

**EVOLUTION OF ACOUSTIC COMMUNICATION AND HABITAT
TYPE INFLUENCE IN THE AVIAN SPECIES, SABOTA
LARK *CALENDULAUDA SABOTA* (ALAUDIDAE)**

MASTER OF SCIENCE IN ZOOLOGY

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**EVOLUTION OF ACOUSTIC COMMUNICATION AND HABITAT
TYPE INFLUENCE IN THE AVIAN SPECIES, SABOTA
LARK *CALENDULAUDA SABOTA* (ALAUDIDAE)**

BY

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RESEARCH DISSERTATION

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2024



The Sabota Lark *Calendulauda sabota*. Photograph © Derek Engelbrecht

DEDICATION

I DEDICATE THIS WORK TO MY PARENTS AND SIBLINGS, WHO HAVE SUPPORTED ME IN MANY WAYS AND ALL THE PEOPLE WHO CONTRIBUTED TO ITS COMPLETION. FINALLY, THANKS BE TO THE TRIUNE GOD!

DECLARATION

I **Mogaletloa Eugene Madiseng** hereby declare that this research project titled **“EVOLUTION OF ACOUSTIC COMMUNICATION AND HABITAT TYPE INFLUENCE IN THE AVIAN SPECIES, SABOTA LARK *CALENDULAUDA SABOTA* (ALAUDIDAE)”** is my own work and that all materials contained herein are duly acknowledged as stipulated in the University of Limpopo’s Plagiarism Policy. This work has not been submitted to this or any other university. I therefore present this dissertation to be submitted for assessment for the degree of Master of Science in Zoology.

Mogaletloa Eugene Madiseng

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Full name

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Signature

29/11/2023

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Date

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PREFACE

This dissertation consists of four chapters. Chapter 1 provides a general review of acoustic communication and the study species, and to some extent, also serves as a framework of the present study. Chapter 2 presents results for spectrogram-based analyses of vocalisations of Sabota Lark *Calendulauda sabota* (Alaudidae) which includes the description of vocalisations in terms of their structure and composition. In Chapter 3 results of test of the applicability of the Acoustics Adaptation Hypothesis in Sabota Lark are presented. The last chapter (Chapter 4) presents summary of the main findings of the entire study, conclusions, recommendations, and future prospects. The data chapters i.e. Chapters 2 and 3, were written and formatted for submission for publication. Figures and tables are presented just after the table of contents while the list of references for the entire dissertation is presented in the last pages of the dissertation.

The preliminary results from this master's research project were presented at a national conference and the Faculty of Science and Agriculture Postgraduate Research Day in May and September 2023, respectively. The following presentations were made:

1. Madiseng ME, Engelbrecht GD, Darikwa T, Henry L, Mandiwana-Neudani TG. Habitat type influence on the structure of vocalisations: A case of the Sabota Lark, *Calendulauda sabota* (Alaudidae). 6th Biennial Learn About Birds (LAB) Conference, 23-28 May 2023, The Wilderness Hotel (George, Western Cape Province, South Africa), Standard oral presentation.
2. Madiseng ME, Engelbrecht GD, Darikwa T, Laurence H, Mandiwana-Neudani TG. Habitat type influence on the structure of vocalisations: A case of the Sabota Lark, *Calendulauda sabota* (Alaudidae). 13th Faculty of Science and Agriculture (FSA) Postgraduate Research Day, 20-22 September 2023, Bolivia Lodge (Polokwane, Limpopo Province, South Africa), Standard oral presentation.

ABSTRACT

Habitat acoustics has been proposed to be involved in producing selective forces that mould bird vocalisations into the sounds we hear when birds vocalise. The influence of habitat on bird vocalisations is well-documented, mostly in bird species in the Americas rather than in Africa. The Sabota Lark *Calendulauda sabota* is near-endemic to southern Africa and has a widespread distribution in habitats ranging from well-developed Savanna woodland to Karoo and semi-desert scrub. However, to my knowledge, no records of published studies have endeavoured to quantitatively describe the vocal structure of the Sabota Lark or the effects of habitat on its vocalisations. This makes the Sabota Lark an ideal candidate to investigate the effect of habitat type and structure on bird vocal structure. This study investigated the effect of habitat on the vocalisations of the Sabota Lark and whether the Acoustic Adaptation Hypothesis applies to the Sabota Lark. Fieldwork was conducted during breeding seasons in the sites that represented semi-arid (*Vachellia*) and moist Savanna (broad-leaved woodland) and the dry Nama Karoo shrublands. Songs were analysed using a bioacoustics sound analyses software. A total of 992 song strophes were extracted, and spectrograms were generated from which descriptions of songs were done. Seven spectrogram parameters of 878 song strophes were analysed using univariate one-way ANOVA and t-test. Multivariate (Principal Component Analyses – PCA and Linear Discriminant Analyses – LDA) statistical analyses were performed in two parts to respectively include: 1) analyses of a comprehensive dataset with all the remaining seven vegetation types included and 2) analyses of a reduced dataset comprising only the two vegetation types with the highest sampling (viz., Bushmanland Basin Shrubland – BBS and Musina Mopane Bushveld – MMB).

The Sabota Lark emerged as a species with large and complex song variations between individual birds and within and between different habitat types. The individuals gave many unique song types and song strophes. Furthermore, this species explored both types of song presentation or singing styles as some individuals repeated song types at least twice before switching to another song type. This singing style is called “eventual variety”. The

other birds rendered their song types once and never twice in succession. This is called “immediate” variety, meaning they switched to new song types immediately without repeating songs that have already been sung. This was observed both within individuals and among individuals in different habitat types. The means of the parameters of song strophes of the Sabota Larks among the vegetation types were highly significantly different, indicating that variances in songs between vegetation types were not equal. However, most parameters were significantly different contrary to the study predictions; Therefore, future studies should include a large sample size with equal representation across habitats, and the vegetation structure should be quantified.

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CHAPTER 1

General Introduction

1.1. Background information

1.1.1. Animal communication systems

Animals use a variety of signals to communicate, including smell, taste, sound, and vision (Walb *et al.* 2021). It is through communication that information is transmitted among organisms, and this has a considerable impact on their survival (Chen and Wiens 2020) and ultimately plays a significant role in ensuring cooperation within their communities. Many important behaviours of animals, like reproduction, would be near-impossible without communicating specific signals. Although animals use a variety of signals, acoustic communication, i.e., the use of sound waves to transmit information, is the predominant means used to communicate information (Chen and Wiens 2020, Walb *et al.* 2021). However, not all organisms have specialised organs or structures for producing and perceiving sound (Moore *et al.* 2016). For example, some insects make sounds by rubbing their body parts, such as legs, wings, or legs and wings together (Moore *et al.* 2016). On the other hand, in some birds and mammals, the production of sound is facilitated by specialised vocal structures, namely, the syrinx in birds and the larynx in mammals (Moore *et al.* 2016). According to Vernes *et al.* (2021), this is one of the features that make acoustic communication an interesting topic in the evolution of sound and vocal communication.

True or oscine songbird species studied to date show the ability to learn vocalisations, and species can either be closed-ended/age-limited or open-ended/continuous vocal learners (Catchpole and Slater 2008). Vocal learning generally refers to producing novel sounds by learning or imitating (Shen 2017). It may be broadly split into two categories: 1) learning sounds of conspecifics and 2) learning sounds of heterospecifics or inanimate objects, i.e., mimicry (Kelley *et al.* 2008). In closed-ended learners, such as the White-crowned Sparrow *Zonotrichia leucophrys*, song learning is limited to the early stage of life, and beyond that no new notes become learned (White and Mooney 1999). In many species song learning occurs before

sexual maturity and their repertoires remain the same there after (e.g., Zebra finch *Taeniopygia guttata*). In open-ended learners, learning extends even into adulthood (e.g., Brown-headed cowbirds *Molothrus ater*) (Soha 2020). Vocal learning has been recorded only in some bird orders, e.g., the hummingbirds (Trochilidae, Apodiformes), parrots (Psittacidae, Passeriformes), and the perching birds (Passeriformes), mammals, e.g., humans (Primates), some cetaceans (Cetacea), pinnipeds (Carnivora), elephants (Proboscidea), and bats (Chiroptera) (Päckert 2018, Martins and Boeckx 2020). In perching birds (Passeriformes), not all species in this group learn their vocalisations; only the oscines, i.e., the true songbirds of the suborder Passeri (Päckert 2018). However, there is empirical evidence of vocal learning abilities in other species besides those mentioned above (Martins and Boeckx 2020).

According to Alström and Ranft (2003), establishing a comprehensive classification of bird vocalisations is necessary for avifaunal surveys and makes it possible to perform comparative analyses between species and conspecifics, while Laiolo (2010) mentioned that it contributes to planning effective management and conservation strategies. A variety of information about birds can be gleaned from their vocalisations, ranging from sex, age, behavioural state, and health, to relationships with co-existing wildlife (Catchpole and Slater 2008). Avian vocalisations are also important in phylogenetic studies in establishing phylogenetic relationships and discovering new species (Alström and Ranft 2003). What has been found over time is that vocalisations of many animals, birds included, vary in space and time within and among species, populations, and individuals (Podos *et al.* 2004, Podos and Warren 2007). The variations range from differences in spectral and temporal characteristics to differences in the structure and number of elements, syllables and phrases that comprise species vocalisations (Kumar 2003). The variations are also distinct enough to aid in distinguishing among species or in species recognition (Woolley and Sakata 2019).

Several hypotheses proposed to explain how variations in bird vocalisations originated and how bird vocalisations evolved. Thorpe (1961) suggested that song can evolve as individuals variably rearrange accurately learned material and when individuals include never-seen-before material (i.e., inventing new material) in their repertoire. Morton (1975) proposed the environment to be the source of selective forces driving the evolution of bird vocalisations, while Ryan and Brenowitz (1985)

included body size, phylogeny, and ambient noise in their study on the evolution of bird song and argued that no single selective force could be treated as the sole driver of the evolution of bird vocalisations. Various selective forces coupled with the limitations of the vocal systems to evolve, contribute to the evolution of bird vocal systems in different degrees. Social selective forces were also emphasised to be the cause (Kirschel *et al.* 2009).

1.2. Sources of selective forces on bird vocalisations

1.2.1. Habitat acoustics

The study of vocal signal structure and usage in relation to the environment is key to understanding animal communication systems (Arasco *et al.* 2022). Morton (1975) suggested that selective forces must be identified and studied to understand how communication through sound evolves in animals. With the knowledge that not all sounds transmit equally well within a particular habitat because of habitat acoustics, Morton proposed that habitat acoustics favour transmission of sound signals that have features adapted for maximum transmission. For instance, Morton found that sound signals of birds living near the ground in forests were characterised by pure tone-like sounds within a relatively narrow frequency range, while sound signals of birds in open habitats had highly modulated or trilled sounds. The sound signals had these characteristics because they allowed optimum transmission relative to habitat acoustics. Furthermore, with many important interactions between species and conspecifics occurring in the context of a habitat, this makes habitats frameworks within which other sources of selection (e.g., sexual selection, selection for species distinctiveness, territory size, and pair bond length) can operate to mould birds sound signals to have the kind of characteristics we hear when birds sing (Morton 1975). It is essential to shed light on these environmental pressures acting on signal evolution to understand how signals evolve and diversify more broadly (Arasco *et al.* 2022).

The distance a bird can communicate by sound depends on the attenuation rate of the sound used, the amplitude of the sound at the source, the level of masking by ambient noise, and the auditory sensitivity of the intended receiver (Morton 1975). Progressive degradation and/or attenuation of acoustic signals during communication,

as signals propagate from the signaller to the receiver, is inevitable (Naguib and Wiley 2001). This impairs acoustic signals and makes it difficult, if not eventually impossible, for the receiver to decode the biological information encoded in the signals. Therefore, acoustic signals that are less susceptible to environmentally-induced degradation, enabling transfer information, should be favoured to ensure optimal communication (Arasco *et al.* 2022). Although this impairment of signals interrupts communication between signallers and receivers, it has been proposed that signallers optimise communication by adapting their signals to reduce impairments (Morton 1975). The ranging hypothesis proposes that the impaired signals can inform the receiver about the signaller's distance and/or direction (Naguib and Wiley 2001).

The other influences on acoustic signal structure during propagation include the complex ground effects, spherical attenuation, attenuation by atmospheric absorption, attenuation by scattering of directional sounds, accumulation of reverberation from reflections from relatively stationary objects near the path of transmission, accumulation of irregular amplitude fluctuations as a result of diffraction from nonstationary turbulence in the atmosphere; and diffraction of sound by temperature and other velocity gradients in the environment (Naguib and Wiley 2001). These influences produce four kinds of changes in the sound received at a distance: overall attenuation; frequency-dependent attenuation (greater attenuation of higher frequencies); reverberation; and fluctuations in amplitude (Naguib and Wiley 2001). Although the ground influences acoustic signals in complex ways, its influence is inversely proportional to the height of the signaller, with sounds rendered at least 1 m above the ground experiencing less influence (Naguib and Wiley 2001). Thus, simply by changing their spatial position when vocalising, signallers can enhance the transmission of their signals and potentially increase their detection by conspecifics or intended receivers (Arasco *et al.* 2022). This erases the effects of the so-called "shadow zone" while increasing the broadcasting area (Morton 1975). Another way to improve signal transmission is proposed by the Acoustic Adaptation Hypothesis (AAH) (Morton 1975). The AAH suggests that birds respond to the distortion and attenuation present in the environment by changing the temporal and spectral or frequency components of their acoustic signals. Morton's data supported his explanations for acoustic adaptations, and since then, many other studies sought to test the validity of

AAH. Still, empirical tests of the AAH to date have provided mixed results (Boncoraglio and Saino 2007).

According to Arasco *et al.* (2022), the inconsistencies among studies may be explained by i) a relatively broad categorisation of habitats such as ‘open’ versus ‘closed’, which oversimplifies complex habitat conditions, ii) prioritising one species or one call type, and iii) usage of different parameters during acoustic analyses across studies. Other factors like phylogenetics, morphology, physiology, social system and call and song context also bring about further complications. To isolate the specific effect of habitat on acoustic signals’ structure, all these other confounding factors must be limited, and one proposed way to restrict them is to study acoustic communication in closely related species (Arasco *et al.* 2022). Based on the difficulty or impossibility of obtaining direct experimental evidence to support a hypothesis dealing with selective forces, in part, and the fact that the element of time cannot be built into the experiment, one test of the hypothesis proposed by Morton (1975) was to compare congeneric species of birds occupying different habitats. According to Nicholls and Goldizen (2006), several studies have found that birds from denser habitats call at lower frequencies than those from more open habitats and that temporal properties of vocalisations, such as trill rates, are influenced by habitat type, as predicted. However, most of these studies have involved comparisons across different species. Hence, a within-species comparison provides a better test of the effect of habitat as it provides greater control of other factors that can influence vocalisations, such as phylogenetic history (Ryan and Brenowitz 1985) or body size (Podos 2001).

1.2.2. Other selective forces

Some studies have found the impact of habitat on vocal signals to be little (Boncoraglio and Saino 2007). A study on the evolution of song in tanagers (family Thraupidae) showed that body size had a greater effect on song evolution in this species (Mason *et al.* 2017). This may be linked to the fact that changes in body size affect syrinx size, which affects the transmission of acoustic signals. An increase in body size is associated with a larger syrinx, which can produce lower frequencies (Billings 2018). Derryberry *et al.* (2018) found that beak size can also limit the temporal and performance components of the song. Song features like frequency modulations

are affected by how fast the bill opens and closes (Palacios and Tubaro 2000). This means song features largely depend on the size of the bill. Larger bills, which are necessary for feeding on food items like seeds with hard covering (Huber and Podos 2006), open and close at slower rates than smaller bills during song delivery (Ballentine 2006).

1.3. The study species

1.3.1. The Sabota Lark – distribution, morphology, diversity, and breeding

The Sabota Lark *Calendulauda sabota* (Smith, 1836) is a species in the family Alaudidae, known as the larks. It is the most common and widespread lark in southern Africa. It is near-endemic to the subregion, extending marginally into the coastal regions of Angola and western Democratic Republic of the Congo (DRC) (Ryan 2020) (Fig. 1.1). In most cases, scientists focus their interest and research on species of conservation concern, either because the species may be declining in its breeding range, may occupy declining or vulnerable habitats, have specialised habitat requirements, or it is living in extreme environments (Tieleman *et al.* 2003) or some combination of these (Khanaposhtani *et al.* 2019). However, the Sabota Lark is listed as a species of Least Concern by the IUCN (BirdLife International 2023).

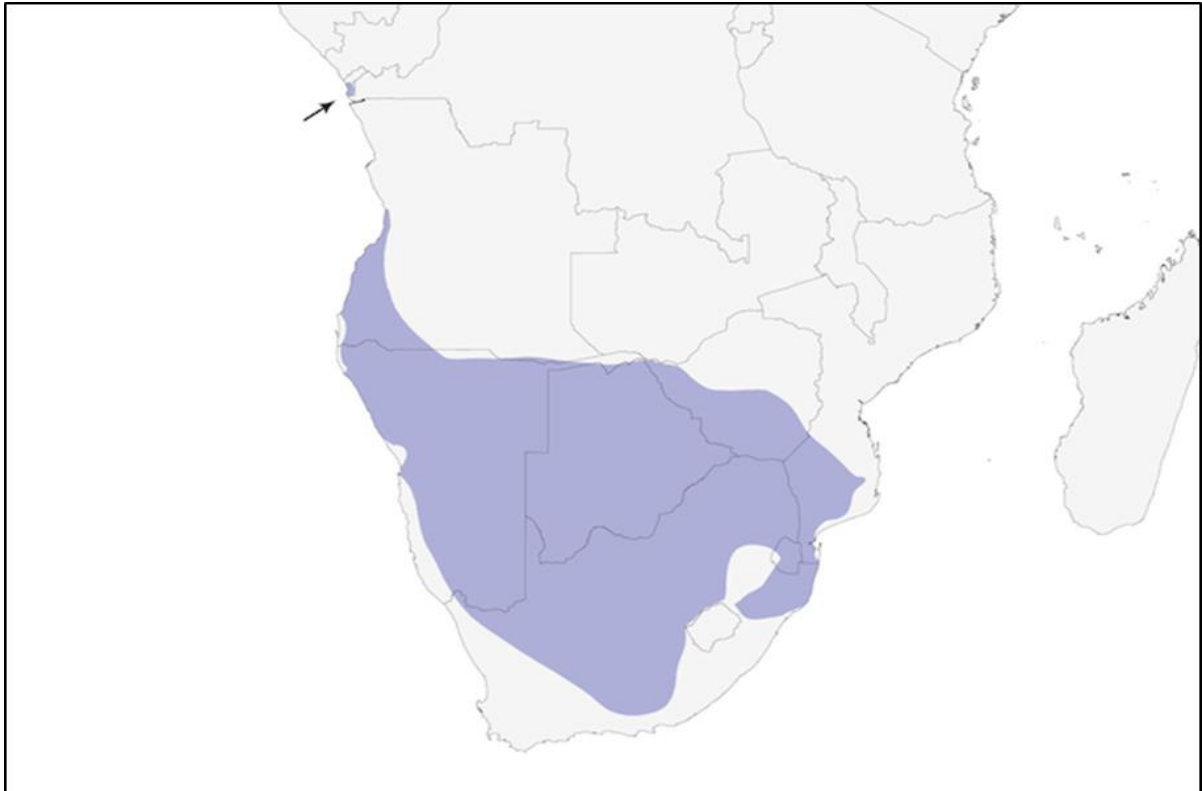


Figure 1.1. Distribution map of the Sabota Lark *Calendulauda sabota* (Ryan 2020).

The Sabota Lark, as understood based on specimens from south-eastern Botswana and from the eastern districts of the country, is a lighter and brighter bird on the upperparts (Clancey 1958). Races differ primarily in upperpart colour and extent of streaking (typically are paler and less streaked in more arid areas), also in bill size (short and slender in the east, longer and heavier in the west) (Marr *et al.* 2017) (Fig. 1.2).



Figure 1.2. The Sabota Lark *Calendulauda sabota*. Top: from Vachellia Savanna. Bottom: from Karoo (Photograph/s © Derek Engelbrecht).

The Sabota Lark breeds from October to May, mostly November to January in the east of the subregion and February to March in the west, coinciding with the later onset of summer rains in the arid and semi-arid western regions (Mashao 2014, Ryan 2020). Territorial males sing from an elevated perch, e.g., the top of a tree or a telephone line, or during an aerial song flight. During song flights, males circle over their territories and typically do not sing during the initial climb. These birds nest in shallow depressions on the ground, usually at the base of a rock, bush or grass tuft, a cup lined with dry grass and rootlets, typically with a domed roof at the back and sides, with material woven into overhanging vegetation. A clutch consists mainly of 2–4 eggs. Among the larks in the central Namib Desert, there is clear sexual size dimorphism, with the male being the larger sex (Willoughby 1971). Most nests of the species are orientated towards the east and south to obtain maximal shade, especially in summer (Maclean 1970).

Taxonomically, *C. sabota* is a complex species with nine presently recognised subspecies, *C. s. sabota* (Smith, 1836), which occurs in eastern Botswana, central Zimbabwe and north-eastern South Africa; *C. s. plebeja* (Cabanis, 1875), found isolated in Cabinda in north-western Angola and eastern DRC; *C. s. ansorgei* (Sclater, WL, 1926), occurs in western Angola; *C. s. naevia* (Strickland, 1853), occurs in north-western Namibia; *C. s. waibeli* (Grote, 1922), occurs in northern Namibia and northern Botswana; *C. s. herero* (Roberts, 1936), occurs in southern and eastern Namibia, north-western South Africa; *C. s. sabotoides* (Roberts, 1932), found in central and southern Botswana, western Zimbabwe and northern South Africa; *C. s. suffusca* (Clancey, 1958), occurs in south-eastern Zimbabwe, southern Mozambique and eastern South Africa and *C. s. bradfieldi* (Roberts, 1928) which occurs in central South Africa (see Marr *et al.* 2017). However, differences between some of these subspecies are negligible and based on small sample sizes. It is possible that detailed morphological and genetic studies will show that some of these subspecies may not be valid (Barnes 2007, Marr *et al.* 2017). Nevertheless, in this study the above taxonomic arrangement is adopted. These subspecies have been subdivided into two groups: the western thick-billed group, whose distribution is centred mainly in the more arid western parts of southern Africa, and the eastern slender-billed group occupying the more mesic Savannas in the east of the subcontinent (Marr *et al.* 2017).

Calendulauda sabota thrives in diverse habitats that range from reasonably dense, broad-leaved woodland and more open, semi-arid *Vachellia* (*Acacia*) Savanna to structurally simple Karoo scrub and desert margins (Mashao 2014, Marr *et al.* 2017, Ryan 2020). Males are resident and defend territories year-round although they may make local movements following rainfall (Ryan 2020). Territories are advertised mainly by song and other vocalisations. However, the vocalisation structure across the geographical range of this species and how it has evolved relative to habitat structure remains unknown. This is irrespective of the vast collection of vocalisations of Sabota Larks available in online sound libraries and private collections. The Sabota Lark vocalisations vary across individuals (Maclean 1970), but how these variations came about is unknown. There are no records of published studies that have endeavoured to describe the vocal structure of this species quantitatively. In addition, the influence of habitat on vocalisations is well-documented in species of birds that are endemic to other continents, particularly the Americas (Daniel and Blumstein 1998, Kopuchian *et al.* 2004, Derryberry *et al.* 2018). The occurrence of the Sabota Lark in structurally diverse habitats provides an opportunity to investigate the relationship between vocalisations and habitat intraspecifically and to test the applicability of the AAH to this species. This research positions itself as an example from the perspective of the Sabota Lark being an African endemic species.

1.4. Study aim

This study aimed to investigate the effect of habitat on vocalisations in Sabota Larks *Calendulauda sabota* and to determine whether the Acoustic Adaptation Hypothesis applies to the Sabota Lark.

1.5. Study objectives

The objectives of this study were to:

- i) describe the vocal structure of vocalisations of the Sabota Lark across the different types of habitats studied,
- ii) investigate the composition of vocalisations of Sabota Larks inhabiting different types of sampled habitats,

- iii) determine if there are significant differences in vocalisations of Sabota Larks that occupy different habitats,
- iv) investigate whether the vocalisations of Sabota Larks can be differentiated based on the types of habitats from which they were collected and probably evolved in.
- v) explore the applicability of an AAH in the Sabota Lark vocalisations.

