C

Black Sunbird	A	B	B	B	A	B	C	A	A	B	C	B	B	B	B	A	C
Black Sunbird	A	A	A	C	B	B	A	B	A	A	C	B	B	B	A	B	A
Black Sunbird	B	A	B	B	C	A	B	A	B	B	B	A	A	B	A	A	B
Black Sunbird	A	A	A	B	B	B	B	C	A	A	C	B	B	B	A	A	B
Copper-throated Sunbird	B	B	B	A	A	B	A	B	A	B	C	B	B	B	B	A	A
Purple Sunbird	B	C	C	C	B	A	C	D	C	C	B	A	A	A	C	D	C
Purple Sunbird	C	B	C	C	A	B	C	C	D	B	C	B	B	B	B	D	C
Purple Sunbird	B	B	D	C	A	D	C	C	C	D	B	A	A	A	B	C	C
Olive-backed Sunbird	B	A	B	C	C	B	C	B	C	B	C	B	B	B	A	C	C
Olive-backed Sunbird	A	B	C	C	B	C	B	C	C	B	C	B	B	B	B	D	B
Olive-backed Sunbird	A	B	C	C	B	C	B	C	C	B	C	B	B	B	B	D	B
Olive-backed Sunbird	B	D	C	C	B	B	C	C	A	C	C	B	B	B	D	C	C
Olive-backed Sunbird	A	C	C	C	B	C	D	C	B	C	D	B	B	B	C	B	D
Olive-backed Sunbird	B	D	A	C	C	C	C	C	B	C	C	B	B	B	D	B	C
Olive-backed Sunbird	A	B	D	C	B	C	C	D	B	D	C	B	B	B	B	C	C
Apricot-breasted Sunbird	B	B	B	C	B	B	A	B	C	B	C	B	B	B	B	A	A
Flame-breasted Sunbird	A	B	B	C	A	B	A	B	B	C	B	B	B	B	B	B	A
Flame-breasted Sunbird	B	A	B	A	C	B	B	A	B	C	B	B	B	B	A	B	B
Souimanga Sunbird	C	C	B	C	C	B	C	D	C	B	C	B	B	B	C	C	C
Souimanga Sunbird	C	B	C	D	B	C	C	C	C	C	C	A	A	A	B	C	C
Souimanga Sunbird	B	C	B	C	C	D	C	C	C	B	C	A	A	A	C	C	C
Humblot's Sunbird	D	D	D	D	D	D	D	D	C	C	D	A	A	A	D	C	C

Humblot's Sunbird	D	D	D	D	D	D	C	C	D	D	C	A	A	A	C	D	C
Anjouan Sunbird	C	D	D	D	D	C	D	D	D	C	D	A	A	A	C	C	C
Mayotte Sunbird	C	D	C	C	C	D	D	D	D	D	D	A	A	A	D	D	D
Long-billed Sunbird	B	C	B	A	B	C	D	B	D	C	C	A	A	A	C	C	D
Long-billed Sunbird	C	C	B	C	A	B	B	D	D	B	C	B	B	B	C	B	B
Grey-hooded Sunbird	A	B	B	C	B	B	B	C	C	B	B	B	B	B	B	C	B
Apo Sunbird	B	A	C	B	C	C	C	B	B	C	B	B	B	B	A	B	C
Apo Sunbird	A	B	A	B	A	B	B	C	B	B	B	B	B	B	B	C	B
Flaming Sunbird	B	C	C	C	C	B	B	C	C	C	D	B	B	B	C	B	B
Flaming Sunbird	C	C	B	B	B	C	C	B	C	C	C	A	A	A	C	C	C
Metallic-winged Sunbird	C	D	D	D	C	D	C	D	D	D	C	A	A	A	D	D	C
Metallic-winged Sunbird	D	D	C	D	C	C	D	D	D	D	D	A	A	A	D	C	D
Elegant Sunbird	B	A	B	C	B	C	C	B	C	C	B	A	A	A	A	B	C
Lovely Sunbird	C	B	C	B	C	C	B	B	C	C	C	A	A	A	B	C	B
Gould's Sunbird	D	D	D	C	B	D	C	C	C	D	C	A	A	A	D	C	C
Green-tailed Sunbird	C	D	D	D	D	C	C	D	C	D	C	A	A	A	C	C	D
Green-tailed Sunbird	D	C	D	C	D	D	C	D	C	D	C	A	A	A	C	D	C
Green-tailed Sunbird	C	D	C	D	C	D	C	D	C	C	D	A	A	A	D	D	C
White-flanked Sunbird	B	A	B	C	C	D	A	B	C	B	C	A	A	A	A	B	A
Forked-tailed Sunbird	C	C	C	D	C	C	B	B	C	C	C	A	A	A	C	B	B
Forked-tailed Sunbird	C	B	C	C	D	C	B	C	B	B	C	A	A	A	B	C	B
Black-throated Sunbird	D	C	C	C	D	D	B	C	C	C	B	A	A	A	C	D	B