CHAPTER 2

Spectrogram-based analyses of vocalisations of the Sabota Lark *Calendulauda sabota* (Alaudidae): description, structure, and composition

2.1. Introduction

The vocalisation of birds is divided into songs and calls (Amy *et al.* 2018). The term ‘song’ is generally reserved for the more complex vocalisations that occur in the context of reproduction (Catchpole and Slater 2008), are usually learned, and last longer. The song is mainly used to defend territory, attract mates, stimulate mating, and maintain pair bonds (Naguib and Riebel 2014, Amy *et al.* 2018, Päckert 2018). The term ‘call’, on the other hand, is uttered by both sexes throughout the year in various contexts (Marler 2004), and it is usually less musical, often short, and might consist of one syllable. Song, because of its involvement in reproduction and territory establishment, is subject to intense sexual selection, and this is one of the reasons it displays a variety of acoustic adaptations that no call can rival. However, on the functional level, calls are far more informative than songs. Although they are not involved in reproduction, their functions extend even into behaviours that may seem trivial, like feeding (hunger calls), raising the alarm (alarm calls), and maintaining social proximity (flight calls) (Soha 2020). The involvement of a call in almost all life situations of birds makes it “a goldmine of insights into animal semantics, and many other aspects of vocal communication as it is more deeply involved than song with immediate issues of life and death” (Marler 2004).

The vocalisations of many avian taxa can help reassess the taxonomic status of species to make clear delimitations, determine the presence or absence of species, identify preferred habitats, recognise juveniles, and determine the abundance of predators based on alarm calls (Teixeira *et al.* 2019).

Repertoire includes all the different song or syllable types a bird can sing (Päckert 2018). Repertoire size is a widely used measure of song complexity (Garamszegi *et al.* 2005, Wada 2010). The structure and versatility of bird song can be as simple as one song composed of one note or element henceforth (Wada 2010), defined as the simplest unit of a song repeated a few or many times. Female mate choice has been widely recognised as the selective force driving the evolution of the many extravagant ornaments and displays of males (Forstmeier *et al.* 2021). Thus, female birds are expected to choose the best male singers as mates in the case of singing. Males must devote most of their resources to learning to sing in preparation for the mating season. However, the extent to which the number of song or syllable types sung by a bird i.e., the bird's repertoire, is subject to sexual selection is unknown, and the literature has provided inconsistent evidence (Creanza *et al.* 2016).

The singing behaviour of birds is considered a multifunctional display (Todt and Naguib 2000), with Otte (1974) describing six basic types of information that may be conveyed in animal signals: 1) deictic, drawing attention to an individual or object, 2) identification, specifying age, sex, relationship, individual, species, and so on, 3) spatial, referring to a location, a direction, or a distance, 4) response level, reflecting the motivation of the signaller or the character of some exploitable resource, 5) temporal, indicating the timing of some event, and 6) event, informing on events taking place. In most species, the acoustic features of a single song indicate the species, or the population, to which a singer belongs and an indication of the singer's identity (Todt and Naguib 2000). In addition, there is evidence for a differential use of at least categories of song types concerning social context, time of day, season, or the singer's location within its territory. Furthermore, information reveals that in some species a male's age (quality and fitness) correlates with repertoire size (Collins 2004), i.e., the older the male, the more songs the male bird sings (Collins 2004).

Acoustic signalling is common and of ecological importance, thus making the quantification and comparison of animal vocalisations the major parts of animal behaviour and communication systems research (Keen *et al.* 2021). Among the conspicuous displays, birdsong is an outstanding system that has shown to be an excellent model to address the classical questions about animal behaviour. Therefore, understanding the evolution of complexity in animal communication necessitates knowledge of species repertoire sizes (Botero *et al.* 2008, Harris *et al.* 2016). In

scientific literature, this trait (vocal repertoire) correlates with male quality, parental provisioning, parasite load, body condition, age, lifetime reproductive success which is linked tightly to resource holding potential, and brain morphology (Botero *et al.* 2008).

Estimating repertoire size necessitates defining a biologically relevant unit, e.g., song or syllable types, but the chosen unit should represent a functional unit (Kershenbaum *et al.* 2014, Sainburg *et al.* 2020). The unit of interest can be identified by visual inspection of sound spectrograms in which the units receive unique codes (Garamszegi *et al.* 2005, Kershenbaum *et al.* 2014). However, this classification involves some subjectivity, as it is based on specific criteria defined by the observer. Thus, the reliability of categorisation should be tested by calculating inter-observer repeatability and the reliability of scoring spectrograms by eye (Reid *et al.* 2004, Garamszegi *et al.* 2005). It is required that the appropriate unit be chosen from the recorded song according to the species and biological questions at hand, and further sampling schemes should be adjusted. Species-specific song organisation determines the definition of the basic unit and the subsequent sampling protocol, thus the meaning of repertoire size (Garamszegi *et al.* 2005).

Presentation or singing style is important when quantifying repertoire size in any species (Botero *et al.* 2008). It determines the rate at which new song types accumulate over time and, thus, is the ultimate determinant of the fraction of the total repertoire in a sample of any given size (Botero *et al.* 2008, Harris *et al.* 2016). This means that more repetitive presentation styles will require larger samples than others to achieve comparable levels of accuracy (Botero *et al.* 2008).

Three standard methods are used in assessing repertoire size: simple enumeration, curve-fitting, and capture-recapture analyses (Botero *et al.* 2008, Harris *et al.* 2016). Simple enumeration is counting the number of song types present in a sample of signals and is said to be ideal for species with small repertoires (Harris *et al.* 2016). However, when the repertoire size is large, counting all song types requires large samples and a significant investment of time and effort. In those cases, repertoire size is often estimated, rather than measured directly, via model-based techniques like curve-fitting or capture-recapture analyses (Botero *et al.* 2008). The most basic technique is simple enumeration, which involves counting the unique types of

vocalisations an individual produces (Harris *et al.* 2016). Ideally, the sampling effort should be high enough that the researcher obtains many new recordings without detecting new vocalisation types (Botero *et al.* 2008, Harris *et al.* 2016). The amount of effort required to quantify repertoire size using simple enumeration is influenced by the size of the animal's repertoire, the pattern with which the animal selects its vocalisations, the frequency with which the animal vocalises and whether an animal is a closed-ended learner (i.e., all songs are learned early in life and adult repertoire size is fixed) or an open-ended learner (i.e., songs continue to be learned throughout life) (Harris *et al.* 2016). However, Botero *et al.* (2008) pointed out that their findings did not support the model-based estimation of repertoire size as an ideal replacement for simple enumeration.

Estimating species' vocal repertoires and categorising signals can be complex or time-consuming because acoustic variation across environments, individuals, or even different renditions of a signal by the same individual can be considerable (Keen *et al.* 2021). Furthermore, not all variation in acoustic structure is discrete (Reid *et al.* 2004, Keen *et al.* 2021)). Often, acoustic signals do not fall into distinct categories but rather exhibit continuous variation on multiple axes and, therefore, can be difficult to classify (Keen *et al.* 2021). Bird species differ enormously in the variety of their songs, and diversity and versatility are key features of singing in passerines (Garamszegi *et al.* 2005). However, the quantitative characterisation of the extreme variability of this temporal and structural vocal organisation is a challenging task that makes comparisons among individuals and species difficult (Garamszegi *et al.* 2005, Keen *et al.* 2021).

A typical problem is that it is impossible to measure repertoire size explicitly in birds with virtuoso performances with large repertoires (Botero *et al.* 2008). In such cases, instead of simple enumeration, repertoire size must usually be estimated from a fraction of the whole repertoire (Garamszegi *et al.* 2005, Harris *et al.* 2016). More difficulties may arise when species and individuals differ in singing styles. For instance, similar repertoire sizes may cover different song compositions and virtuosity in different birds. On the other hand, the total amount of song material that two birds produce may be remarkably similar, but dramatic differences may be detected in repertoire size because of the specific organisation of the song output (Garamszegi *et al.* 2005).

Researchers have not agreed on a standard set of units of analyses by which bird songs of various species might be described (Thompson *et al.* 1994). Some terms such as note, syllable, phrase, motif and elements are used by different authors (Williams 2008, Brewer and Fudickar 2022).

In spite of the many terms that have been used to describe bird song, only three methods of generating bird song units have ever been used: temporal method and two methods based on morphological characteristics (Thompson *et al.* 1994, Kershenbaum *et al.* 2014). The temporal method takes account of the pauses in the song stream, whereby the researcher visually scans or measures the spectrographic record and assesses the relative frequency of pauses of different durations (Thompson *et al.* 1994). Such an assessment usually reveals one or more modes in the frequency distributions of pauses; that is, pauses of some durations are much more frequent than others. The traditional way to differentiate temporal units of different orders of duration is to set boundaries between the modes, in the pause distribution, and at points where few pauses are observed (Thompson *et al.* 1994).

In the other two methods, which are based on morphological characteristics, i.e., Morphological Sequence Analyses and Morphological Runs Analyses, the sound stream is broken into segments by taking account of repeated sound patterns (Thompson *et al.* 1994, Sainburg *et al.* 2020). Morphological analyses is most often used to generate higher-order units in a sound stream that has already been divided into basic temporal units. The investigator makes a sound spectrograph of each temporal unit and sorts the spectrograms into piles based on their similarities and differences (Thompson *et al.* 1994, Reid *et al.* 2004). By this method, each pile comes to represent a morphological type, and the members of the pile are the instances of the morphological type. For many songs, this procedure leads to the creation of a basic unit of morphological types (Kershenbaum *et al.* 2014). Even though the members of the different piles may differ in small details, members of the same pile vary so little that independent sorters can usually duplicate one another's work exactly (Thompson *et al.* 1994).

It is estimated that majority of bird species worldwide are passerines ('true perching birds'), with the 'true' or oscine songbirds estimated to consist of about 5000 species and its sister group of suboscines, about 1000 species (Shen 2017). Oscine

songbird species studied show the ability to learn their vocalisations (Catchpole and Slater 2008), whereby species can be closed-ended/age-limited or open-ended/continuous vocal learners. Vocal learning generally refers to producing novel sounds by learning or imitating (Shen 2017). Generally, vocal learning may be limited to the copying of sounds of conspecifics and/or copying of heterospecific or inanimate sounds (Kelley *et al.* 2008). Some scientists maintain that vocal learning includes modifying innate sounds in response to social experience, while others limit the definition to creating entirely new sounds (Shen 2017).

In contrast to vocal non-learners which develop their species-typical vocalisations reliably without the need to hear models (Arato and Fitch 2021), vocal learners need to be exposed to a model of their species-typical vocalisations through hearing to develop reliable species-typical vocalisations. Vocal learning has been recorded in only three bird orders: i) hummingbirds – Apodiformes, Trochilidae, ii) parrots – Psittaciformes, Psittacidae), and iii) perching birds - Passeriformes and some mammals including humans, some cetaceans, pinnipeds, elephants, and bats (Päckert 2018, Martins and Boeckx 2020). In perching birds (Passeriformes), not all species in this group learn their vocalisations; only Oscines, the true songbirds of the suborder Passeri, learn their vocalisations (Päckert 2018). There is, however, empirical evidence of vocal learning abilities in other species outside the taxa, as mentioned above (Martins and Boeckx 2020).

Birds that make seasonal alterations to their vocalisations, either adding to or replacing their repertoires, are called open-ended/continuous vocal learners (Williams 2021), unlike closed-ended/age-limited vocal learners, which memorise a song model early in their lifetime, producing a crystallised version of that song when they first breed, and singing that same song for the rest of their lives e.g., Savannah sparrows *Passerculus sandwichensis* (Williams 2021, Thomas *et al.* 2021). In ‘age-limited learners’, like the White-crowned sparrow *Zonotrichia leucophrys*, individuals can only learn their song during early stages of development, after which song learning comes to a halt (White and Mooney 1999). In many other bird species song learning occurs before sexual maturity and their repertoires remain the same there after (e.g., Zebra finch *Taeniopygia guttata*). In open-ended song learning species song learning occurs even in adulthood (e.g., Brown-headed cowbirds *Molothrus ater*) (Soha 2020).

Nevertheless, age-limited song learners may continue to memorise songs of conspecifics or coexisting species to for use in individual recognition (Soha 2020).

Several wild bird species are known to imitate or mimic not only vocalisations of other species of birds, but also sounds produced by other animals (including humans), and even those of inanimate objects e.g., Albert's lyrebirds *Menura alberti* (Kelly *et al.* 2008, Backhouse *et al.* 2022). Some authors maintain that mimicry may be used in threats, with many imitated calls being those of aggressive species or predators e.g., snake-hissing calls of the nestlings of the open-nesting zitting cisticola *Cisticola juncidis* (Nuttall 1996, Igic *et al.* 2015, Barlow *et al.* 2023). There is mimicry through learning and mimicry because of convergence over generations (Kelly *et al.* 2008). Mimicry through learning is commonly regarded as true vocal mimicry, involving direct learning of sounds from heterospecifics within the lifetime of the mimicking individual (Kelly *et al.* 2008). This is different from evolutionary convergence, whereby bird species (usually closely related) end up rendering similar vocalisations because of being subjected to similar selection pressures, which lead only to the accumulation of mutations and no learning taking place (Kelly *et al.* 2008). There is also vocal matching/convergence evident among conspecifics rather than heterospecifics, whereby individuals alter their vocalisations to match those of their conspecifics e.g., Dupont's Lark *Chersophilus duponti* (Laiolo and Tella 2005). True vocal mimicry is proposed to have functions involved in interspecific and intraspecific communications, but these functions lack significant empirical support (Kelly *et al.* 2008, Barlow *et al.* 2023). The diversity surrounding mimicking species has been shown to influence the repertoire of the mimics. This has been demonstrated the in Crested Lark *Galerida cristata* and the Thekla Lark *G. theklae*, whereby the surrounding bird diversity was found to have a positive effect on the vocal repertoire size of these two mimicking species (Laiolo *et al.* 2011).

According to Thompson and Boughey (1976), Marler (1960) suggested that despite the vast difference in the degree of variability between the songs of highly versatile singers like the mimic thrushes and the songs of non-versatile singers like White-throated Sparrows *Zonotrichia albicollis* and Oregon Juncos *Junco hyemalis*, the songs of the versatile singers, like the songs of the non-versatile singers, include constant features which maintain the species specificity of the songs. As heterospecific mimicry illustrates, the acoustic parameters of sounds that different

species will learn can overlap. Still, restrictions on how mimicked songs are delivered within a repertoire and the inclusion of species-specific songs maintain species distinctiveness (Soha 2020).

The Sabota Lark is a resident species, and males defend their territories throughout the year. This species breeds from October to May, mostly November to January in the east and February to March in the west of the range in southern Africa, associated with the later onset of summer rains in the west (Ryan 2020). The peak breeding is mostly during southern Africa's wet season (October - March) (Engelbrecht and Mashao 2019). The Sabota Lark *Calendulauda sabota* (Smith, 1836) (Alaudidae) is the most common and widespread lark in southern Africa and is near-endemic to the region, extending marginally into the coastal regions of Angola (de Juana *et al.* 2020) (Fig.1.2). Sabota Larks thrive in diverse habitats that range from reasonably dense, broad-leaved woodland and more open, semi-arid *Vachellia* Savanna, to structurally simple Karoo scrub and desert margins. These larks are discontinuous singers instead of warbling, presenting their songs with silent inter-song intervals. While the literature contains information about vocalisations of some species' songs and calls, the song or syllable types making up the songs and their repertoire sizes, the Sabota Lark vocalisations, to my knowledge, have not been studied extensively. These include species-specific vocalisations, the frequency with which they vocalise, the pattern with which they select and present their vocalisations, whether they are closed-ended learners or open-ended learners, their repertoire size, and whether their repertoire size relates to age, mimicry, and dialects. In this chapter, the focus was on studying vocalisations of Sabota Larks that thrive in different habitats with special emphasis on understanding the songs' visual structure and composition.

2.1.1. Aim

To investigate the structure and composition of the Sabota Lark *Calendulauda sabota* songs across the different types of habitats in which the species occurs.

2.1.2. Objectives

The objectives investigated were:

- i) to describe the song of Sabota Lark
- ii) to determine the presentation or singing style exhibited in songs of Sabota Larks and the number of song strophes across the different types of habitats
- iii) to identify and classify unique song types that make up the songs of Sabota Larks recorded across the different types of habitats studied
- iv) to find out if there were shared or overlapping song types given by birds recorded in different habitats.

2.2. Materials and methods

2.2.1. Data collection – selection of collection sites, recording of songs, and capturing of Global Positioning System (GPS) coordinates of song recordings.

Fieldwork was mainly conducted during the breeding seasons in the Limpopo and Northern Cape Provinces South Africa, in the dry and moist Savanna woodlands and the arid Nama-Karoo shrublands. Appendix 2.1 shows that most of the recordings of vocalisations (henceforth songs) were made during the months ranging mainly from September to March (and May), with some recordings obtained in June. Nine sites from which the Sabota Lark songs (sung by males) were recorded were selected: six in the Limpopo Province and three in the Northern Cape Province. The six sites in Limpopo Province were Limpokwena Nature Reserve (LNR), Kruger National Park (KNP), De Loskop (DLK), Polokwane Nature Reserve (PNR), Blouberg Nature Reserve (BNR), Maribana and the three sites in the Northern Cape Province were Pofadder, Kenhardt, and Brandvlei. The sampled sites needed to include the major habitat types occupied by the species, i.e., *Vachellia* Savanna, broad-leaved Savanna woodland and scrub, and Karoo scrub.

All recordings of songs, except the 16 recordings obtained from the Northern Cape Province in September 2022, were recorded before the present study. Efforts were made to ensure that the songs were obtained from at least five randomly

recorded territorial males at the study sites (Kent and Carmel 2011), but this was not always possible. When it was possible to identify a songster individually, e.g., a colour-marked individual, it is possible that multiple recordings may have been obtained from the same individual. In instances where the songster was not a marked individual, care was taken to allow > ~250 m between individuals to ensure that repertoires and recordings of different individuals were not pooled. The 75 recordings represent 49 birds: nine from KNP, three from LNR, seven from DLK, one from BNR, one from Maribana, five from PNR, one from Kenhardt, two from Pofadder, and 20 from Brandvlei (Appendix 2.1, Table 2.1). A Marantz PMD670 Professional digital recorder and a Sennheiser ME66 directional microphone were used to record vocalisations. Of the 75 recordings, 14 were recorded in the KNP, 18 at LNR, seven at DLK, one at BNR, one at Maribana, eight in the PNR, 23 in the Brandvlei region, one near Kenhardt, and two in Pofadder (Table 2.1). Songs were recorded between 15 and 25 metres from the songster. No playback was used to illicit singing in this study. Recordings made in the Northern Cape were for one breeding season, late September to early October 2022.

Table 2.1. The collection sites from which the Sabota Lark songs were recorded and field identification codes of songs.

Province	Collection sites	Song recordings and field identification codes
Limpopo Province	Limpokwena Nature Reserve (LNR)	1045, 1046, 1047, 1049, 1053, 1054, 1055, 1056, 1057, 1061, 1062, 1064, 1065, 1069, 1070, 1072, 1073, 1077
	Kruger National Park (KNP)	1001, 1007, 1008, 1009, 1013, 1015, 1017, 1034, 1078, 1079, 1076, 1004, 1005, 1006
	Polokwane Nature Reserve (PNR)	1002 (2), 1013, 1016, 1017, 1018, 1019, 1021, 1027
	Blouberg Nature Reserve (BNR)	1036
	De Loskop (DLK)	1002, 1019, 1026, 1030, 1046, 1051, 1044
	Maribana	1037
Northern Cape	Pofadder	1095, 1143
	Kenhardt	1136
	Brandvlei	1001, 1002, 1003, 1006, 1007, 1008, 1137, 1138, 1006w, 1207, 1168, 1205, 1023, 1145, 1146, 1153, 1155, 1156, 1165, 1210, 1187, 1152, 1151

The GPS coordinates associated with the exact localities in sites where the recordings of songs were made were captured in MS Excel; this information is contained in Appendix 2.1.

2.2.2. Data analyses – spatial mapping, analyses of songs and generation of spectrograms, observed aspects of the Sabota Lark song that were considered, classification of song strophes and song types, and terminology.

The two terms, habitat and vegetation, are sometimes considered synonymous, but Kirk *et al.* (2018) recommended the definition of habitat as defined by Hall *et al.* (1997): "... habitat is the resources and conditions present in an area that produce occupancy including survival and reproduction by a given organism". Habitat is organism-specific and relates the presence of a species, population, or an individual (animal or plant) to an area's physical and biological characteristics. This is the definition adopted in this study, with vegetation being one of the variables that make up a habitat. Habitat implies more than vegetation or vegetation structure; it is the sum of the specific resources organisms need.

A vegetation map showing only the collection sites from which the recordings of songs were obtained (*viz.*, KNP, LNR, DLK, BNR, PNR, Maribana, Brandvlei, Kenhardt, and Pofadder), was generated using ArcGIS (version 10.8) (ESRI 2020). The vegetation shapefile was obtained from the South African National Biodiversity Institute (SANBI 2018). A layer consisting of the GPS coordinates associated with the recorded songs was added to the analyses.

The generated map shown in Figure 2.1 revealed that the birds recorded in the six sites in Limpopo Province were inhabiting nine types of vegetation within two bioregions (Mopane-mp and Central Bushveld-cb) of the Savanna biome (Mucina and Rutherford 2006). LNR and KNP fall within the Mopane (mp) bioregion while Maribana, DLK, BNR, and PNR fall within the Central Bushveld (cb) bioregion. In LNR, the vegetation type is Musina Mopane Bushveld (MMB). At the same time, in KNP, the birds were recorded in three vegetation types: Mopane Basalt Shrubland (MBS), Mopane Gabbro Shrubland (MGS), and Tsende Mopaneveld (TM). Regarding the sites in the Central Bushveld-cb bioregion, the PNR vegetation type is Polokwane Plateau Bushveld (PPB), for BNR, is Roodeberg Bushveld (RB), while in DLK and Maribana, the birds were recorded in Makhado Sweet Bushveld (MSB). In the Northern Cape Province, the recorded birds were inhabiting two types of vegetation, Bushmanland Arid Grassland (BAG) and Bushmanland Basin Shrubland (BBS) that

are classified in the Bushmanland-b bioregion of the Nama-Karoo biome (Mucina and Rutherford 2006) (Table 2.2).

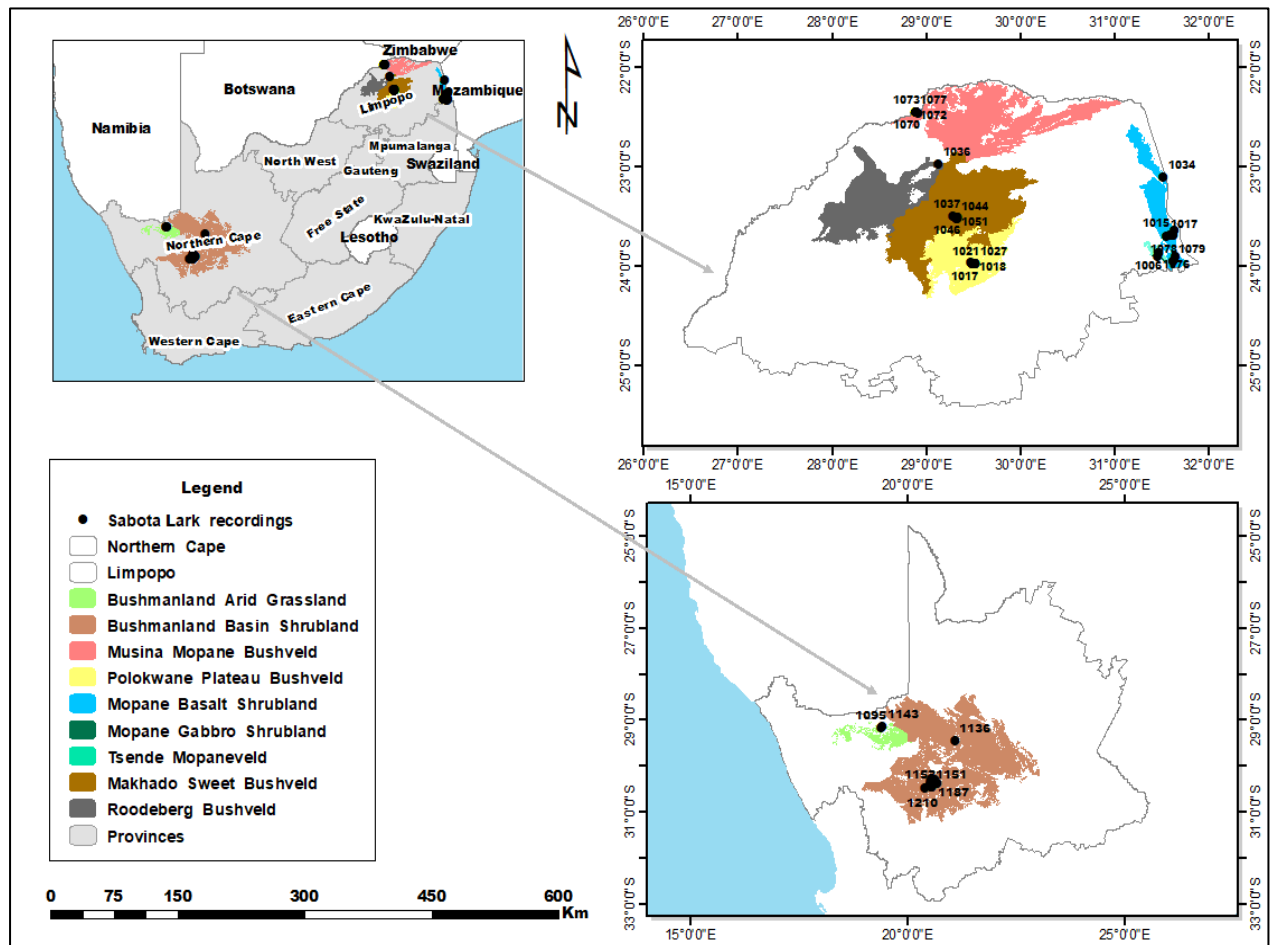


Figure 2.1. A spatial map showing the collection sites, vegetation types and the exact locality points from which the songs were recorded.

In the field, efforts were made to ensure the recording of good-quality recordings of songs that are free from high levels of background noise from other species. Along these lines, only 16 of the 23 recordings made in Brandvlei were included in the analyses, and only one of the two made in Pofadder was included. This resulted in an analyses of a total of 67 recordings. Songs were imported and analysed in Avisoft SAS Lab Pro (Bioacoustics sound analyses software, version 5.2.11) (Specht 2017). The maximum number of good quality song strophes were cut out from each song recorded for individual birds. In cases where recordings of songs were marred by background noise, caution was taken to remove noise, avoiding tempering with the actual song information. Song strophes are defined in this study as a

continuous flow of elements, mostly repeated multiple times, often making up the entire song or piece and are separated from the other strophes by pauses of varying lengths (Rutkowska-Guz and Osiejuk 2004; Alström *et al.* 2010). A total of 992 song strophes were extracted with 265 song strophes extracted from KNP song recordings, 275 strophes from LNR song recordings, 103 strophes from DLK, 10 strophes Maribana, 40 strophes from BNR, 77 strophes from PNR, one strophe from Pofadder, 5 strophes from Kenhardt, and 216 strophes from Brandvlei (Table 2.2).

Spectrograms were generated with the following settings being considered: the Fast Fourier Transform (FFT) with a length of 1024, 100% frame size and a Blackman window, while the overlap was kept at 87.5%. All original song recordings had different sampling frequencies but were resampled to a sampling frequency of 32,000 Hz during the generation of spectrograms. Based on the visual characteristics of the spectrograms and their respective temporal and spectral or frequency characteristics, the general descriptions of the song strophes were made.

Table 2.2. A list of all the sites and the associated vegetation types as shown in Figure 2.1, from which the Sabota Lark song recordings were obtained. This table only shows the number of birds and song recordings included in the analyses. The number of song strophes extracted from the recorded song is also provided.

Province	Recording site	Vegetation type (acronym)	Number of birds recorded	Number of song recorded	Number of song strophes
Limpopo Province	Limpokwena Nature Reserve (LNR)	Musina Mopane Bushveld (MMB)	3	18	275
	Kruger National Park (KNP)	Tsende Mopaneveld (TM)	1	3	61
		Mopane Basalt Shrubland (MBS)	7	10	193
		Mopane Gabbro Shrubland (MGS)	1	1	11
	Polokwane Nature Reserve (PNR)	Polokwane Plateau Bushveld (PPB)	5	8	77
	Blouberg Nature Reserve (BNR)	Roodeberg Bushveld (RB)	1	1	40
	De Loskop (DLK)	Makhado Sweet Bushveld (MSB)	7	7	113
	Maribana	Makhado Sweet Bushveld (MSB)	1	1	10

Northern Cape Province	Pofadder	Bushmanland Arid Grassland (BAG)	1	1	1
	Kenhardt	Bushmanland Arid Grassland (BAG)	1	1	5
	Brandvlei	Bushmanland Basin Shrubland (BBS)	13	16	216

Some species of larks, including the Sabota Lark, are known to mimic the songs of other species. Investigation into mimicry did not form part of this study.

The vocal unit of interest in this study was song strophe. Based on the spectrograms, the inter-element intervals within the song strophes were shorter than the interval between the song strophes. Inter-song strophe intervals were, on mean, greater than 1 s, while inter-element intervals were less than 1 s on mean. Individual birds appeared to repeat some song types before switching to new ones when singing. Based on these observations, song strophe was defined as a sequence of syllables separated from others by a period of silence (>1 s) substantially exceeding the usual time interval between the syllables (approximately <1 s). Song type was defined as the set of syllable types consistently repeated in songs or songs composed from the same syllable types. However, the songs differ in the total number and sequence of syllables. Song types usually have the same syllable composition and order; thus, there is little variance between different renditions of a particular song type (Průchová *et al.* 2017). Spectrograms were morphologically analysed, considering repeated patterns of sound. They were then sorted into piles based on their similarities and differences. Each pile came to represent a morphological type, and the members of the pile, the instances of the morphological type. Even though the members of the different piles may differ in some details, members of the same pile have at least most elements in common (Thompson *et al.* 1994).

Song strophes – the work of Moyer *et al.* (2022) was followed to determine the beginning and the end of song strophes, which were then considered the biological units of interest in this study. The song strophes were classified visually based on i) having elements that are at least presented in the same order most of the time within strophes making up the songs that were sampled, and ii) the global structure of the spectrograms which shows the dominant features in the spectrograms. The song

strophes that share parts marked by similar order or sequence of elements were classified as the same song types and given a number for easy identification and reference purposes, such as song type 1. Every new strophe was compared with all the other strophes, and if different, it was then regarded as a separate song type and given a different song type number, e.g., song type 2. The song strophes and song types shared between the study sites were also identified and given the same identification name as the song strophe or song type identified earlier.

Different terms for studying vocal communication in birds that sing are available in various publications. In this study, the terms that were used included:

- i) song was defined as a series of three or more different elements sung without interruption (cf. Barrington 1773),
- ii) bout, which is an undisturbed sequence of song strophes sung by a male (Rutkowska-Guz and Osiejuk 2004).
- iii) song strophe is a continuous flow of elements, mostly repeated multiple times, separated from other strophes by pauses of varying lengths (Rutkowska-Guz and Osiejuk 2004; Alström *et al.* 2010). In this study, song strophe was defined as a sequence of syllables separated from others by a period of silence or pause (>1 s), substantially exceeding the usual time interval between the syllables (approximately <1 s).
- iv) syllables consist of the smallest units, i.e., elements, that occur together in a regular pattern and could be repeated several times.
- v) song type was defined as a different version of the song and varies within and among individual birds.
- vi) An element refers to the smallest unit of the song (Wada 2010) or the song strophe separated from the others by pauses.
- vii) phrase or motif consists of one syllable or a series of more than one identical syllables.
- viii) the repertoire was defined as the sum of all different songs (or song types) produced by individual birds and recorded and analysed in the context of this study.

However, the definitions of the terms used in Brenowitz *et al.* (1997), Wada (2010) and ten Cate and Okanoya (2012) were adopted to define an element, a syllable, and a phrase or motif. Some of the terms are annotated in Figure 2.2.

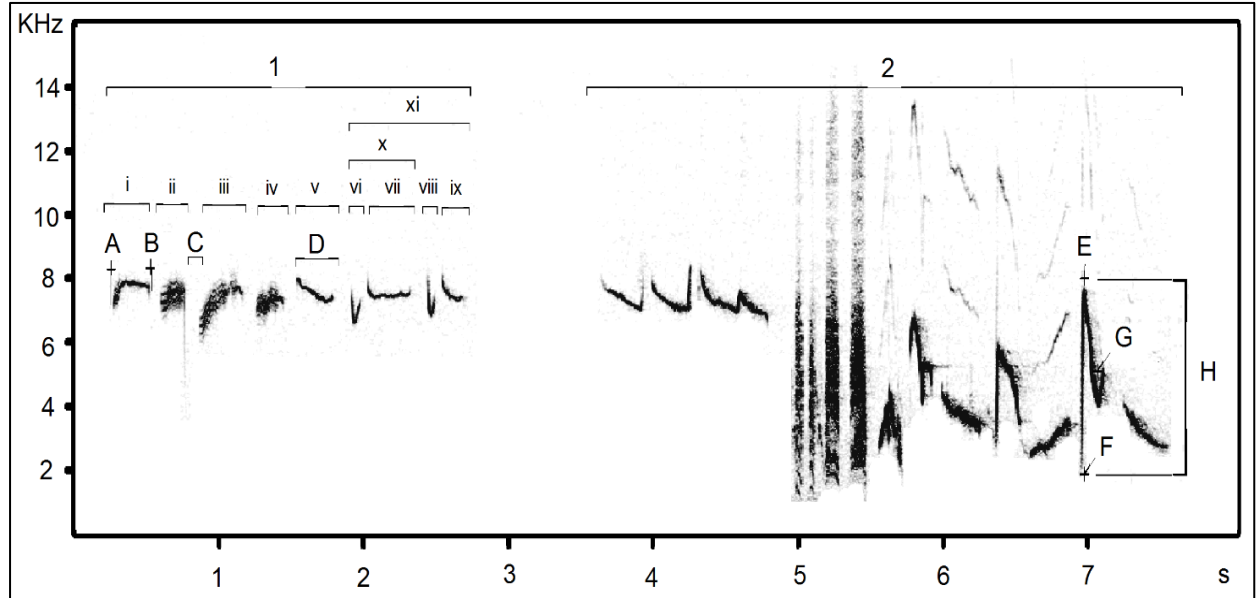


Figure 2.2. Examples of annotated spectrograms of two song strophes. 1 refers to strophe 1 (Calsab 1046_1_40to43s), 2 - strophe 2 (Calsab 1046_2_46to50s), i-ix - individual elements (i.e., i is the first element), x - syllable, xi - phrase, A - element start time, B - element end time, C - inter-element interval, D - element duration, E - element maximum frequency, F - element minimum frequency, G - element peak frequency and H - element bandwidth frequency. In Calsab 1046_1_40to43s, Calsab abbreviates *Calendulauda sabota*, 1046 - field identification code, 1 - the first strophe in a specific song recording, 40to43s - refers to the time range or block (in s - seconds) occupied by a specific strophe along the song recording. The interval between strophe 1 and strophe 2 was artificially shortened for illustrative purposes.

2.3. Results

2.3.1. The Sabota Lark song

A typical Sabota Lark song was described in this study as a highly complex and modulated structurally diverse piece (ranging from less than 1 minute to at least 5 to 6 minutes) (Table 2.3a-k, Appendix 2.2), characterised by having few to multiple song strophes that are mostly repeated varying number of times in random to some order.

In most or rather some cases, the song strophes and or unique song types were led by two to several independent introductory whistled elements and what follows could not be predicted, i.e. it could be a variety of few to multiple syllables and/or phrases (see Calsab 1045_1_6to9s_MBS1 – Appendix 2.2, Calsab 1079_17_112to115s_MBS7 – Appendix 2.3), Calsab 1002_1_3to6s_PP1 – Appendix 2.3).

2.3.2. Presentation or singing style of Sabota Larks

The presentation or singing style of Sabota Larks was found to vary within and among individual birds. Individually, some birds repeated certain song types at least twice before switching to a new or another song type, and this style of singing is called “eventual variety” (see Figs. 2.3a, b). There were also song types that were only rendered once and never twice or multiple times in succession. This is called “immediate” variety, which means that the birds switched straight to new song types without having to repeat song types. Therefore, Sabota Larks explored both types of presentation and singing styles. (Figs. 2.3a, b)

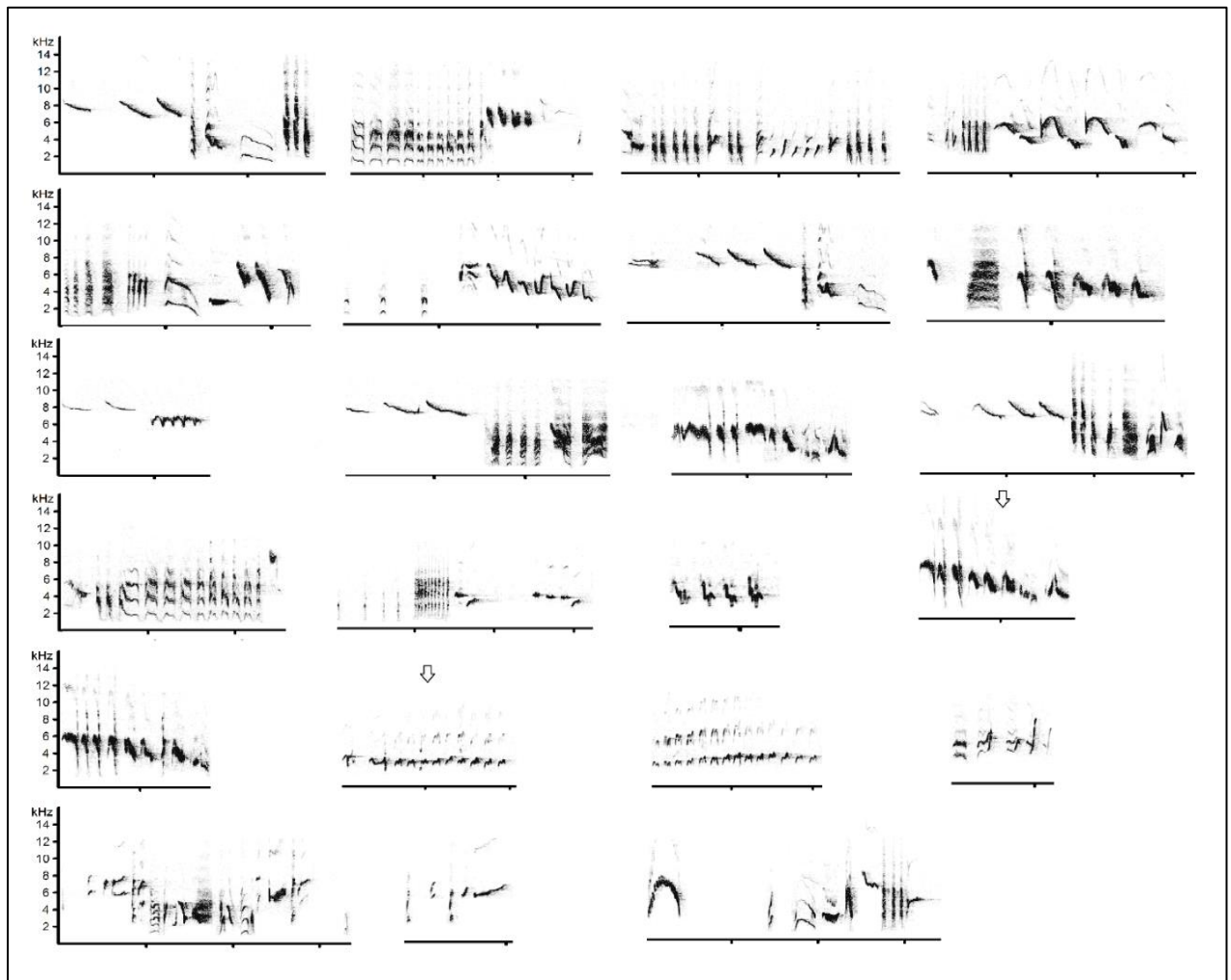


Figure 2.3(a). An example of song presentation style by an individual Sabota Lark recorded in Musina Mopane Bushveld-MMB1 (Calsab 1045). Pauses between strophes have been artificially shortened for illustration purposes. The arrows point to song types repeated at least twice in succession (eventual variety), and intercalated parts with no arrows show immediate variety style.

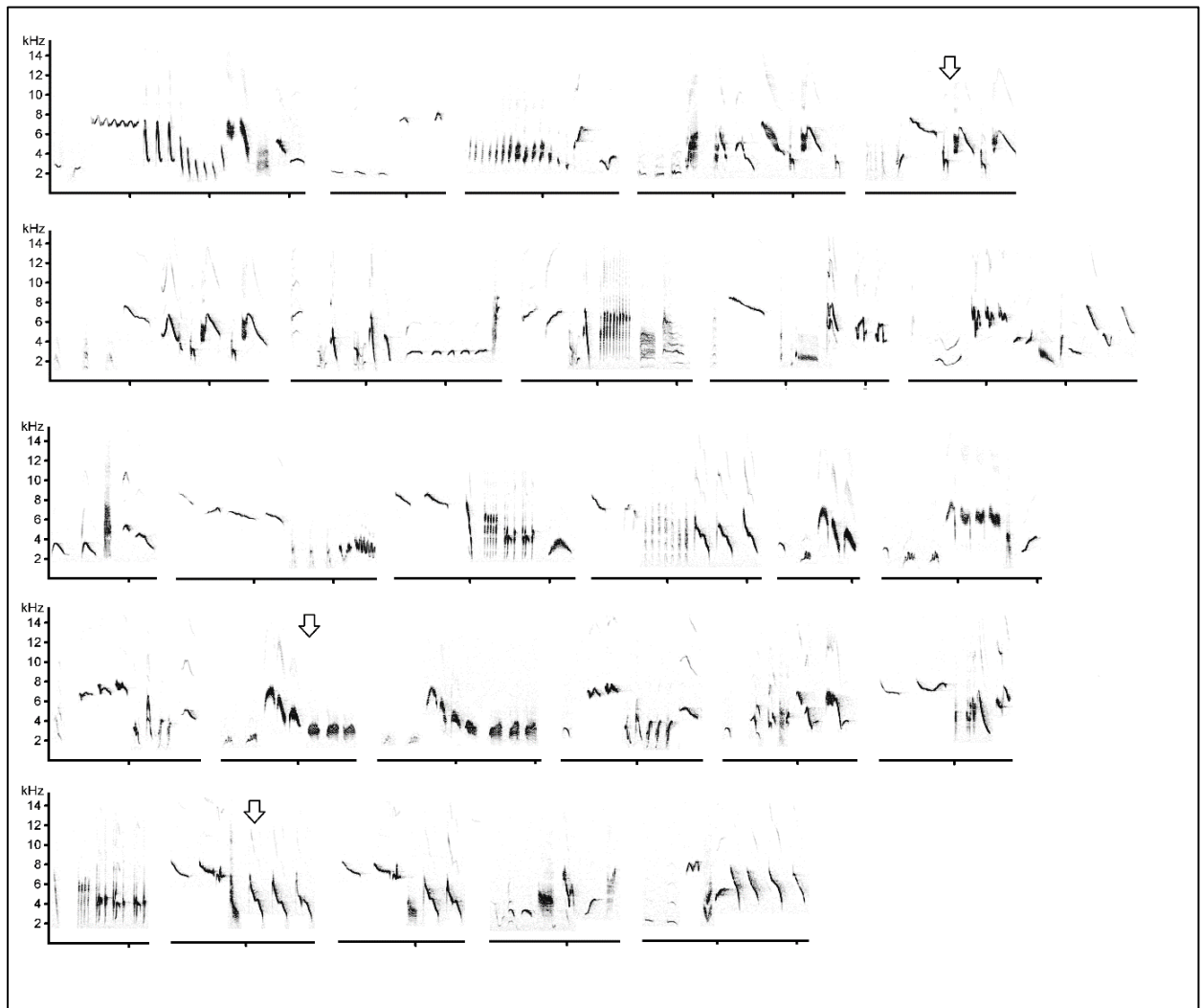


Figure 2.3(b). An example of song presentation style by an individual Sabota Lark recorded in Musina Mopane Bushveld-MMB 1 (Calsab 1057). Pauses between strophes have been artificially shortened for illustration purposes. The arrows point to song types repeated at least twice in succession (eventual variety), and intercalated parts with no arrows show immediate variety style.

2.3.3. Song strophes, unique and shared song types

The simple enumeration technique that involved counting parts (song strophes and song types) from the songs coupled with Morphological Sequence Analyses and Morphological Runs Analyses yielded 992 song strophes (Tables 2.3a-k). From these, 481 song types (Table 2.5 and Appendix 2.2) were identified visually from the generated spectrograms. The song types were assigned unique codes (Table 2.4a-k).

The rest of the results sections were extracted from Tables 2.3a-k and 2.4a-k; therefore, these tables were clearly explained in those sections.

Table 2.3(a-k). The number of individual birds recorded in each vegetation type accompanied by the number of song strophes and the number of song types produced by each bird. Calsab 1045 stands for *Calendulauda sabota* individual bird number 1045. The acronym and associated vegetation types are as follows: a) MMB-Musina Mopane Bushveld, b) MBS-Mopane Basalt Shrubland, c) TM-Tsende Mopaneveld, d) MG-Mopane Gabbro Shrubland, e) RB-Roodeberg Bushveld, f) and g) MSB-Mopane Sweet Bushveld, h) PPB-Polokwane Plateau Bushveld, i) BBS-Bushmanland Basin Shrubland, and j) and k) BAG-Bushmanland Arid Grassland.

a) Musina Mopane Bushveld (SVmp1) Limpopo Nature Reserve					
Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
MMB1	4	Calsab 1045	5.28	23	39
		Calsab 1046	2.55	12	
		Calsab 1047	5.07	17	
		Calsab 1057	2.55	23	
MMB2	1	Calsab 1049	4.38	35	23
MMB3	13	Calsab 1054	5.35	41	78
		Calsab 1055	2.31	4	
		Calsab 1056	1.08	2	
		Calsab 1053	2.36	23	
		Calsab 1061	0.37	2	
		Calsab 1062	0.43	3	
		Calsab 1064	4.49	23	
		Calsab 1065	1.36	4	
		Calsab 1069	1.45	5	
		Calsab 1070	2.33	20	
		Calsab 1072	2.46	12	
		Calsab 1073	0.41	5	
		Calsab 1077	5.34	21	
Total	18			275	

b) Mopane Basalt Shrubland (SVmp4) Kruger National Park

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
MBS1	1	Calsab 1001	3.51	31	17
MBS2	3	Calsab 1007	1.36	4	6
		Calsab 1008	0.52	2	
		Calsab 1009	5.47	3	
MBS3	1	Calsab 1013	3.13	30	9
MBS4	1	Calsab 1015	5.32	54	18
MBS5	1	Calsab 1017	4.13	19	17
MBS6	1	Calsab 1034	2.12	18	2
MBS7	2	Calsab 1078	1.14	6	18
		Calsab 1079	3.41	26	
Total	10			193	

c) Tsende Mopaneveld (SVmp5) Kruger National Park

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types
TM1	3	Calsab 1004	6.50	37	32
		Calsab 1005	3.55	12	
		Calsab 1006	2.11	12	
Total	3			61	

d) Mopane Gabbro Shrubland (SVmp8) Kruger National Park

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types
MGS1	1	Calsab 1076	3.18	11	11
Total	1			11	

e) Roodeberg Bushveld (SVcb18) Blouberg Nature Reserve

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types
RB1	1	Calsab 1036	5.15	40	31
Total	1			40	

f) Makhado Sweet Bushveld (SVcb20) De Loskop

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
MSB1	1	Calsab 1030	0.44	2	3
MSB2	1	Calsab 1046	2.08	20	14
MSB3	1	Calsab 1051	5.13	38	12
MSB4	1	Calsab 1002	2.29	10	8
MSB5	1	Calsab 1019	2.59	18	18
MSB6	1	Calsab 1026	2.14	9	7
MSB7	1	Calsab 1044	4.57	6	1

Total	8			113	
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g) Makhado Sweet Bushveld (SVcb20) Maribana

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
MSB8	1	Calsab 1037	6.06	10	6
Total	1			10	6

h) Polokwane Plateau Bushveld (SVcb23) Polokwane Nature Reserve

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
PPB1	1	Calsab 1002 (2)	0.52	4	3
PPB2	1	Calsab 1013 PNR	2.16	10	7
PPB3	1	Calsab 1016 PNR	1.58	15	2
PPB4	4	Calsab 1017 PNR	4.15	18	28
		Calsab 1018 PNR	3.19	8	
		Calsab 1021 PNR	3.28	8	
		Calsab 1019 PNR	4.41	13	
PPB5	1	Calsab 1027 PNR	3.00	1	1
Total	8			77	

i) Bushmanland Basin Shrubland (NKb6) Brandvlei

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
BBS1	1	Calsab 1001	0.45	4	4
BBS2	2	Calsab 1002	1.29	8	25
		Calsab 1003	2.44	24	
BBS3	1	Calsab 1006	0.32	3	3
BBS4	1	Calsab 1007	1.11	15	6
BBS5	1	Calsab 1008	2.58	24	22
BBS6	1	Calsab 1138	6.33	53	43
BBS7	1	Calsab 1006 Windpomp	1.51	16	15
BBS8	1	Calsab 1168	3.09	14	8
BBS9	2	Calsab 1205	2.56	20	5
		Calsab 1203	3.26	9	
BBS10	1	Calsab 1145	0.27	2	1
BBS11	1	Calsab 1153	0.15	1	1
BBS12	1	Calsab 1156	2.48	11	10
BBS13	2	Calsab 1152	1.33	4	9