Black-throated Sunbird	D	C	C	D	D	D	C	B	C	D	C	B	B	B	C	C	C
Black-throated Sunbird	C	D	D	C	E	D	B	C	C	D	D	B	B	B	D	C	B
Crimson Sunbird	B	B	C	D	C	B	C	B	C	C	B	B	B	B	B	C	C
Crimson Sunbird	C	B	C	C	C	B	C	C	B	C	B	B	B	B	B	D	C
Javan Sunbird	B	D	D	C	B	B	B	B	C	D	D	B	B	B	D	C	B
Temminck's Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Scarlet-tufted Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Scarlet-tufted Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Plain-backed Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Plain-backed Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Anchieta's Sunbird	A	B	B	C	B	B	B	C	C	B	B	B	B	B	B	C	B
Mouse-brown Sunbird	B	A	C	B	C	C	C	B	B	C	B	B	B	B	A	B	C
Western Violet-backed Sunbird	A	B	A	B	A	B	B	C	B	B	B	B	B	B	B	C	B
Kenya Violet-backed Sunbird	B	C	C	C	C	B	B	C	C	C	D	B	B	B	C	B	B
Violet-tailed Sunbird	C	C	B	B	B	C	C	B	C	C	C	A	A	A	C	C	C
Little Green Sunbird	C	D	D	D	C	D	C	D	D	D	C	A	A	A	D	D	C
Little Green Sunbird	D	D	C	D	C	C	D	D	D	D	D	A	A	A	D	C	D
Green Sunbird	B	A	B	C	B	C	C	B	C	C	B	A	A	A	A	B	C
Green Sunbird	C	B	C	B	C	C	B	B	C	C	C	A	A	A	B	C	B
Collared Sunbird	C	D	D	D	D	C	C	D	C	D	C	A	A	A	C	C	D

Collared Sunbird	D	C	D	C	D	D	C	D	C	D	C	A	A	A	C	D	C
Collared Sunbird	C	D	C	D	C	D	C	D	C	C	D	A	A	A	D	D	C
Collared Sunbird	B	A	B	C	C	D	A	B	C	B	C	A	A	A	A	B	A
Collared Sunbird	C	C	C	D	C	C	B	B	C	C	C	A	A	A	C	B	B
Collared Sunbird	C	B	C	C	D	C	B	C	B	B	C	A	A	A	B	C	B
Collared Sunbird	D	C	C	C	D	D	B	C	C	C	B	A	A	A	C	D	B
Pygmy Sunbird	D	C	C	D	D	D	C	B	C	D	C	B	B	B	C	C	C
Nile Valley Sunbird	C	D	D	G	D	D	D	D	D	D	D	A	A	A	D	D	D
Amani Sunbird	D	D	D	D	D	D	D	D	D	C	D	A	A	A	D	D	D
Reichenbach's Sunbird	C	D	D	C	E	D	B	C	C	D	D	B	B	B	D	C	B
Principe Sunbird	B	B	C	D	C	B	C	B	C	C	B	B	B	B	B	C	C
Newton's Sunbird	C	B	C	C	C	B	C	C	B	C	B	B	B	B	B	D	C
Sao Tome Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Orange-breasted Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Green-headed Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Green-headed Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Green-headed Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Bannerman's Sunbird	B	C	B	E	E	C	D	C	D	C	B	A	A	A	C	D	D
Blue-throated Brown Sunbird	B	B	C	D	D	B	C	C	D	C	C	A	A	A	B	C	C