		Calsab 1151	3.30	8	
Total	16			216	

j) Bushmanland Arid Grassland (NKb3) Kenhardt

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
BAG1	1	Calsab 1136	0.52	5	5
Total	1			5	

k) Bushmanland Arid Grassland (NKb3) Pofadder

Individual bird no.	No. of recordings	Recording Identity no.	Duration of recordings (minutes)	No. of strophes	No. of song types per bird
BAG2	1	Calsab 1095	2.08	1	1
Total	1			1	

Table 2.4(a-k). Number of song types per individual bird in each vegetation type. Calsab 1045 stands for *Calendulauda sabota* individual bird number 1045, 1 (MM) means song type 1 from MMB-Musina Mopane Bushveld, 117 (MS) - song type 117 from MSB-Makhado Sweet Bushveld, TM-Tsende Mopaneveld, MGS-Mopane Gabbro Shrubland, MBB-Mopane Basalt Bushveld, RB-Roodeberg Bushveld, PPB-Polokwane Plateau Bushveld, BAG-Bushmanland Arid Grassland, BBS-Bushmanland Basin Shrubland. The order of song types in the tables is not necessarily the order in which song types were presented in the recordings by individual birds.

a) Musina Mopane Bushveld (SVmp1) Limpokwena Nature Reserve

Individual bird no.	Recording ID no.	Song types	Total
MMB1	Calsab 1045	1, 2, 9, 11, 12, 15, 18, 19, 20, 21, 31, 32, 43, 52	39
	Calsab 1046	1, 2, 5, 9, 11, 15, 18, 19, 31, 34, 35, 105	
	Calsab 1047	1, 2, 17, 18, 27, 28, 35, 36, 64, 106, 107, 108	
	Calsab 1057	1, 4, 18, 22, 26, 45, 50, 69, 70, 71, 72, 73, 74, 75, 90	
MMB2	Calsab 1049	1, 3, 20, 22, 38, 39, 40, 41, 42, 54, 56, 97, 98, 101, 102, 103, 104, 109, 110, 111, 112, 113, 114	23
MMB3	Calsab 1054	1, 2, 7, 9, 11, 14, 17, 18, 19, 20, 21, 23, 25, 30, 32, 33, 43, 44, 48, 51, 53, 57, 58, 59, 60, 61, 62, 63, 66, 75, 99	78
	Calsab 1055	4, 50, 67	
	Calsab 1056	19, 68	
	Calsab 1053	1, 2, 9, 12, 13, 18, 19, 20, 21, 24, 25, 32, 33, 53, 55, 78, 115, 116	
	Calsab 1061	27, 76	
	Calsab 1062	46, 77	
	Calsab 1064	1, 2, 9, 11, 13, 16, 18, 19, 21, 29, 30, 33, 34, 43, 44, 49, 51, 52, 79, 80, 81,	
	Calsab 1065	1, 9, 30, 82	

	Calsab 1069	1, 9, 11, 35	
	Calsab 1070	1, 2, 9, 10, 12, 13, 19, 20, 25, 33, 47, 48, 49, 83, 84, 100	
	Calsab 1072	1, 11, 27, 37, 44, 51, 65, 85, 86, 87, 88, 96	
	Calsab 1073	25, 43, 47	
	Calsab 1077	1, 6, 8, 9, 13, 21, 22, 29, 48, 50, 89, 91, 92, 93, 94, 95, 96,	

b) Roodeberg Bushveld (SVcb18) Blouberg Nature Reserve

Individual bird no.	Recording ID no.	Song types	Total
RB1	Calsab 1036	1 (MM), 123 (MS), 25 (MM), 7 (MM), 18 (MM), 26 (MM), 124 (MS), 125, 129, 130, 131, 132, 143 (MS), 146, 151, 156, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179, 180, 181, 182, 183, 184	31

c) Makhado Sweet Bushveld (SVcb20) De Loskop

Individual bird no.	Recording ID no.	Song types	Total
MSB1	Calsab 1030 De Loskop	2 (MM), 169	3
MSB2	Calsab 1046 De Loskop	1 (MM), 121, 123, 124, 137, 138, 139, 147, 160, 185, 186, 187, 188, 189	14
MSB3	Calsab 1051 De Loskop	120, 123, 9 (MM), 32 (MM), 124, 126, 127, 128, 140, 141, 142, 143	12
MSB4	Calsab 1002 De Loskop	117, 2 (MM), 122, 128, 148, 149, 157, 190	8
MSB5	Calsab 1019 De Loskop	119, 122, 124, 142, 150, 152, 153, 154, 155, 156, 158, 159, 161, 162, 163, 164, 165, 191	18
MSB6	Calsab 1026 De Loskop	1 (MM), 118, 12 (MM), 166, 167, 168	7
MSB7	Calsab 1044	136	1

d) Makhado Sweet Bushveld (SVcb20) Maribana

Individual bird no.	Recording ID no.	Song types	Total
MSB8	Calsab 1037	117, 133, 134, 135, 144, 145	6

e) Polokwane Plateau Bushveld (SVcb23) Polokwane Nature Reserve

Individual bird no.	Recording ID no.	Song types	Total
PPB1	Calsab 1002 (2) PNR	1 (MM), 203, 9 (MM)	3
PPB2	Calsab 1013 PNR	2 (MM), 1 (MM), 117 (MS), 194, 204, 205, 206	7
PPB3	Calsab 1016 PNR	196, 197	2
PPB4	Calsab 1017 PNR	2 (MM), 1 (MM), 192, 117 (MS), 198, 200, 201, 207, 209	28

	Calsab 1018 PNR	1 (MM), 117 (MS), 195, 199, 124 (MS)	
	Calsab 1021 PNR	123 (MS), 215, 216, 30a, 217, 218	
	Calsab 1019 PNR	1 (MM), 193, 117 (MS), 124 (MS), 202, 208, 210, 211, 212, 213, 214, 219	
PPB5	Calsab 1027 PNR	117 (MS)	1

f) Mopane Basalt Shrubland (SVmp4) Kruger National Park			
Individual bird no.	Recording ID no.	Song types	Total
MBS1	Calsab 1001	220, 229, 230, 231, 234, 142 (MS), 235, 236, 237, 264, 265, 280, 305, 306, 307, 315, 316	17
MBS2	Calsab 1007	221, 19 (MM), 279, 319	6
	Calsab 1008	19 (MM), 263	
	Calsab 1009	223, 263	
MBS3	Calsab 1013	222, 224, 225, 228, 123 (MS), 26 (MM), 248, 249, 320	9
MBS4	Calsab 1015	1 (MM), 226, 123 (MS), 250, 251, 252, 19 (MM), 253, 259, 260, 133 (MS), 281, 289, 292, 296, 304, 321, 334	18
MBS5	Calsab 1017	227, 232, 123 (MS), 133 (MS), 267, 275, 276, 277, 278, 285, 294, 295, 310, 311, 312, 322, 335	17
MBS6	Calsab 1034	254, 255	2
MBS7	Calsab 1078	123 (MS), 258, 261, 262, 268, 272	18
	Calsab 1079	1 (MM), 123 (MS), 247, 256, 257, 258, 261, 262, 271, 282, 296, 297, 313, 314, 325, 330	

g) Tsende Mopaneveld (SVmp5) Kruger National Park			
Individual bird no.	Recording ID no.	Song types	Total
TM1	Calsab 1004	233, 238, 239, 240, 241, 242, 123 (MS), 258 (MB), 266, 269, 283, 284, 286, 287, 290, 291, 12 (MM), 308, 309, 318, 323, 329, 331, 332, 333, 336	32
	Calsab 1005	238, 242, 123 (MS), 258, 270, 274, 17 (MM), 298, 301, 324	
	Calsab 1006	243, 245, 246, 258, 293, 299, 302, 317	

h) Mopane Gabbro Shrubland (SVmp8) Kruger National Park			
Individual bird no.	Recording ID no.	Song types	Total
MGS1	Calsab 1076	1 (MM), 142 (MS), 123 (MS), 273, 11 (MM), 288, 300, 303, 326, 327, 328,	11

i) Bushmanland Basin Shrubland (NKb6) Northern Cape			
Individual bird no.	Recording ID no.	Song types	Total
BBS1	Calsab 1001	348, 364, 382, 421	4
BBS2	Calsab 1002	11 (MM), 365, 366, 395, 422, 452	25
	Calsab 1003	11 (MM), 337, 365, 366, 367, 368, 369, 383, 384, 397, 398, 399, 400, 424, 425, 426, 427, 434, 447, 454, 455, 467	
BBS3	Calsab 1006	428, 448, 449	3
BBS4	Calsab 1007	342, 343, 344, 345, 372, 435	6
BBS5	Calsab 1008	1 (MM), 349, 158 (MS), 387, 396, 405, 406, 407, 408, 409, 423, 436, 437, 438, 439, 444, 445, 446, 450, 457, 459, 460	22
BBS6	Calsab 1138	139 (MS), 2 (MM), 350, 351, 362, 363, 367, 371, 372, 373, 374, 375, 376, 377, 378, 379, 380, 381, 388, 389, 390, 391,	43

		392, 394, 411, 414, 415, 416, 417, 418, 419, 420, 440, 441, 442, 443, 451, 461, 462, 463, 464, 465, 466	
BBS7	Calsab 1006 Windpomp	339, 364, 370, 385, 386, 401, 402, 403, 429, 430, 431, 433, 453, 456, 458	15
BBS8	Calsab 1168	340, 341, 345, 358, 361, 479, 480, 481	8
BBS9	Calsab 1205	345, 355, 356, 357	5
	Calsab 1023	345, 347	
BBS10	Calsab 1145	347	1
BBS11	Calsab 1153	471	1
BBS12	Calsab 1156	338, 359, 360, 372, 373, 374, 375, 376, 377, 378	10
BBS13	Calsab 1152	346, 353, 354, 470	9
	Calsab 1151	352, 353, 381, 432, 468, 469	

j) Bushmanland Arid Grassland (NKb3) Kenhardt			
Individual bird no.	Recording ID no.	Song types	Total
BAG1	Calsab 1095	345 (BS)	1

k) Bushmanland Arid Grassland (NKb3) Pofadder			
Individual bird no.	Recording ID no.	Song types	Total
BAG2	Calsab 1136	393, 404, 410, 412, 413	5

2.3.3.1. Song types unique to the vegetation types and song types shared

The songs recorded from Sabota Larks that occur in Musina Mopane Bushveld (SVmp1) were analysed first (an arbitrary choice), and a total of 116 song types were gained from this vegetation type (Table 2.5). Mopane Basalt Shrubland (SVmp4) yielded 80 song types, of which three were shared (similar song types rendered by birds that occur in different vegetation types) with those from Musina Mopane Bushveld (SVmp1) and another three were shared with those from Makhado Sweet Bushveld (Table 2.5). In Tsende Mopaneveld (SVmp5), 30 song types were gained, two overlapped with those from Musina Mopane Bushveld (SVmp1) (viz., song types 12 and 17), one song type overlapped with another one from Mopane Basalt Shrubland (song type 258), and the last one was shared with one song type from Makhado Sweet Bushveld (SVcb20) (song type 123). In Mopane Gabbro Shrubland (SVmp8), 11 song types were recovered with two being shared with those from Musina Mopane Bushveld (SVmp1) (viz., song types 1 and 11) and another two overlapped with those from Makhado Sweet Bushveld (SVcb20) (viz., song types 123 and 142). In Polokwane Plateau Bushveld (SVcb23), 35 song types were gained, four overlapped with those from Musina Mopane Bushveld (SVmp1) (viz., song types 1, 2, 9, and 30) and three overlapped with those from Makhado Sweet Bushveld (SVcb20) (viz., song types 117, 123, and 124). In Roodeberg Bushveld (SVcb18), 31

song types were recovered, of which five were shared with those from Musina Mopane Bushveld (SVmp1) (viz., song types 2, 7, 18, 25, and 26) and three were shared with those from Makhado Sweet Bushveld (SVcb20) (viz., song types 123, 124, and 143). From Makhado Sweet Bushveld (SVcb20) birds, 57 song types were recovered from which five were shared with those from Musina Mopane Bushveld (SVmp1) (viz., song types 1, 2, 9, 12, and 32). In Bushmanland Arid Grassland (NKb3), six song types were gained of which one overlapped with one song type gained from Bushmanland Basin Shrubland (song type 345) birds. Bushmanland Basin Shrubland (NKb6) birds yielded 145 song types, three of these were shared with those gained from Musina Mopane Bushveld (SVmp1) birds while two were shared with those produced by birds that occupy occur in Makhado Sweet Bushveld (SVcb20) (Table 2.5).

The numbers in shaded cells in Table 2.5 are the total song types gained from the songs of Sabota Larks recorded in each vegetation type. The other numbers represent overlapping or shared song types between Sabota Larks recorded from different vegetation types. For example, two song types in Tsende Mopaneveld (column SVmp5) overlap with those in Musina Mopane Bushveld (row SVmp1), three song types in Roodeberg Bushveld (column SVcb18) overlap with those in Makhado Sweet Bushveld (row SVcb20). When calculating the total number of song types, for every vegetation type that overlaps with another vegetation type in song types, the overlapping song types were subtracted from the total song types recovered per vegetation (numbers in shaded cells). For example, in Mopane Basalt Shrubland (column SVmp4), the three song types overlapping between this vegetation and Musina Mopane Bushveld (row SVmp1) and the other three overlapping with Makhado Sweet Bushveld (row SVcb20) were subtracted from the 80.

Among the sampled vegetation types, it was observed that Makhado Sweet Bushveld (SVcb20) birds produced unique song types that were shared among almost all the sampled vegetation types except Musina Mopane Bushland (SVmp1) and Bushmanland Arid Grassland (NKb3) (Table 2.5). Another observation was that Musina Mopane Bushland (SVmp1) birds were the only ones that produced unique song types that were shared among almost all the sampled vegetation types except Bushmanland Arid Grassland (NKb3) (Table 2.5). Exceptionally, the Bushmanland Arid Grassland (NKb3) birds shared song types with their Nama-Karoo biome-linked, Bushmanland Basin Shrubland (NKb6) birds only while Bushmanland Basin

Shrubland (NKb6) birds shared song types with at least two of the Savanna biome-linked Musina Mopane Bushland (SVmp1) birds and Makhado Sweet Bushveld (SVcb20) birds.

Table 2.5. Total number of song types unique to each vegetation type and song types shared among the vegetation types. Musina Mopane Bushland (SVmp1), Mopane Basalt Shrubland (SVmp4), Tsende Mopaneveld (SVmp5), Mopane Gabbro Shrubland (SVmp8), Polokwane Plateau Bushveld (SVcb23), Roodeberg Bushveld (SVcb18), Makhado Sweet Bushveld (SVcb20), Bushmanland Arid Grassland (NKb3), and Bushmanland Basin Shrubland (NKb6). ‘ - ‘ shows no record of shared or overlapping song types.

Biome	Vegetation type	SVmp1	SVmp4	SVmp5	SVmp8	SVcb18	SVcb20	SVcb23	NKb3	NKb6
Savanna	SVmp1	116	3	2	2	5	5	3	-	3
	SVmp4	-	80	1	-	-	-	-	-	-
	SVmp5	-	-	39	-	-	-	-	-	-
	SVmp8	-	-	-	11	-	-	-	-	-
	SVcb18	-	-	-	-	31	-	-	-	-
	SVcb20	-	3	1	2	3	57	3	-	2
	SVcb23	-	-	-	-	-	-	35	-	-
Nama-Karoo	NKb3	-	-	-	-	-	-	-	6	-
	NKb6	-	-	-	-	-	-	-	1	145

As shown in Tables 2.5 and 2.6(a-b), song types were shared mostly between Musina Mopane Bushveld (SVmp1) and Makhado Sweet Bushveld (SVcb20) birds and all the other vegetation types. Birds recorded in the Limpopo Province vegetation types within the Savanna biome system have more song types in common than birds associated with the Northern Cape vegetation types in the Nama-Karoo biome system.

Table 2.6(a-b). Shared song types between sites and individual birds singing the shared song types in each site. ‘ - ‘ shows no record of shared or overlapping song types.

a) Shared song types between Musina Mopane Bushland (SVmp1) birds and birds associated with the other vegetation types. Mopane Basalt Shrubland (SVmp4), Tsende Mopaneveld (SVmp5), Mopane Gabbro Shrubland (SVmp8), Polokwane

Plateau Bushveld (SVcb23), Roodeberg Bushveld (SVcb18), Makhado Sweet Bushveld (SVcb20), and Bushmanland Basin Shrubland (NKb6).

Song type in Musina Mopane (SVmp1)	Individuals singing the song type in each vegetation type							
	SVmp1	SVmp4	SVmp5	SVmp8	SVcb18	SVcb20	SVcb23	NKb6
1	All 3	MBS4, MBS7	-	MGS1	RB1	MSB2, MSB6	PPB1, PPB2, PPB4	BBS5
2	MMB1, MMB2	-	-	-	-	MSB1, MSB4	PPB2, PPB4	BBS6
7	MMB3	-	-	-	RB1	-	-	-
9	MMB1, MMB3	-	-	-	-	MSB3	PPB1	-
11	MMB1, MMB3	-	-	MGS1	-	-	-	BBS2
12	MMB1, MMB3	-	TM1	-	-	MSB6	-	-
17	MMB1, MMB3	-	TM1	-	-	-	-	-
18	MMB1, MMB3	-	-	-	RB1	-	-	-
19	MMB1, MMB3	MBS2, MBS4	-	-	-	-	-	-
25	MMB3	-	-	-	RB1	-	-	-
26	MMB1	MBS3	-	-	RB1	-	-	-
32	MMB1, MMB3	-	-	-	-	MSB3	-	-

b) Shared song types between Makhado Sweet Bushveld birds and birds from the other vegetation types. Tsende Mopaneveld (SVmp5), Mopane Gabbro Shrubland (SVmp8), Polokwane Plateau Bushveld (SVcb23), Roodeberg Bushveld (SVcb18), Makhado Sweet Bushveld (SVcb20), and Bushmanland Basin Shrubland (NKb6).

Song type in Makhado Sweet Bushveld (SVcb20)	Individuals singing the song type in each vegetation type						
	SVcb20	SVmp4	SVmp5	SVmp8	SVcb18	SVcb23	NKb6
117	MSB4, MSB8	-	-	-	-	PPB2, PPB4, PPB5	-
123	MSB2, MSB3	MBS3, MBS4, MBS5, MBS7	TM1	MGS1	RB1	PPB4	-
124	MSB2, MSB3, MSB5	-	-	-	RB1	PPB4	-
133	MSB8	MBS4, MBS5	-	-	-	-	-
139	MSB2	-	-	-	-	-	BBS6

142	MSB3, MSB5	MBS1	-	MGS1	-	-	-
143	MSB3	-	-	-	RB1	-	-
158	MSB5	-	-	-	-	-	BBS5

2.3.3.2. Composition and the estimated number of song types

The songs of individual Sabota Larks collected over different breeding seasons (from 2011 to 2022 excluding 2016) yielded many unique song types, and these, in turn, contribute towards the total estimated number and size of song types Sabota Larks have in the context of the songs and habitats sampled in this study.

As reflected in Table 2.7, a maximum of 78 song types were gained from the song recordings of one individual Sabota Lark song recorded in Musina Mopane Bushveld viz., MMB3 (c. Tables 2.3 and 2.4). The minimum number of song types was found to be 23 in individual MMB2, the mean number of song types among the three individuals being 47 song types. In Bushmanland Basin Shrubland, one individual (BBS6) sang a maximum of 43 song types. In Tsende Mopaneveld, the one individual (TM1) recorded in this vegetation type sang a maximum of 32 song types. The one Sabota Lark individual (RB1) recorded in Roodeberg Bushveld rendered 31 song types. In Polokwane Plateau Bushveld, 28 song types were gained from one bird's song recordings, viz., individual PPB4. Eighteen (18) song types were sung by two Sabota larks in Mopane Basalt Shrubland, viz., individuals MBS4 and MBS7. In Makhado Sweet Bushveld, a maximum of 18 song types were rendered by one individual Sabota Larks viz., individual MSB5. In Mopane Gabbro Shrubland, one individual (MGS1) sung 11 song types. Lastly, in Bushmanland Arid Grassland, one bird (BAG2) sung five song types.

Table 2.7. The minimum, maximum, and mean number of song types constitute the total estimated number and size of song types sung by Sabota Larks in each vegetation type. Vegetation types are arranged such that vegetation types in which individual birds sing the highest maximum number of song types appear at the top of the table and tail off towards the least maximum song types sung. The “mean song

types” were calculated as the sum of the number of song types per bird/total number of birds (Tables 2.3a-k).

Biome	Vegetation types	Minimum no. of song types	Maximum no. of song types	Mean song types
Savanna	Musina Mopane Bushveld (MMB)	23	78	47
	Tsende Mopaneveld (TM)	32	32	32
	Roodeberg Bushveld (RB)	31	31	31
	Polokwane Plateau Bushveld (PPB)	1	28	8
	Mopane Basalt Shrubland (MBS)	3	18	11
	Makhado Sweet Bushveld (MSB)	1	18	9
	Mopane Gabbro Shrubland (MGS)	11	11	11
Nama	Bushmanland Basin Shrubland (BBS)	1	43	12
Karoo	Bushmanland Arid Grassland (BAG)	1	5	3

2.4. Discussion

Song description and presentation or singing style - the findings from this study showed that the Sabota Lark *Calendulauda sabota* could be one of the songbird species characterised by singing ‘complex’, highly variable and modulated songs (ranging from less than 1 minute to at least 5 to 6 min) that tended to have many different versions. To a greater degree, the song strophes were led by two to several independent introductory whistled elements accompanied by various syllables and/or phrases. The large number of song strophes and unique song types gained from the songs of the Sabota Larks attested to the complex nature of the songs of this species. For example, song types were rarely given without variations in the structure and composition of elements and/or syllables.

The presentation of songs or singing styles of Sabota Larks varied within and among individual birds that occurred within and among the vegetation types associated with the different bioregions that are part of both the Savanna and Nama-Karoo biome systems. The birds could explore both singing styles, immediate and eventual varieties. In some instances, the ability of Sabota Larks to explore different singing styles compared well with that of the Mongolian Lark *Melanocorypha mongolia* (Zhang *et al.* 2011). The song bout of this species was described as having a series of distinct, repeated parts of the song, with unrepeatd phrases or syllables

intercalated among them. This appeared to be the case in some of the Sabota Larks. In some individuals, although there were song types that were sung multiple times, most of the song types were sung a few times. Various song strophes and types showed diversity and variations regarding the syntactical arrangement.

Song composition – in the context of this study, the results showed that one individual Sabota Lark recorded from Musina Mopane Bushveld produced a maximum of 78 song types. This was the highest number of song types sung by an individual bird. In the other vegetation types, song types were fewer, and this could be attributed to factors such as skewed sampling sizes, with many songs having been collected only from the birds that occur in Musina Mopane Bushveld. The acoustic environment associated with the habitats may not be ruled out. However, the results suggested that song plasticity could be a feature of Sabota Larks. Based on observations made in other bird species, song repertoires could be accumulated in two possible ways: 1) through “extended memory and re-expression” (Hough *et al.* 2000) or 2) through open-ended learning (Vargas-Castro *et al.* 2015). The results from this study cannot help determine how Sabota Larks accumulate their song components. To determine whether the Sabota Larks use extended memory and re-expression or open-ended learning to get their song components, like in most species studied to date, will require studies of songs between breeding seasons. According to Vargas-Castro *et al.* (2015), this will also necessitate control of the acoustic environment of the birds from the moment of their birth. Since cases of mimicry have been reported in Sabota Larks, it could be speculated in this study that Sabota Larks are open-ended learners. On the contrary, a study on Marsh Warblers in Dowsett-Lemaire (1979) showed that, although this species can mimic songs and calls of approximately 84 other species, it is nevertheless not open-ended in song learning; rather, it is age-limited.

Song type sharing - individual birds within one area shared some song types. Still, there were structural variations among the shared song types, and this could be attributed to the uniqueness of individual birds and possibly linked to the acoustic environment associated with the birds. Nonetheless, this study is not the first to comment on the complexity of the vocalisations of the Sabota Lark. Maclean (1970) described vocalisations of the Sabota Lark as “difficult to transcribe, varying considerably between conspecifics”, which is probably one of the reasons why this aspect of the species' life history has received little attention.

Regardless of how species accumulate their song types over time, song learning allows the sharing of song types among conspecifics (Nordby *et al.* 2002), a concept known as repertoire overlap. Repertoire overlap measures the similarity between the repertoires of two birds or the fraction of song types they share (Molles and Vehrencamp 1999, Kershenbaum *et al.* 2016). There was song type sharing among neighbouring Sabota Larks but the extent to which individual birds' repertoires overlap varies from one species to another. Some studies have found that in some species, neighbours have their entire repertoire or most song types in common (e.g., Tufted Titmouse *Baeolophus bicolor*), while in species like the Great Tit *Parus major*, the extent of repertoire overlap can be intermediate (McGregor and Avery 1986). These variations in song type sharing among species reflect differences in song learning strategies. The relationship between patterns of song type sharing and the distance between territories of individuals demonstrates these strategies (Molles and Vehrencamp 1999). It is evident that a lack of knowledge of the learning strategy employed by the Sabota Larks to accumulate the components of their song limits how song sharing could be fully interpreted in this species. Therefore, it is recommended that future studies should investigate the learning strategy employed by Sabota Larks.

Within-song type variation was also characteristic of the Sabota Lark songs. When continuously distributed, conspecific populations show geographical variation in song, and these song patterns can be used as markers of sub-populations; such song patterns are called dialects (Planqué *et al.* 2014). This is characteristic of species with small song repertoires, especially those with only one song type. In such species, birds within the same area usually sing the same song type (Slater *et al.* 1984). Should there be a discontinuity in song type sharing among sub-populations with clear boundaries, i.e., different sub-populations singing distinguishable variants of their song, these variants are dialects. In species with large repertoires, birds from the same area tend to have several song types in common, coupled with those unique to individual birds (Slater *et al.* 1984, Luther and Baptista 2010). This individual uniqueness, which also serves as individual signatures, results in a continuous variation in song variants among individuals, with no group of individuals singing one song variant that can be distinguished from another variant sung by another group (Slater *et al.* 1984, Luther and Baptista 2010). The latter could be the case for Sabota Larks in the Savanna system. Shared song variants varied within individuals, among individuals, and across

sub-populations. These variations were so continuous that no specific song patterns could be associated with only a particular group of individuals in a particular area. Since the Sabota Lark includes heterospecific vocal mimicry in its repertoire, it stands to reason that those individuals occupying habitats with high species richness, e.g., the Savanna biome, have a larger “pool of sounds” to draw upon in their songs, compared with individuals occupying regions with lower species richness, e.g., the Nama-Karoo biome.

As maintained by Thompson *et al.* (1994), finding a universal method that could easily be followed when describing the songs of birds remains a daunting task. The number of vocal units (be it song types or syllables) that a bird can sing is its repertoire (Päckert 2018). It could be as simple as one song type, like in the White-throated Sparrow *Zonotrichia albicollis*, or complex like in the Brown Thrasher *Toxostoma rufum*. Kroodsma and Parker’s (1977) estimation of a Brown Thrasher song repertoire was more than 2,000 song units. Boughey and Thompson (1981) found one male Brown Thrasher singing a maximum of 1 147 song types in a sample of 1 910 songs. Unlike complex songs, simple songs are describable, which is evident in literature (Vella *et al.* 2021). Studies of song in birds with complex songs, including mimicry, would not describe their many song types. One possible explanation for this may be a lack of the correct language. Coupled with this, the work may prove to be in vain. For example, the singing behaviour of the Red-eyed Vireo *Vireo olivaceus* is such that few of the many song types of this species can be recognised in the field (Borror 1981). Instead of describing the song types of species with complex singing behaviours, the trend seems to primarily determine the composition of vocalisation e.g., to identify the song types, to identify the shared song types, to determine the singing style and species-specific song types, and to estimate the repertoire sizes.

APPENDICES

Appendix 2.1. Vocalisation recordings of the Sabota Larks made from different study sites including their field identification numbers.

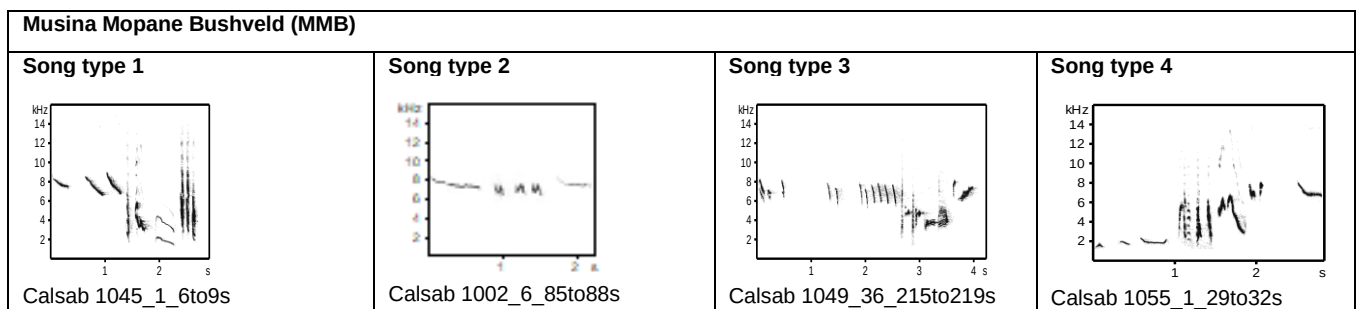
Province	Location name	Individual Sex	Recordings and Catalogue no.	Location coordinates	Date recorded	Inclusion/Exclusion in data analyses
Limpopo Province	Kruger National Park	Male	Calsab 1001	-23.908644°, 31.646146°	23-Dec-2015	Included
		Male	Calsab 1004	-23.873520°, 31.469836°	24-Dec-2015	Included
			Calsab 1005	-23.873520°, 31.469836°	24-Dec-2015	Included
			Calsab 1006	-23.873520°, 31.469836°	24-Dec-2015	Included
		Male	Calsab 1007	-23.693714°, 31.587149°	25-Dec-2015	Included
		Male	Calsab 1008	-23.695153°, 31.615568°	25-Dec-2015	Included
			Calsab 1009	-23.695153°, 31.615568°	25-Dec-2015	Included
		Male	Calsab 1013	-23.651302°, 31.634148°	25-Dec-2015	Included
		Male	Calsab 1015	-23.691444°, 31.596528°	25-Dec-2015	Included
		Male	Calsab 1017	-23.708778°, 31.543444°	25-Dec-2015	Included
		Male	Calsab 1049	-24.569695°, 31.537248°	07-Feb-2016	Excluded
		Male	Calsab 1083	-23.924739°, 31.180797°	16-Oct-2016	Excluded
		Male	Calsab 1085	-23.866638°, 31.195806°	16-Oct-2016	Excluded
		Male	Calsab 1034	-23.114440°, 31.514052°	24-Jun-2015	Included
		Male	Calsab 1076	-23.914432°, 31.456373°	23-Dec-2015	Included
		Male	Calsab 1078	-23.957103°, 31.623874°	23-Dec-2015	Included
			Calsab 1079	-23.957103°, 31.623874°	23-Dec-2015	Included
		Male	Calsab 1081	-23.920060°, 31.279250°	23-Dec-2015	Excluded
		Male	Calsab 1020	-23.505545°, 31.484005°	22-Jun-2015	Excluded
		Male	Calsab 1021	-23.488757°, 31.488125°	22-Jun-2015	Excluded
	Shimuwini	Male	Calsab 1066	-22.954437°, 31.263157°	21-Nov-2015	Excluded
			Calsab 1067	-22.954437°, 31.263157°	21-Nov-2015	Excluded
	Limpokwena Nature Reserve	Male	Calsab 1045	-22.460162°, 28.884667°	24-Dec-2021	Included
			Calsab 1046	-22.460162°, 28.884667°	24-Dec-2021	Included
			Calsab 1047	-22.460162°, 28.884667°	24-Dec-2021	Included
			Calsab 1057	-22.460162°, 28.884667°	24-Dec-2021	Included

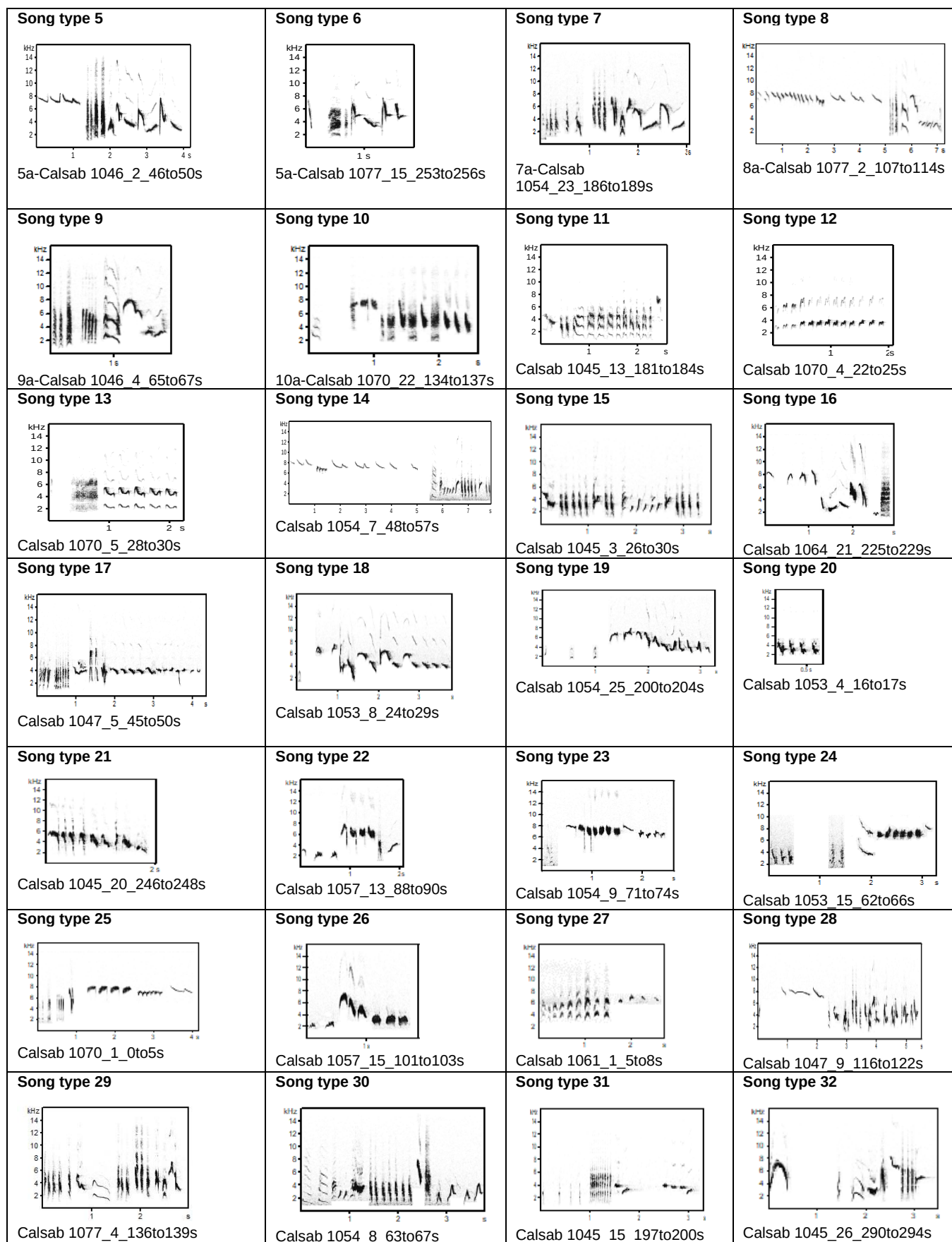
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			Calsab 1077	-22.459513°, 28.884441°	25-Dec-2021	Included
		Male	Calsab 1049	-22.476912°, 28.903645°	24-Dec-2021	Included
	Polokwane Nature Reserve	Male	Calsab 1002 (2)	-23.975888°, 29.467664°	28-Nov-2012	Included
		Male	Calsab 1004	-23.966172°, 29.473272°	28-Nov-2012	Excluded
			Calsab 1005	-23.966172°, 29.473272°	28-Nov-2012	Excluded
		Male	Calsab 1037	-23.979390°, 29.501857°	29-Nov-2016	Excluded
		Male	Calsab 1003 (2)	-23.968210°, 29.471733°	28-Nov-2012	Excluded
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		Male	Calsab 1013	-23.985736°, 29.474099°	23-Nov-2016	Included
		Male	Calsab 1016	-23.986330°, 29.477420°	18-Sep-2007	Included
		Male	Calsab 1017	-23.978749°, 29.508795°	24-Nov-2016	Included
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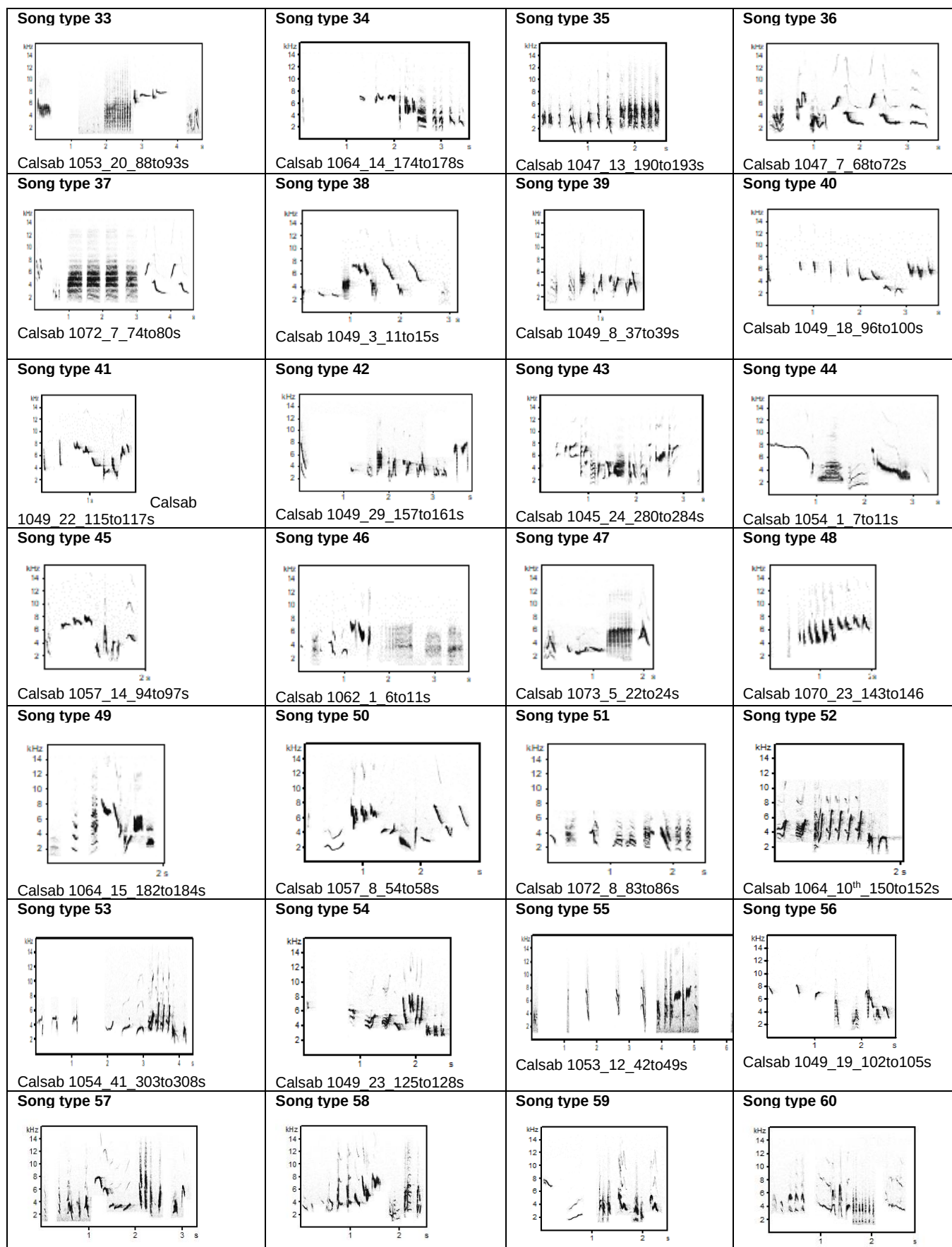
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	Maribana	Male	Calsab 1037	-23.506319°, 29.277717°	04-Apr-2018	Included
	Blouberg Nature Reserve	Male	Calsab 1036	-22.979401°, 29.126648°	23-Dec-2018	Included
Northern Cape	Neus Se Berg Groblershoop	Male	SabotaLark_Ne usseBergGHoo p_20180125	-28.899958°, 21.766583°	25-Jan-2018	Excluded
	Brandvlei	Male	Calsab 1207	-30.354507°, 20.580830°	28-Sep-2022	Included
		Male	Calsab 1168	-30.360396°, 20.578224°	27-Sep-2022	Included
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		Male	Calsab 1205	-30.450606°, 20.537893°	28-Sep-2022	Included
			Calsab 1023	-30.450606°, 20.537893°	28-Sep-2022	Included
		Male	Calsab 1145	-30.377820°, 20.647994°	26-Sep-2022	Included
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		Male	Calsab 1153	-30.468420°, 20.527801°	27-Sep-2022	Included
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		Male	Calsab 1156	-30.407942°, 20.539929°	27-Sep-2022	Included
		Male	Calsab 1159	-30.396548°, 20.556779°	27-Sep-2022	Excluded
		Male	Calsab 1165	-30.392979°, 20.560917°	27-Sep-2022	Included
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		Male	Calsab 1210	-30.481094°, 20.367139°	28-Sep-2022	Included
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		Male	Calsab 1187	-30.339474°, 20.583310°	28-Sep-2022	Included
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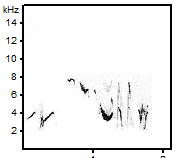
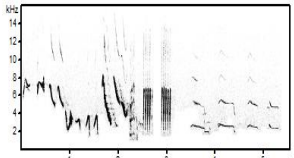
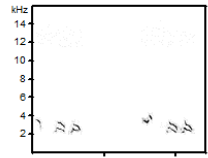
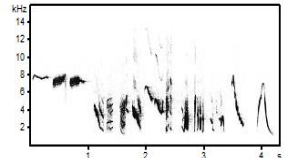
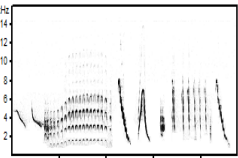
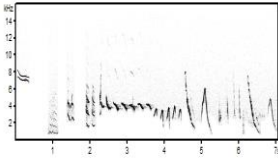
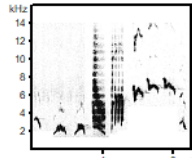
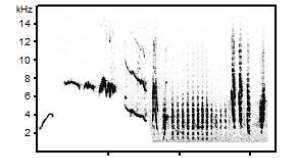
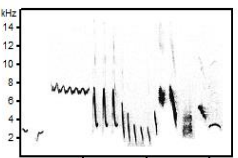
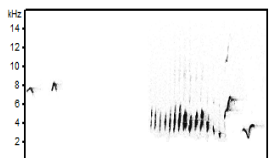
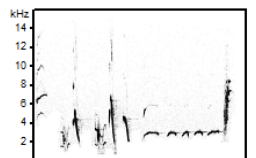
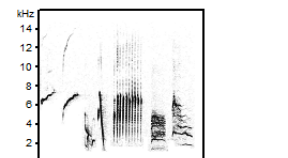
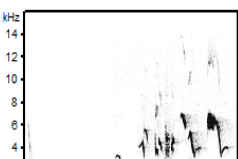
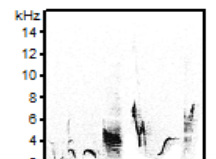
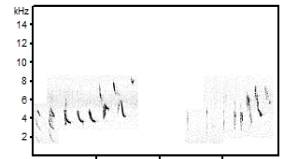
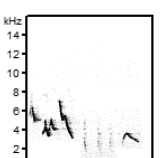
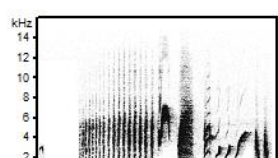
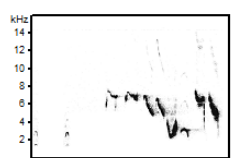
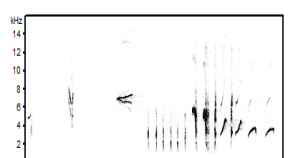
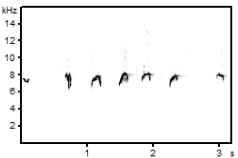
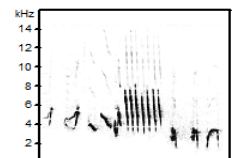
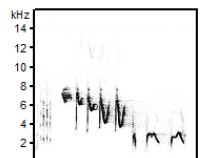
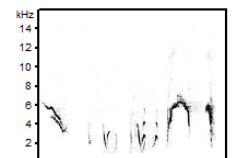
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	Phillipolis	Male	Calsab 1040	-30.263148°, 25.210553°	07-Apr-2011	Excluded
		Male	Calsab 1043	-30.246585°, 25.241398°	07-Apr-2011	Excluded
	Pofadder South	Male	Calsab 1095	-29.165636°, 19.367903°	24-Sep--2022	Included
		Male	Calsab 1143	-29.144305°, 19.405335°	26-Sep-2022	Included
	Keimoes	Male	Calsab 1135	-28.826911°, 21.036569°	21-Mar-2017	Excluded
	Kenhardt	Male	Calsab 1136	-29.467273°, 21.061288°	21-Mar-2017	Included
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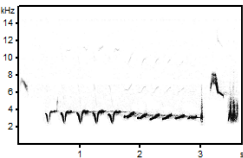
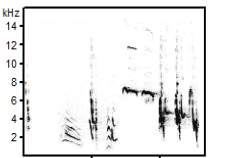
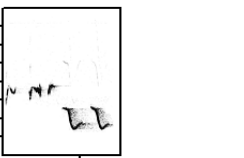
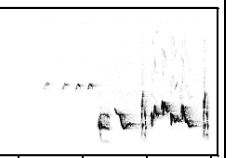
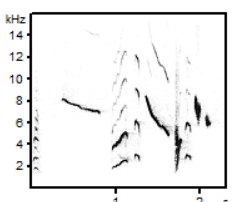
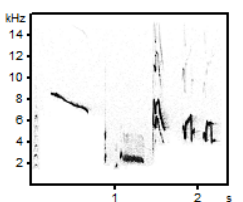
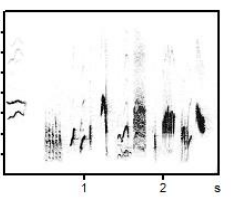
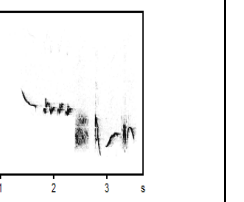
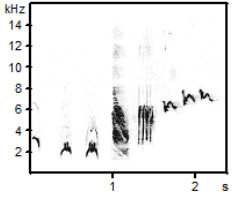
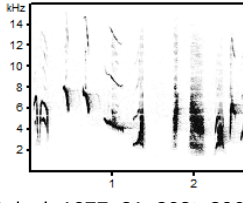
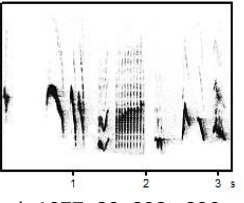
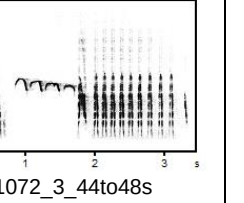
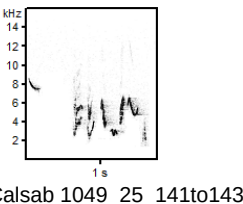
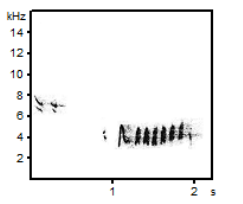
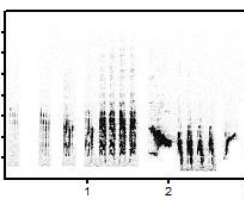
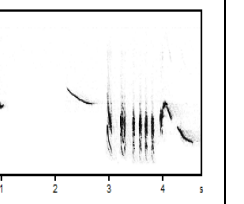
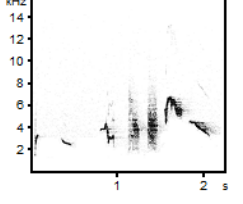
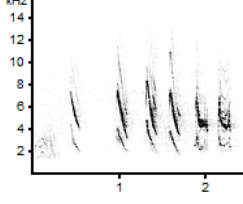
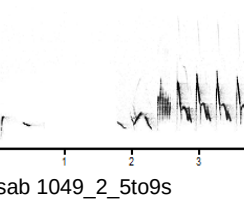
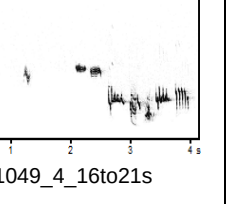
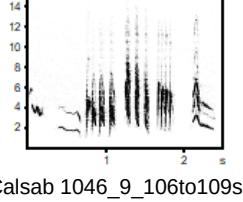
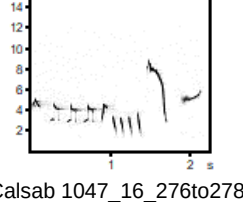
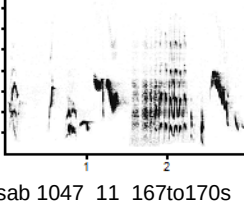
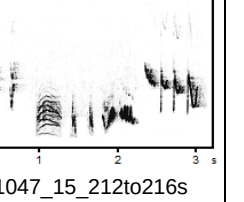
Appendix 2.2. Representative spectrograms of unique song types rendered by different birds. Sites from which song recordings were made, vegetation type and the number of song types (including variants) classified are shown. In Calsab 1045_1_6to9s, Calsab stands for *Calendulauda sabota*, 1045-recording field identification number, 1-strophe 1, 6to9s-approximate start and end time of strophe 1 within recording 1045.