Blue-throated Brown Sunbird	C	C	B	C	D	C	D	C	C	C	C	A	A	A	C	B	D
Cameroon Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Cameroon Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Blue-headed Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Eastern Olive Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Eastern Olive Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Eastern Olive Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Western Olive Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Western Olive Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Western Olive Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Mouse-coloured Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Mouse-coloured Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Buff-throated Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Buff-throated Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Carmelite Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Green-throated Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Amethyst Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Amethyst Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Scarlet-chested Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Scarlet-chested Sunbird	B	C	B	E	E	C	D	C	D	C	B	A	A	A	C	D	D
Scarlet-chested Sunbird	B	B	C	D	D	B	C	C	D	C	C	A	A	A	B	C	C

Hunter's Sunbird	C	C	B	C	D	C	D	C	C	C	C	A	A	A	C	B	D
Socotra Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Bocage's Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Purple-breasted Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Bronze Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Bronze Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Malachite Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Malachite Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Red-tufted Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Golden-winged Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Golden-winged Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Olive-bellied Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Olive-bellied Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Olive-bellied Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Tiny Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Miombo Double-collared Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Miombo Double-collared Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Southern Double-collared Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D

Southern Double-collared Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Neergaard's Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Prigogine's Double-collared Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Montane Double-collared Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Northern Double-collared Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Northern Double-collared Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Greater Double-collared Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Greater Double-collared Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Regal Sunbird	D	D	E	F	G	D	F	G	F	E	F	B	B	B	D	E	F
Rockefeller's Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Eastern Double-collared Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Eastern Double-collared Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Loveridge's Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D

Beautiful Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Beautiful Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Mariqua Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Mariqua Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Shelley's Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Shelley's Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Congo Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Red-chested Sunbird	B	B	C	D	D	B	D	D	D	D	D	B	B	B	B	D	C
Black-bellied Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Purple-banded Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Purple-banded Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Tsavo Purple-banded Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Kenya Violet-breasted Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Voilet-breasted / Pemba Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Orange-tufted Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Palestine Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Shining Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D

Splendid Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Johanna's Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Johanna's Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Superb Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Superb Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Oustalet's Sunbird	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
White-breasted Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Variable Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Variable Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Variable Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Variable Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B
Dusky Sunbird	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Ursula's Sunbird	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Bates's Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Copper Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Copper Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Madagascar Sunbird	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Madagascar Sunbird	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Madagascar Sunbird	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Seychelles Sunbird	D	B	D	C	B	B	B	C	C	C	C	B	B	B	B	C	B

Spiderhunters

Little Spiderhunter	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Little Spiderhunter	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Long-billed Spiderhunter	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Spectacled Spiderhunter	D	D	D	C	D	D	C	D	D	D	D	B	B	B	D	D	C
Naked-faced Spiderhunter	C	D	D	D	C	D	D	C	D	C	C	A	A	A	D	C	C
Naked-faced Spiderhunter	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C
Streaked Spiderhunter	D	D	D	D	D	D	D	C	C	D	D	A	A	A	C	D	D
Grey-breasted Spiderhunter	D	C	D	D	C	D	D	D	C	D	D	A	A	A	D	C	D
Thick-billed Spiderhunter	D	D	D	D	D	D	D	C	D	D	D	B	B	B	D	C	D
Whitehead's Spiderhunter	D	D	D	D	C	D	D	D	C	D	D	A	A	A	D	C	C

* Ampl. – Amplitude

* Bandw – Bandwidth

* Dur. Syll. – Duration of syllable

* Reper't – Repertoire