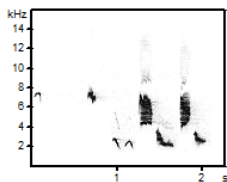
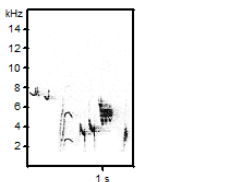
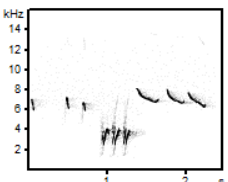
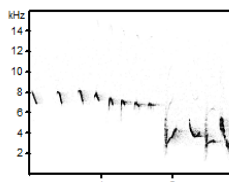
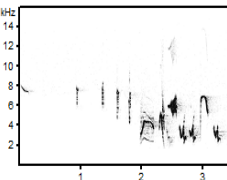
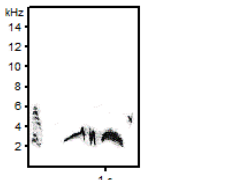
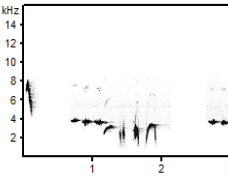
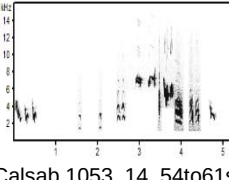
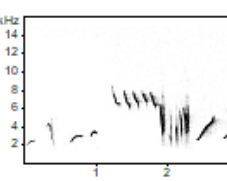
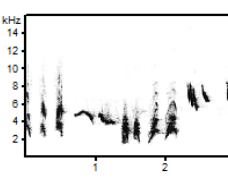
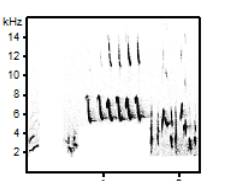
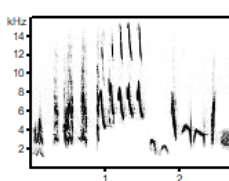
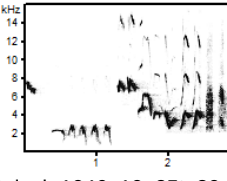
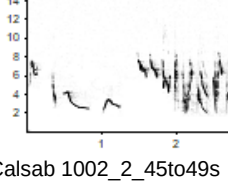
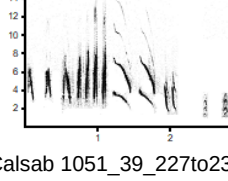
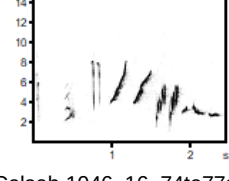
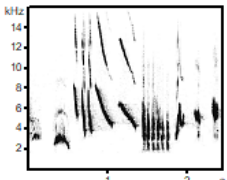
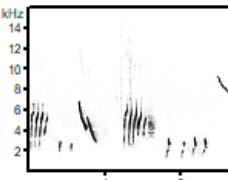
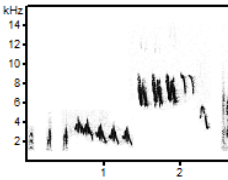
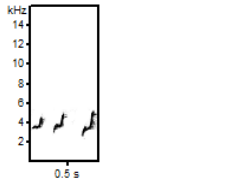
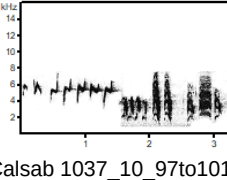
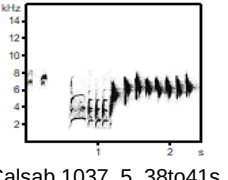
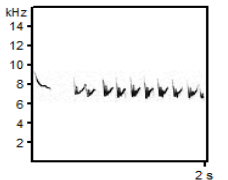
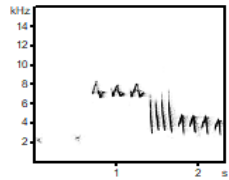


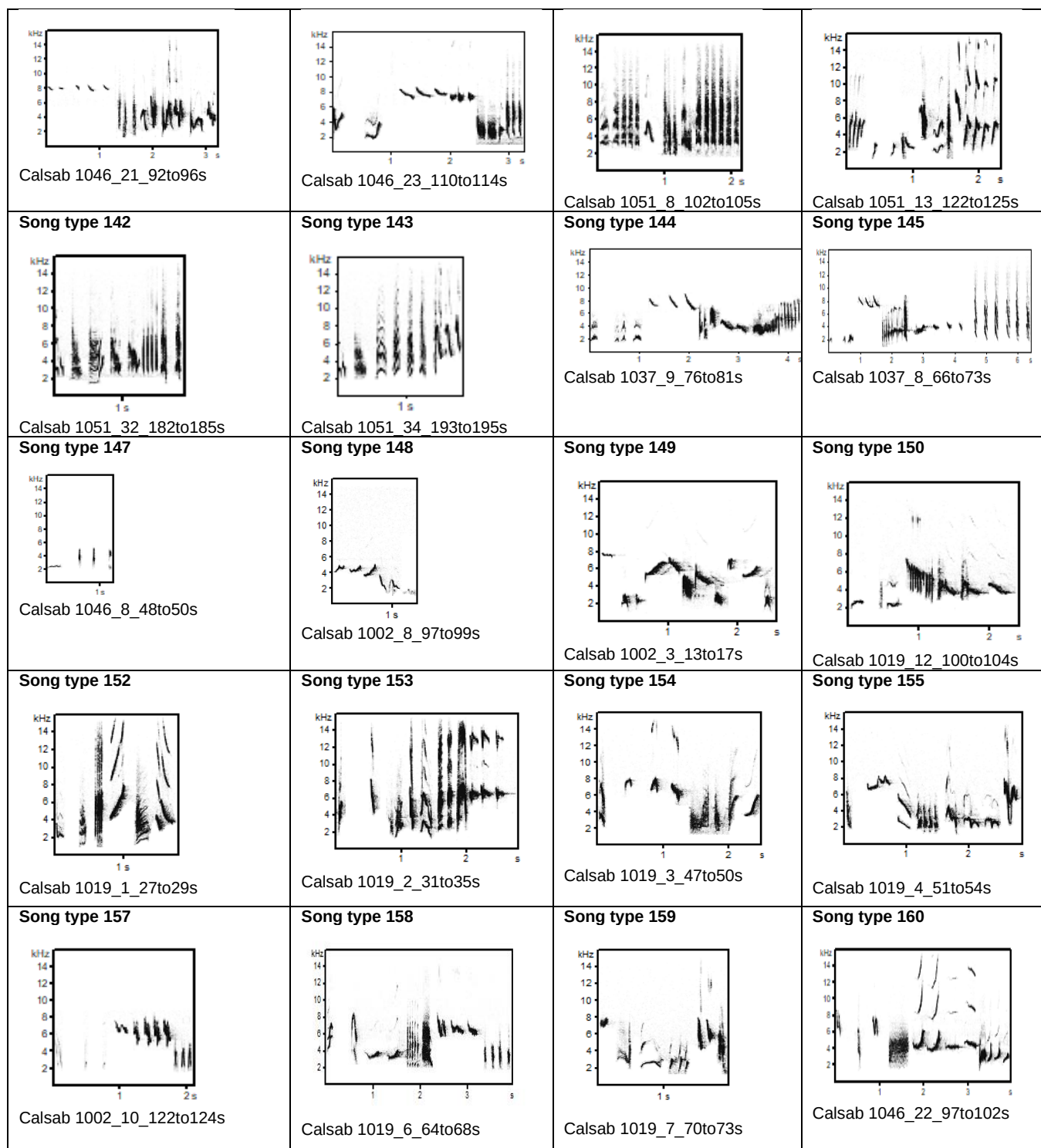


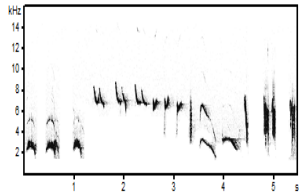
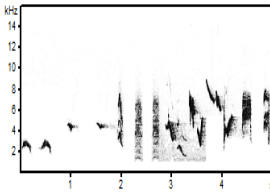
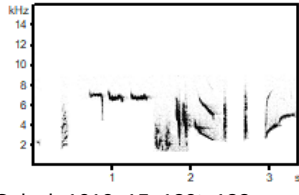
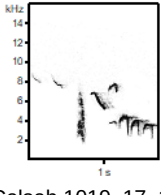
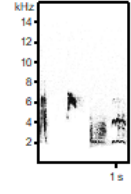
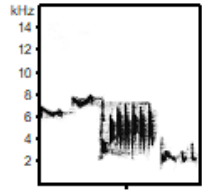
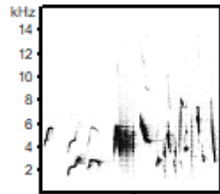
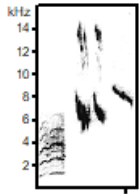
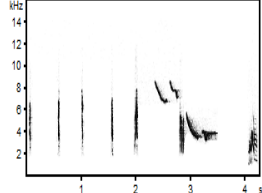
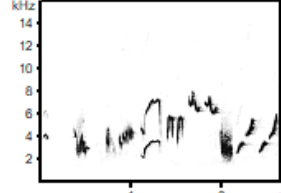
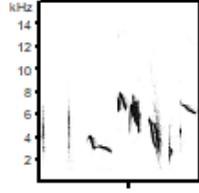
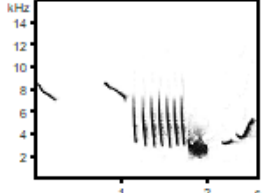
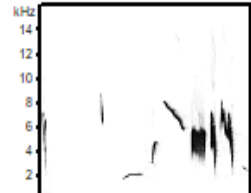
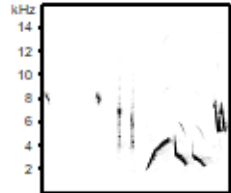
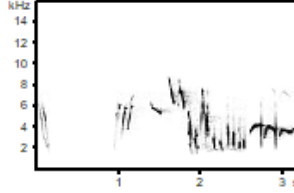
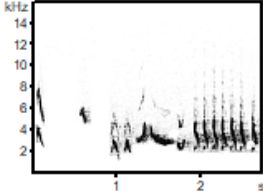
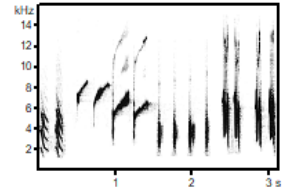
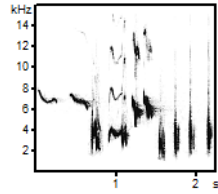
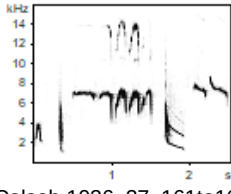
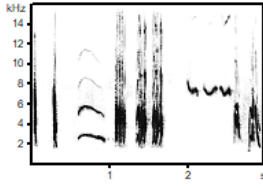


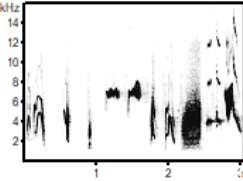
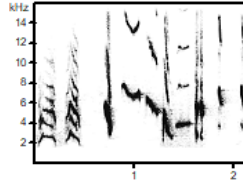
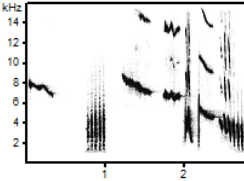
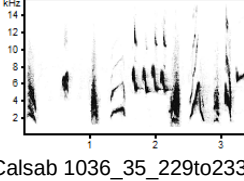
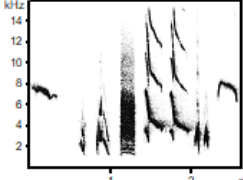
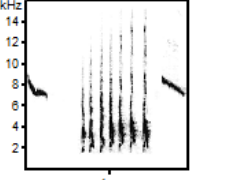
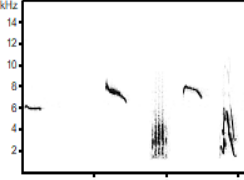
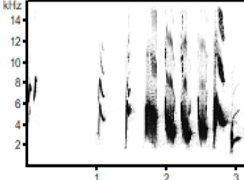
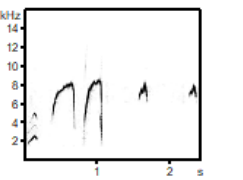
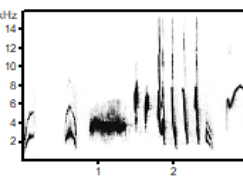
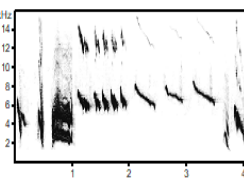
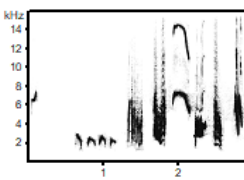
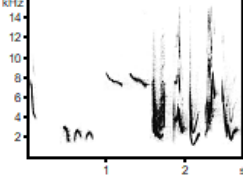
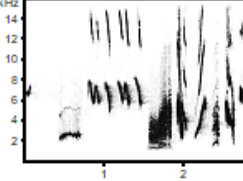
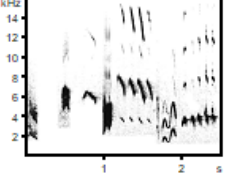
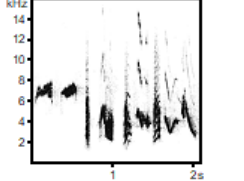
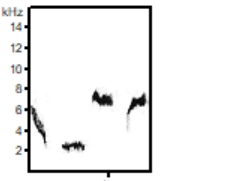
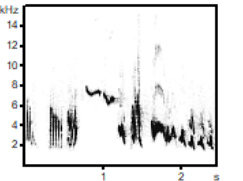
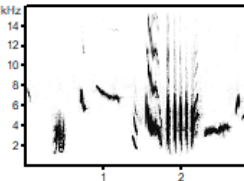
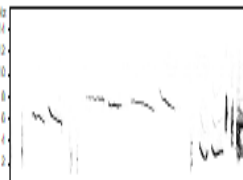
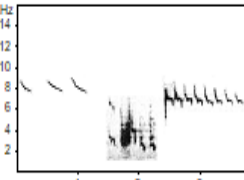
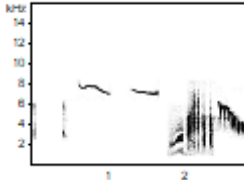
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Song type 61 	Song type 62 	Song type 63 	Song type 64 
Calsab 1054_20_163to165s	Calsab 1054_2_14to20s	Calsab 1054_15_117to120s	Calsab 1047_3_17to22s
Song type 65 	Song type 66 	Song type 67 	Song type 68 
Calsab 1072_2_23to28s	Calsab 1054_21_174to181s	Calsab 1055_5_59to61s	Calsab 1056_1_8to12s
Song type 69 	Song type 70 	Song type 71 	Song type 72 
Calsab 1057_1_8to12s	Calsab 1057_2_15to19s	Calsab 1057_6_36to40s	Calsab 1057_7_42to45s
Song type 73 	Song type 74 	Song type 75 	Song type 76 
Calsab 1057_18_123to127s	Calsab 1057_23_151to153s	Calsab 1054_12_95to99s	Calsab 1061_2_10to14s
Song type 77 	Song type 78 	Song type 79 	Song type 80 
Calsab 1062_3_37to39s	Calsab 1053_2_2to6s	Calsab 1064_5_42to45s	Calsab 1064_12_162to168
Song type 81 	Song type 82 	Song type 83 	Song type 84 
Calsab 1064_23_243to246s	Calsab 1065_4_56to59s	Calsab 1070_9_54to57s	Calsab 1070_12_76to79s
Song type 85	Song type 86	Song type 87	Song type 88

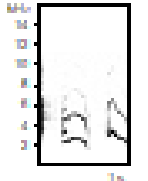
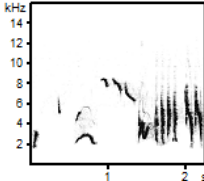
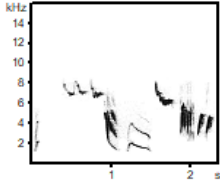
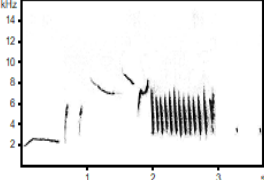
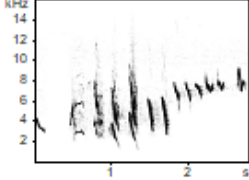
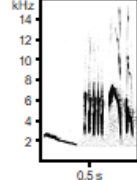
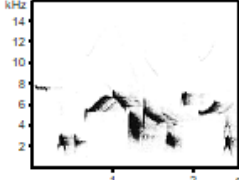
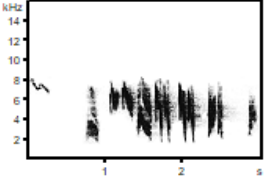
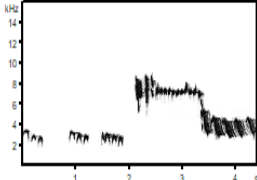
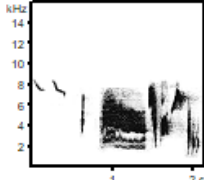
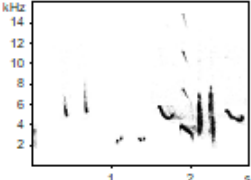
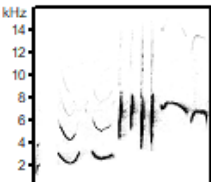
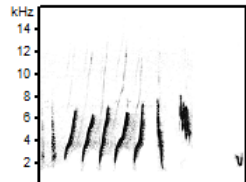
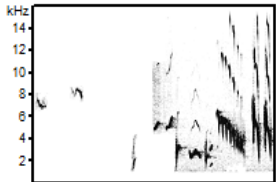
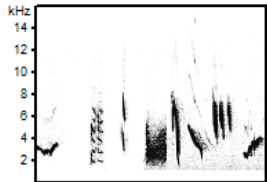
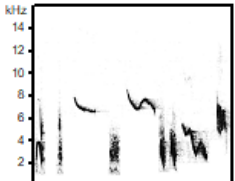
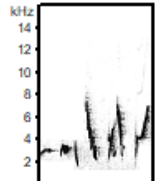
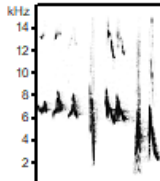
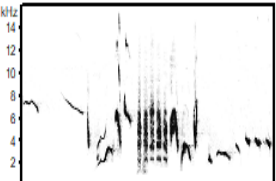
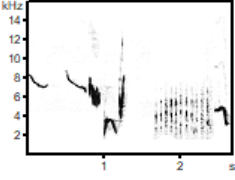
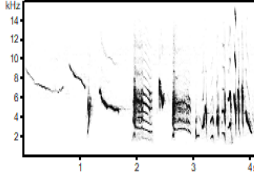
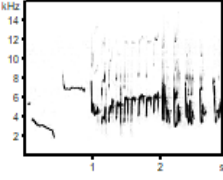
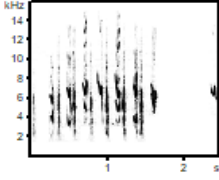
 Calsab 1072_1_4to8s	 Calsab 1072_5_61to64s	 Calsab 1072_6_67to69s	 Calsab 1072_10_103to108s
Song type 89  Calsab 1077_1_4to7s	Song type 90  Calsab 1057_8_47to50s	Song type 91  Calsab 1077_9_203to206s	Song type 92  Calsab 1077_10_225to229s
Song type 93  Calsab 1077_14_246to249s	Song type 94  Calsab 1077_21_303to306s	Song type 95  Calsab 1077_20_293to296s	Song type 96  Calsab 1072_3_44to48s
Song type 97  Calsab 1049_25_141to143s	Song type 98  Calsab 1049_27_148to151s	Song type 99  Calsab 1054_24_194to197s	Song type 100  Calsab 1070_13_80to85s
Song type 101  Calsab 1049_13_65to68s	Song type 102  Calsab 1049_7_33to36s	Song type 103  Calsab 1049_2_5to9s	Song type 104  Calsab 1049_4_16to21s
Song type 105  Calsab 1046_9_106to109s	Song type 106  Calsab 1047_16_276to278s	Song type 107  Calsab 1047_11_167to170s	Song type 108  Calsab 1047_15_212to216s
Song type 109	Song type 110	Song type 111	Song type 112

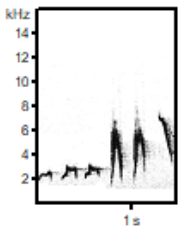
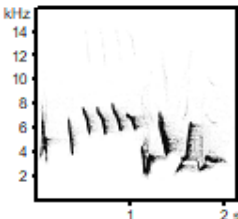
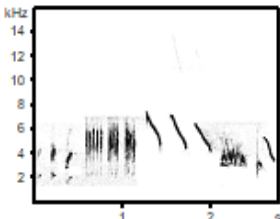
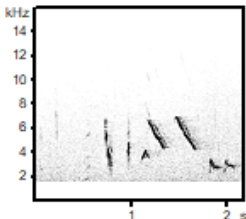
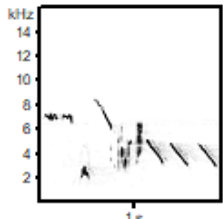
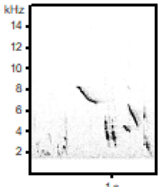
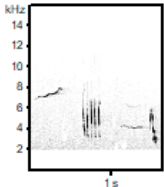
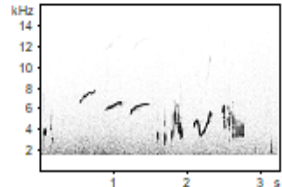
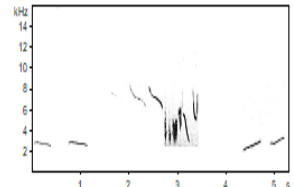
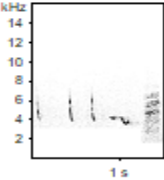
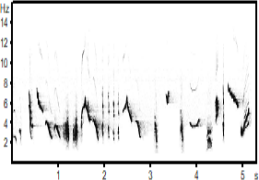
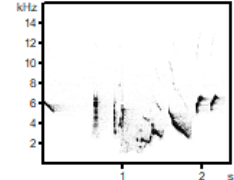
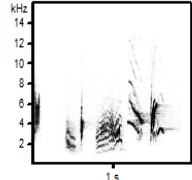
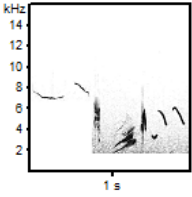
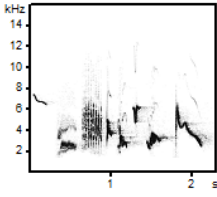
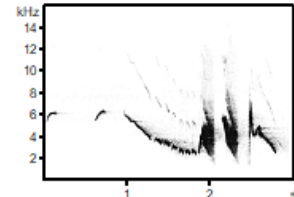
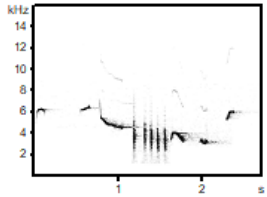
 Calsab 1049_9_41to43s	 Calsab 1049_10_45to47s	 Calsab 1049_11_49to51s	 Calsab 1049_15_75to79s
Song type 113  Calsab 1049_16_80to84s	Song type 114  Calsab 1049_34_200to202s	Song type 115  Calsab 1053_3_11to15s	Song type 116  Calsab 1053_14_54to61s
Makhado Sweet Bushveld (MSB)			
Song type 117  Calsab 1002_3_56to59s	Song type 118  Calsab 1026_5_71to74s	Song type 119  Calsab 1019_5_59to61s	Song type 120  Calsab 1051_30_174to178s
Song type 121  Calsab 1046_19_85to89s	Song type 122  Calsab 1002_2_45to49s	Song type 123  Calsab 1051_39_227to230s	Song type 124  Calsab 1046_16_74to77s
Song type 126  Calsab 1051_2_77to80s	Song type 127  Calsab 1051_12_117to121s	Song type 128  Calsab 1051_38_222to225s	Song type 133  Calsab 1037_4_31to33s
Song type 134  Calsab 1037_10_97to101s	Song type 135  Calsab 1037_5_38to41s	Song type 136  Calsab 1044_1_72to75s	Song type 137  Calsab 1046_9_50to53s
Song type 138	Song type 139	Song type 140	Song type 141

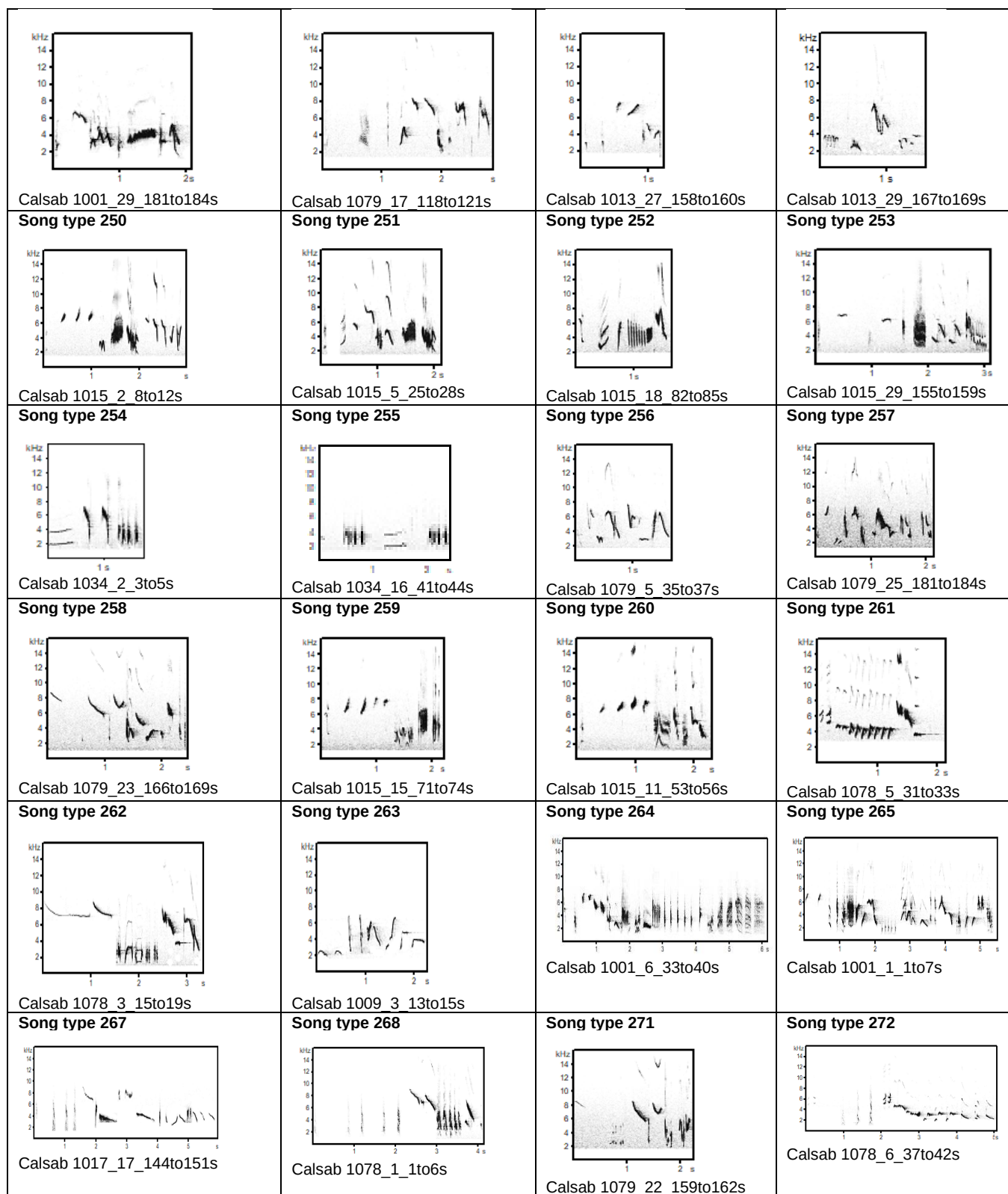


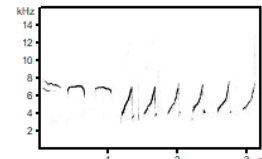
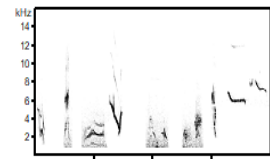
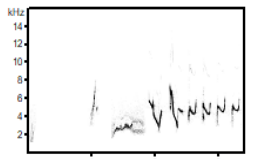
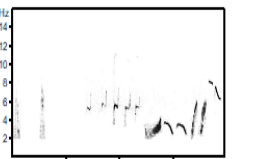
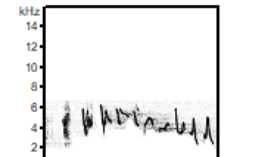
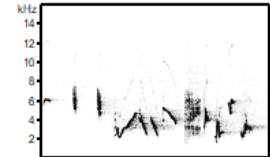
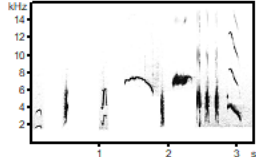
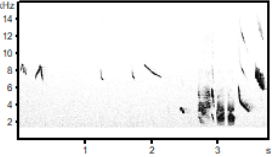
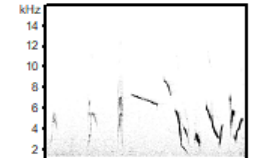
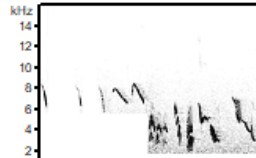
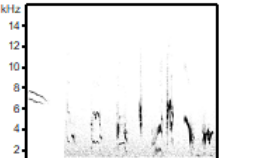
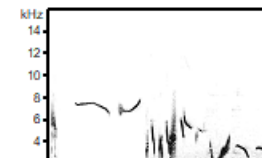
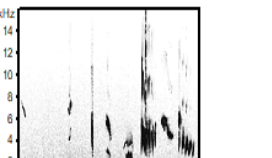
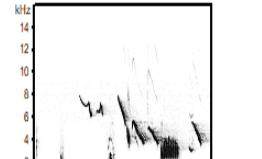
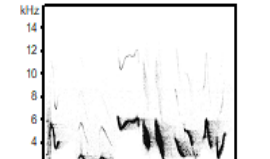
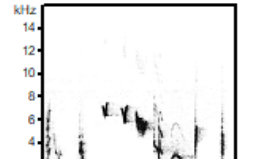
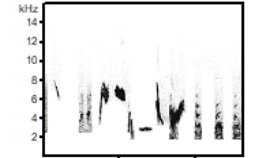
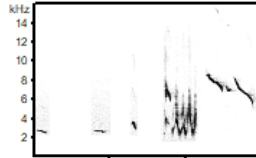
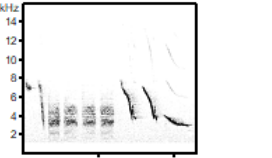
Song type 161  Calsab 1019_10_84to90s	Song type 162  Calsab 1019_11_91to96s	Song type 163  Calsab 1019_15_129to132s	Song type 164  Calsab 1019_17_150to152s
Song type 165  Calsab 1019_18_157to158s	Song type 166  Calsab 1026_1_23to25s	Song type 167  Calsab 1026_2_30to33s	Song type 168  Calsab 1026_4_57to59s
Song type 169  Calsab 1030_4_21to26s	Song type 185  Calsab 1046_3_15to18s	Song type 186  Calsab 1046_4_22to24s	Song type 187  Calsab 1046_5_26to29s
Song type 188  Calsab 1046_7_44to47s	Song type 189  Calsab 1046_13_62to65s	Song type 190  Calsab 1002_9_102to106s	Song type 191  Calsab 1019_9_79to82s
Roodeberg Bushveld (RB)			
Song type 125  Calsab 1036_13_74to77s	Song type 129  Calsab 1036_16_94to97s	Song type 130  Calsab 1036_27_161to164s	Song type 131  Calsab 1036_30_172to174s
Song type 132	Song type 146	Song type 151	Song type 156

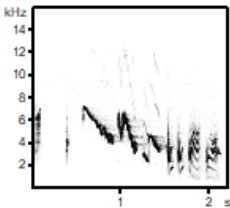
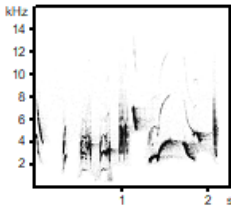
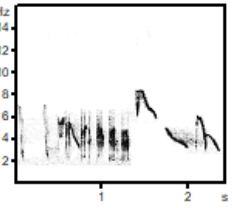
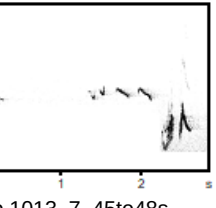
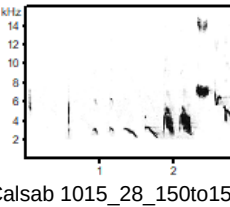
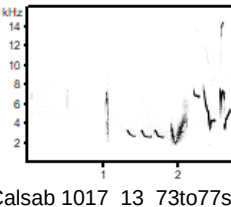
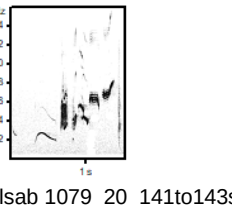
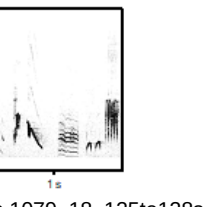
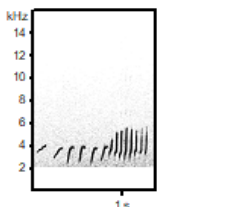
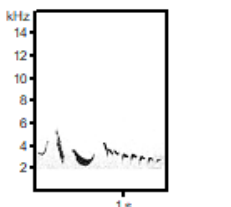
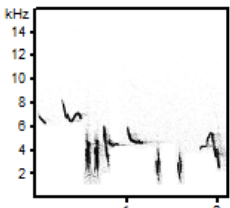
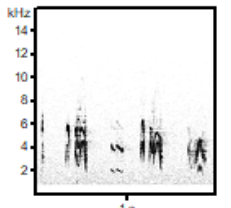
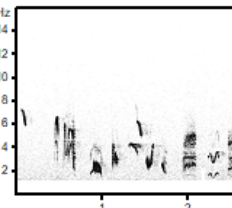
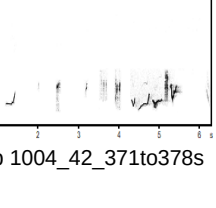
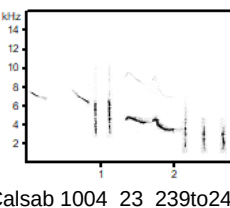
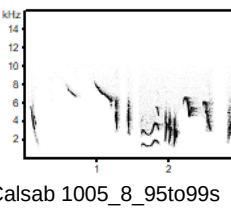
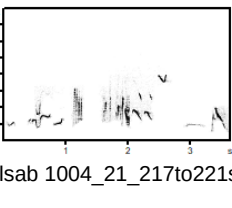
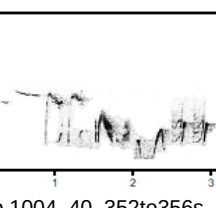
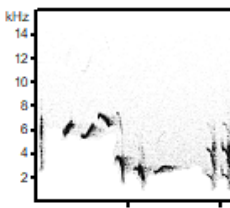
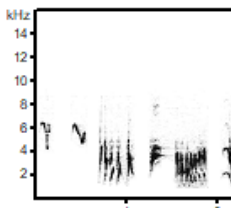
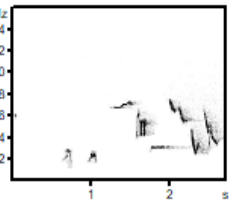
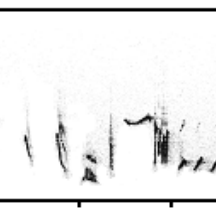
 Calsab 1036_39_258to262s Song type 170	 Calsab 1036_18_107to109s Song type 171	 Calsab 1036_2_4to8s Song type 172	 Calsab 1036_35_229to233s Song type 173
 Calsab 1036_4_11to14s Song type 174	 Calsab 1036_5_15to18s Song type 175	 Calsab 1036_6_20to24s Song type 176	 Calsab 1036_11_58to62s Song type 177
 Calsab 1036_22_131to134s Song type 178	 Calsab 1036_23_134to138s Song type 179	 Calsab 1036_32_209to214s Song type 180	 Calsab 1036_33_215to219s Song type 181
 Calsab 1036_36_237to241s Song type 182	 Calsab 1036_34_222to226s Song type 183	 Calsab 1036_37_244to247s Song type 184	 Calsab 1036_38_254to257s
 Calsab 1036_41_270to272s Song type 182	 Calsab 1036_42_275to279s Song type 183	 Calsab 1036_43_282to286s Song type 184	
Polokwane Plateau Bushveld (PPB)			
 Calsab 1017_5_18to24s Song type 196	 Calsab 1019PNR_2_6to9s Song type 193	 Calsab 1013_1_1to6s Song type 194	 Calsab 1018_2_63to66s Song type 195
	Song type 197	Song type 198	Song type 199

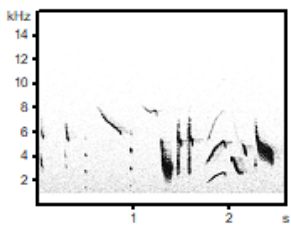
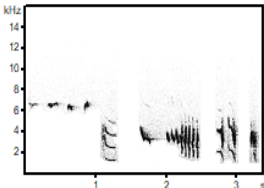
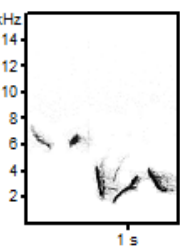
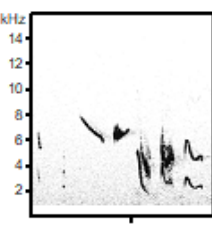
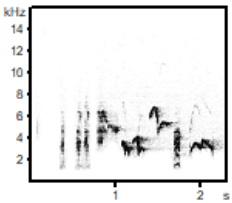
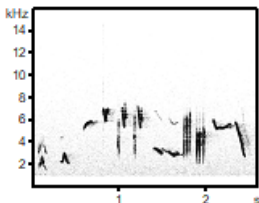
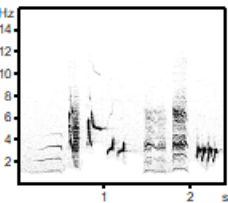
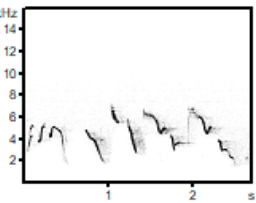
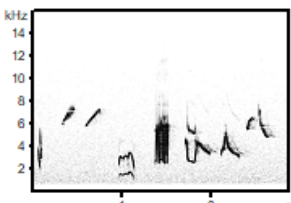
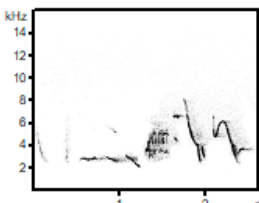
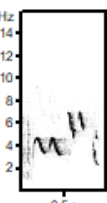
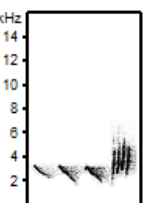
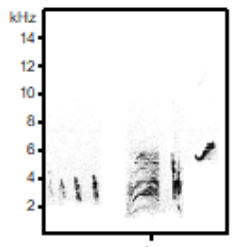
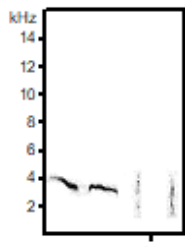
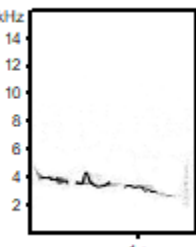
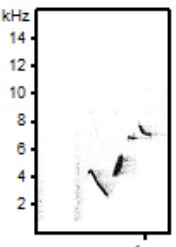
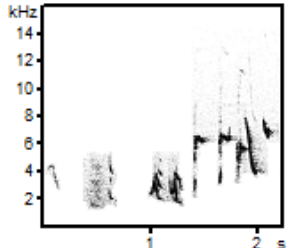
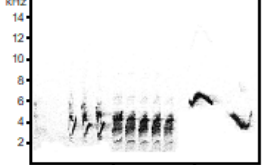
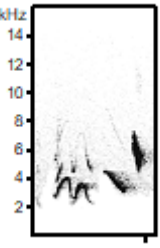
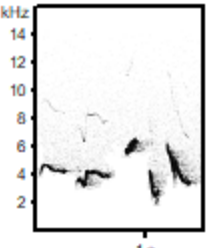
 Calsab 1016_13_27to30s Song type 200	 Calsab 1016_34_88to90s Song type 201	 Calsab 1017_11_102to105s Song type 202	 Calsab 1018_5_84to87s Song type 203
 Calsab 1017_7_48to52s Song type 204	 Calsab 1017_14_156to159s Song type 205	 Calsab 1019PNR_12_72to74s Song type 206	 Calsab 1002_3_13to17s Song type 207
 Calsab 1013_9_57to60s Song type 208	 Calsab 1013_10_64to69s Song type 209	 Calsab 1013_16_121to124s Song type 210	 Calsab 1017_12_106to109s Song type 211
 Calsab 1019PNR_4_11to14s Song type 212	 Calsab 1017_18_177to180s Song type 213	 Calsab 1019PNR_5_23to26s Song type 214	 Calsab 1019PNR_6_39to42s Song type 215
 Calsab 1019PNR_7_43to46s Song type 216	 Calsab 1019PNR_8_47to49s Song type 30a	 Calsab 1019PNR_10_65to67s Song type 217	 Calsab 1021PNR_1_12to16s Song type 218
 Calsab 1021PNR_2_22to25s Song type 219	 Calsab 1021PNR_4_37to42s	 Calsab 1021PNR_5_46to50s	 Calsab 1021PNR_10_92to95s

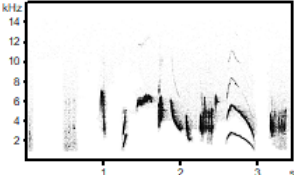
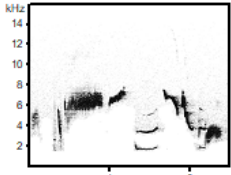
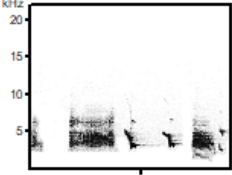
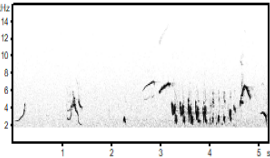
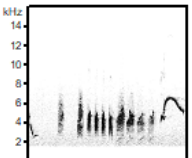
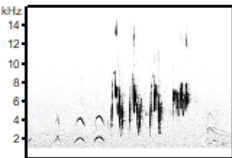
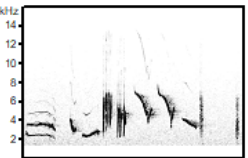
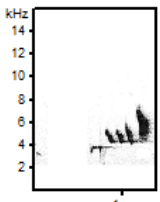
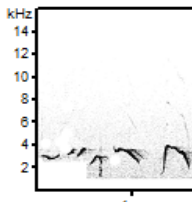
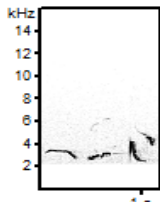
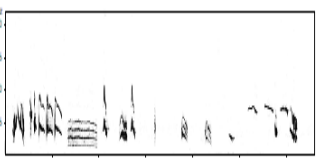
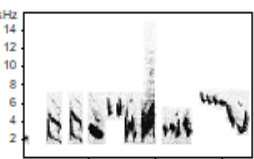
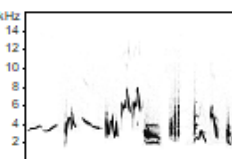
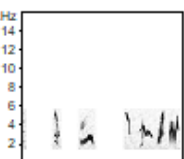
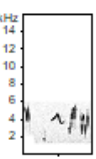
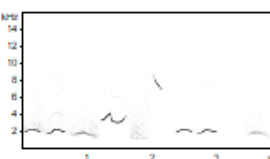
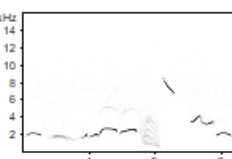
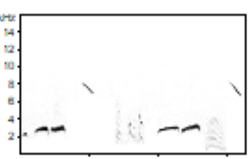
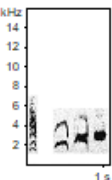
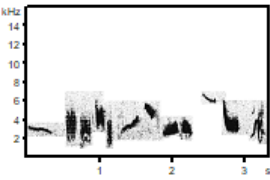
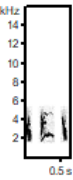
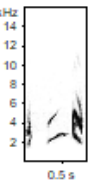
 Calsab 1019PNR_11_68to70s			
Mopane Basalt Shrubland (MBS)			
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Song type 224  Calsab 1013_23_137to139s	Song type 225  Calsab 1013_17_107to109s	Song type 226  Calsab 1015_24_130to134s	Song type 227  Calsab 1017_15_91to93s
Song type 228  Calsab 1013_20_120to123s	Song type 229  Calsab 1001_3_12to18	Song type 230  Calsab 1001_8_47to50s	Song type 231  Calsab 1001_11_61to64s
Song type 232  Calsab 1017_16_119to122s	Song type 234  Calsab 1001_22_147to150s	Song type 235  Calsab 1001_24_155to159s	Song type 236  Calsab 1001_26_165to168s
Song type 237	Song type 247	Song type 248	Song type 249

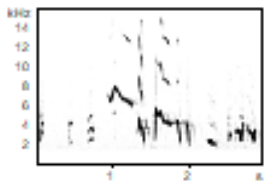
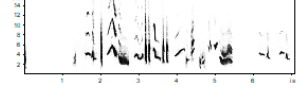
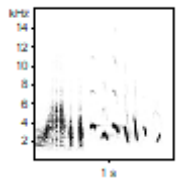
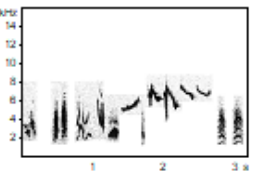
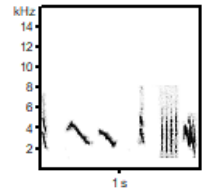
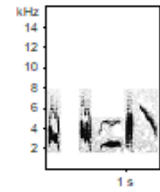
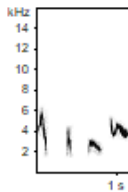
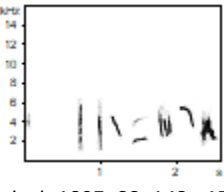
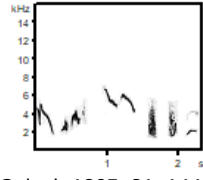
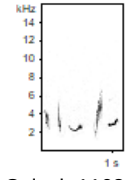
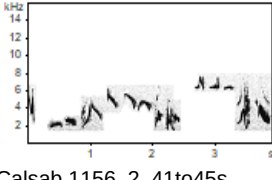
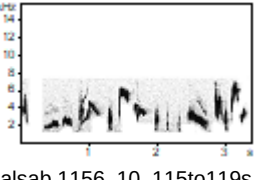
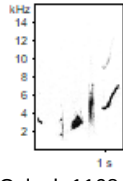
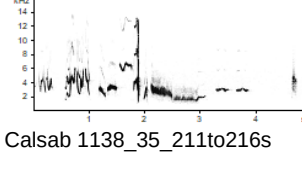
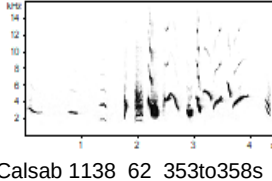
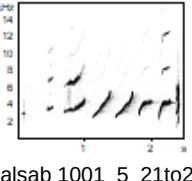
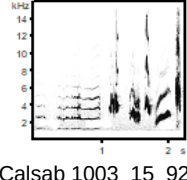
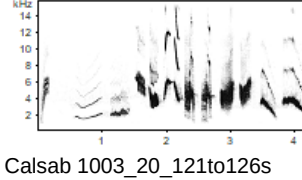
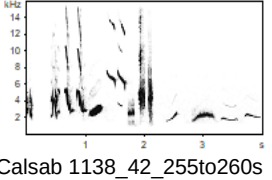
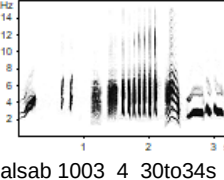
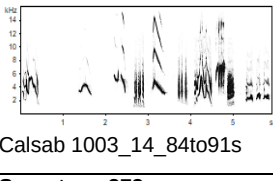
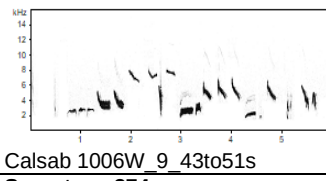
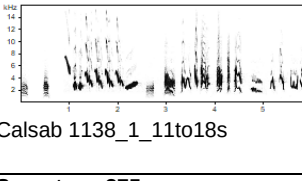
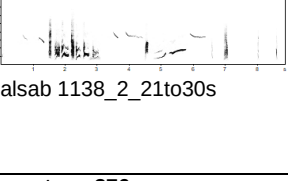
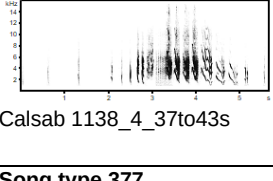
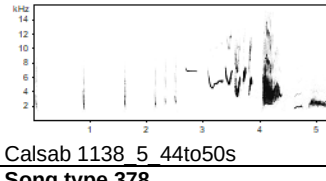
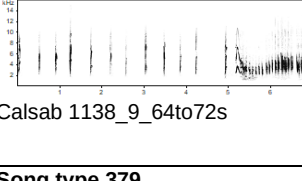
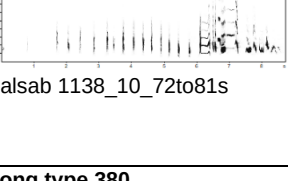


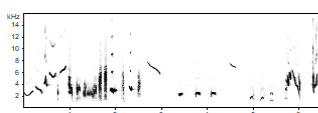
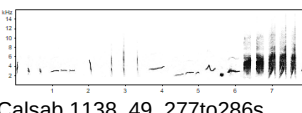
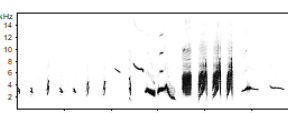
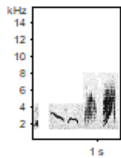
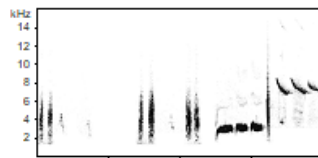
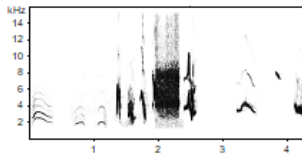
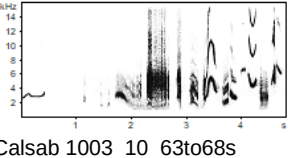
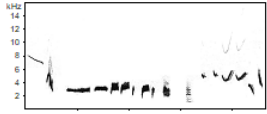
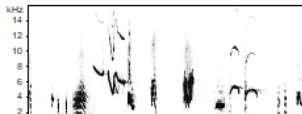
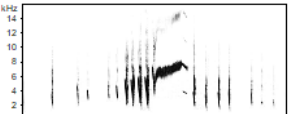
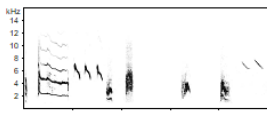
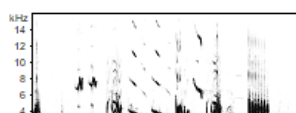
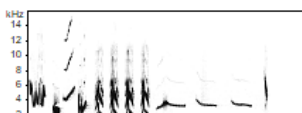
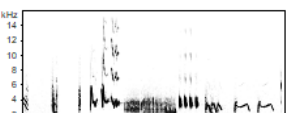
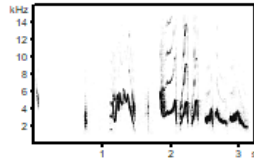
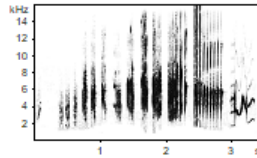
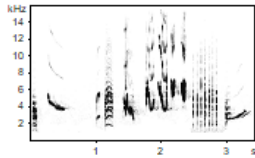
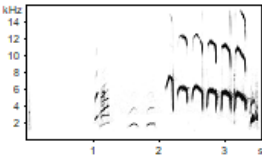
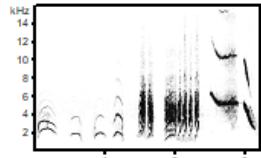
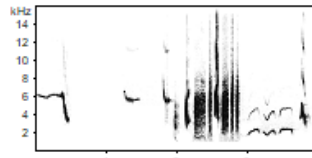
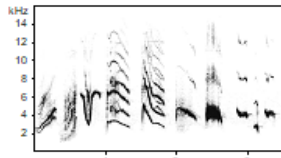
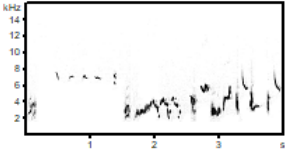
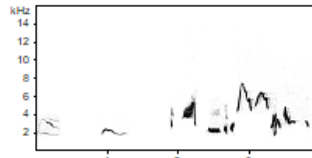
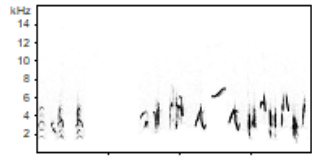
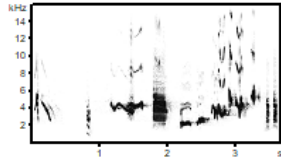
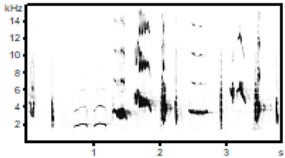
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Song type 279  Calsab 1007_1_20to22s	Song type 280  Calsab 1001_15_83to87s	Song type 281  Calsab 1015_1_2to6s	Song type 282  Calsab 1079_10_68to73s
Song type 285  Calsab 1017_2_13to16s	Song type 289  Calsab 1015_25_135to139s	Song type 292  Calsab 1015_30_184to188s	Song type 294  Calsab 1017_5_33to36s
Song type 295  Calsab 1017_9_55to59s	Song type 296  Calsab 1015_9_45to48s	Song type 297  Calsab 1079_2_13to15s	Song type 304  Calsab 1015_43_259to262s
Song type 305  Calsab 1001_14_78to81s	Song type 306  Calsab 1001_5_25to28s	Song type 307  Calsab 1001_5_25to28s	Song type 310  Calsab 1017_11_65to68s
Song type 311  Calsab 1017_25_206to209s	Song type 312  Calsab 1017_26_212to215s	Song type 313  Calsab 1079_11_77to81s	Song type 314  Calsab 1079_19_131to134s
Song type 315	Song type 316	Song type 319	Song type 320

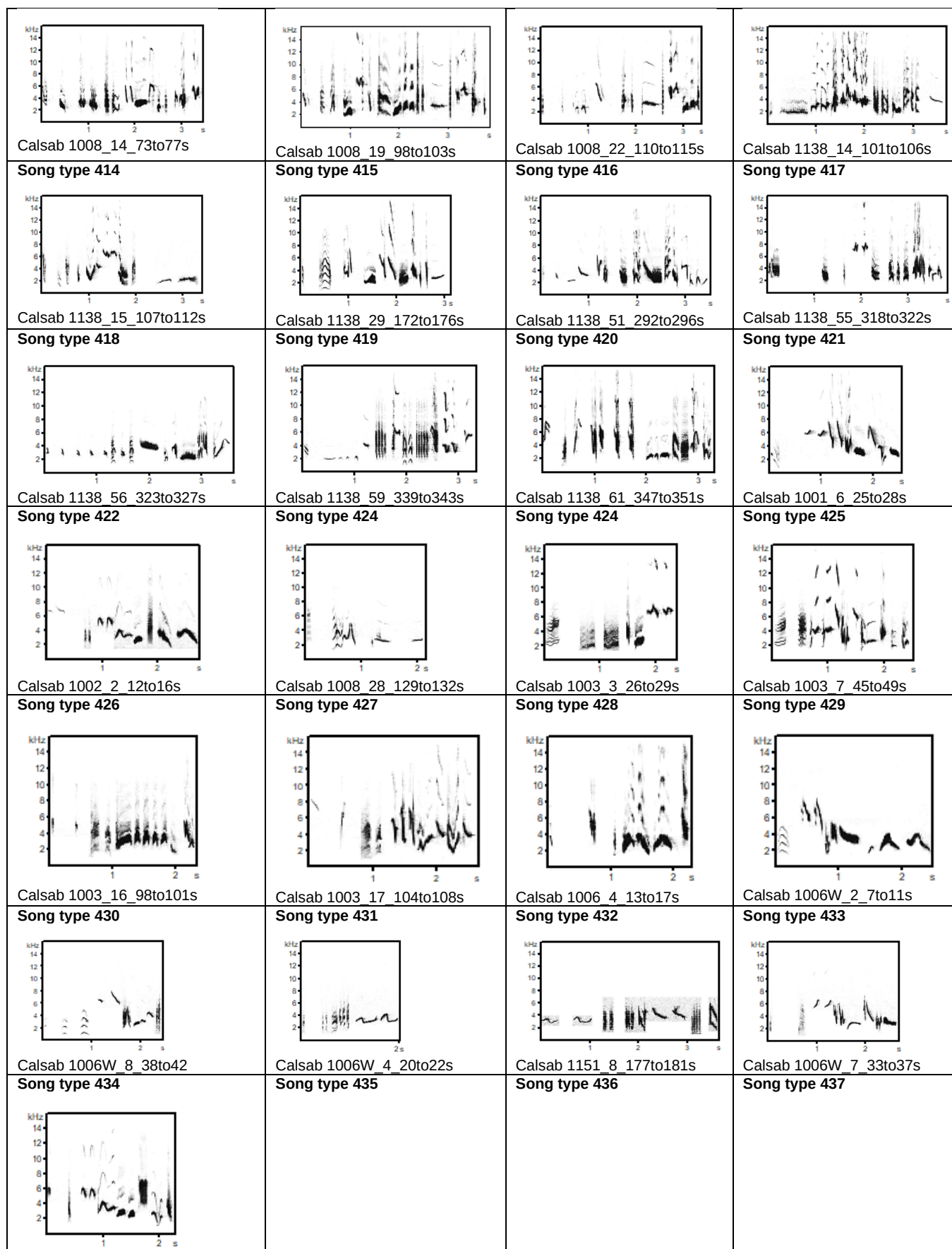
 Calsab 1001_10_57to60s	 Calsab 1001_7_43to46s	 Calsab 1007_4_30to33s	 Calsab 1013_7_45to48s
Song type 321  Calsab 1015_28_150to154s	Song type 322  Calsab 1017_13_73to77s	Song type 325  Calsab 1079_20_141to143s	Song type 330  Calsab 1079_18_125to128s
Song type 334  Calsab 1015_35_212to214s	Song type 335  Calsab 1017_23_197to199s		
Tsende Mopaneveld (TM)			
Song type 243  Calsab 1006_1_8to11s	Song type 245  Calsab 1006_8_56to59s	Song type 246  Calsab 1006_12_83to87s	Song type 266  Calsab 1004_42_371to378s
Song type 269  Calsab 1004_23_239to243s	Song type 270  Calsab 1005_8_95to99s	Song type 283  Calsab 1004_21_217to221s	Song type 284  Calsab 1004_40_352to356s
Song type 286  Calsab 1004_11_106to109s	Song type 287  Calsab 1004_35_321to323s	Song type 290  Calsab 1004_25_265to267s	Song type 291  Calsab 1004_14_148to151s

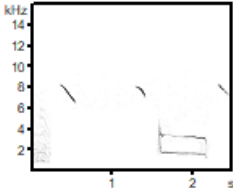
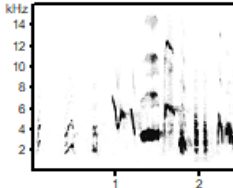
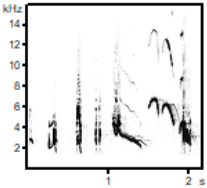
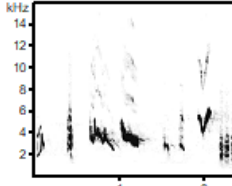
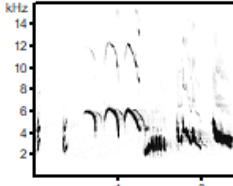
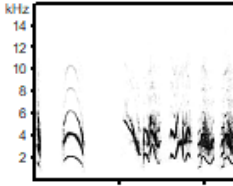
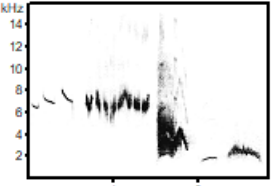
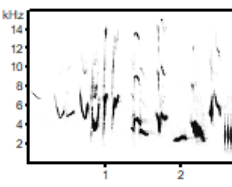
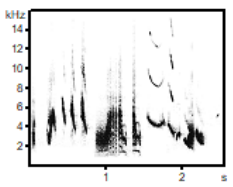
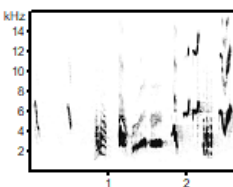
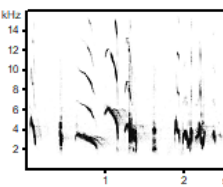
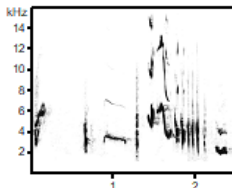
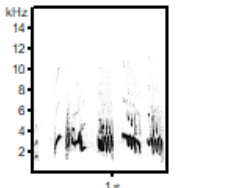
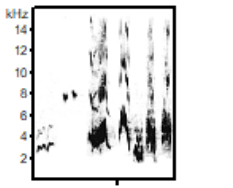
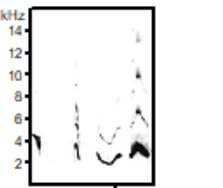
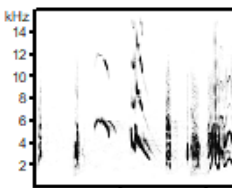
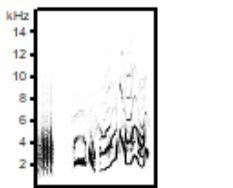
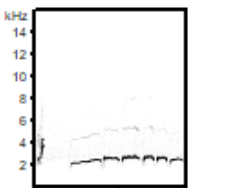
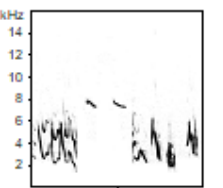
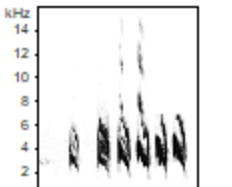
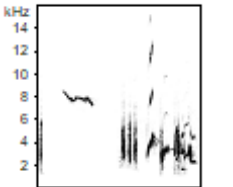
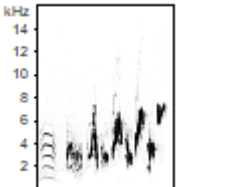
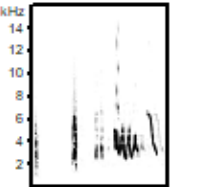
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Song type 301  Calsab 1005_12_158to161s	Song type 302  Calsab 1006_11_77to80s	Song type 308  Calsab 1004_24_254to257s	Song type 309  Calsab 1004_37_335to338s
Song type 317  Calsab 1006_5_32to35s	Song type 318  Calsab 1004_30_300to303s	Song type 323  Calsab 1004_5_53to55s	Song type 324  Calsab 1005_10_133to134s
Song type 329  Calsab 1004_26_267to270s	Song type 331  Calsab 1004_34_315to317s	Song type 332  Calsab 1004_36_325to327s	Song type 333  Calsab 1004_1_7to8s
Song type 233  Calsab 1004_39_348to350s	Song type 238  Calsab 1004_2_14to17s	Song type 239  Calsab 1004_15_160to161s	Song type 240  Calsab 1004_9_90to93s
Song type 241	Song type 242	Song type 336	

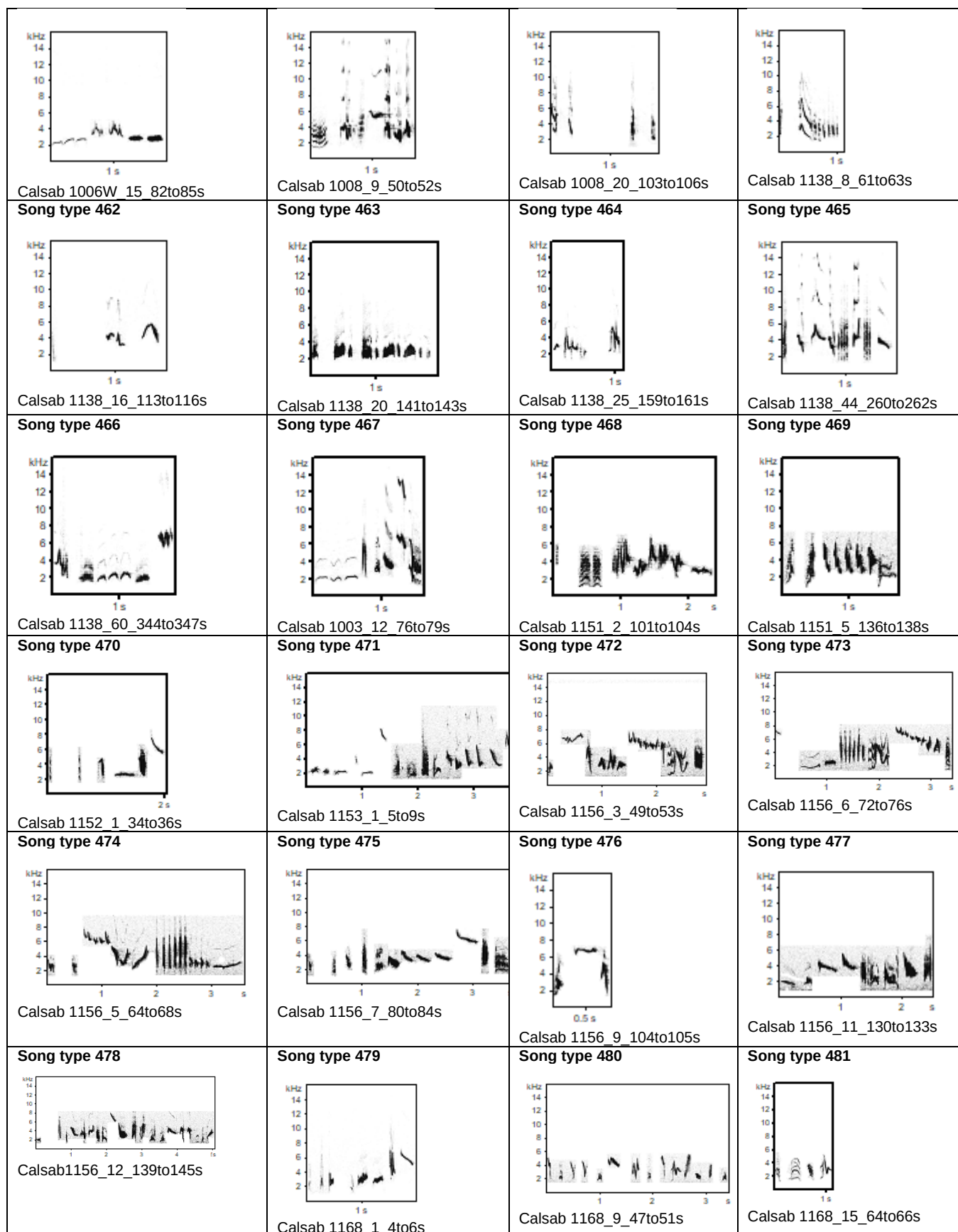
 Calsab 1004_18_182to186s	 Calsab 1004_13_133to136s	 Calsab 1004_17_175to178s	
Mopane Gabbro Shrubland (MGS)			
Song type 273  Calsab 1076_12_113to119s	Song type 288  Calsab 1076_14_129to132s	Song type 300  Calsab 1076_15_143to146s	Song type 303  Calsab 1076_4_16to20s
Song type 326  Calsab 1076_16_175to177s	Song type 327  Calsab 1076_8_100to103s	Song type 328  Calsab 1076_9_105to107s	
Bushmanland Basin Shrubland (BBS)			
Song type 337  Calsab 1003_1_12to19s	Song type 338  Calsab 1156_4_55to59s	Song type 339  Calsab 1006W_5_23to27s	Song type 340  Calsab 1168_16_68to71s
Song type 341  Calsab 1168_13_59to60s	Song type 342  Calsab 1007_1_1to5s	Song type 343  Calsab 1007_4_10to15s	Song type 344  Calsab 1007_11_34to39s
Song type 345  Calsab 1205_12_85to87s	Song type 346  Calsab 1152_2_48to52s	Song type 347  Calsab 1023_22_134to135s	Song type 348  Calsab 1001_1_2to5s
Song type 349	Song type 350	Song type 351	Song type 352

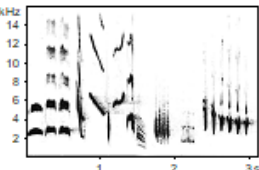
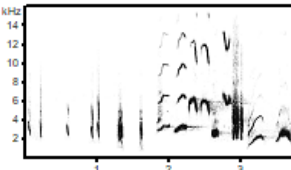
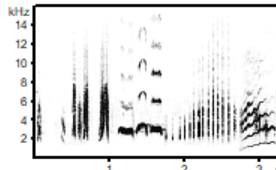
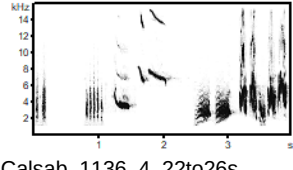
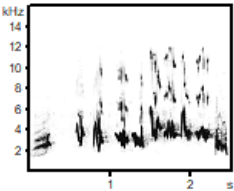
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Song type 353  Calsab 1151_9_184to189s	Song type 354  Calsab 1152_3_53to55s	Song type 355  Calsab 1205_29_137to140s	Song type 356  Calsab 1205_32_148to151s
Song type 357  Calsab 1205_31_144to147s	Song type 358  Calsab 1168_5_27to29s	Song type 359  Calsab 1156_2_41to45s	Song type 360  Calsab 1156_10_115to119s
Song type 361  Calsab 1168_4_11to13s	Song type 362  Calsab 1138_35_211to216s	Song type 363  Calsab 1138_62_353to358s	Song type 364  Calsab 1001_5_21to24s
Song type 365  Calsab 1003_15_92to96s	Song type 366  Calsab 1003_20_121to126s	Song type 367  Calsab 1138_42_255to260s	Song type 368  Calsab 1003_4_30to34s
Song type 369  Calsab 1003_14_84to91s	Song type 370  Calsab 1006W_9_43to51s	Song type 371  Calsab 1138_1_11to18s	Song type 372  Calsab 1138_2_21to30s
Song type 373  Calsab 1138_4_37to43s	Song type 374  Calsab 1138_5_44to50s	Song type 375  Calsab 1138_9_64to72s	Song type 376  Calsab 1138_10_72to81s
Song type 377	Song type 378	Song type 379	Song type 380

 Calsab 1138_12_85to99s	 Calsab 1138_37_220to228s	 Calsab 1138_49_277to286s	 Calsab 1138_57_327to334s
Song type 381  Calsab 1151_6_174to176s	Song type 382  Calsab 1001_3_7to12s	Song type 383  Calsab 1003_5_36to42s	Song type 384  Calsab 1003_10_63to68s
Song type 385  Calsab 1006W_3_12to18s	Song type 386  Calsab 1006W_17_94to99s	Song type 387  Calsab 1008_29_132to138s	Song type 388  Calsab 1138_3_31to36s
Song type 389  Calsab 1138_32_189to195s	Song type 390  Calsab 1138_38_228to233s	Song type 391  Calsab 1138_41_246to251s	Song type 392  Calsab 1138_46_264to269s
Song type 394  Calsab 1138_58_334to338s	Song type 395  Calsab 1002_9_58to61s	Song type 396  Calsab 1008_18_93to97s	Song type 397  Calsab 1003_9_57to61s
Song type 398  Calsab 1003_11_70to74s	Song type 399  Calsab 1003_13_79to84s	Song type 400  Calsab 1003_19_114to118s	Song type 401  Calsab 1006W_10_53to58s
Song type 402  Calsab 1006W_11_61to66s	Song type 403  Calsab 1006W_13_69to74s	Song type 405  Calsab 1008_10_55to59s	Song type 406  Calsab 1008_11_60to65s
Song type 407	Song type 408	Song type 409	Song type 411

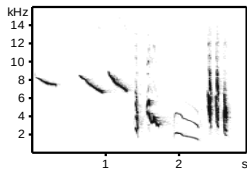
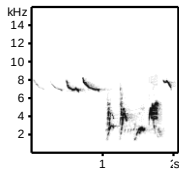
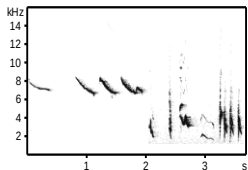
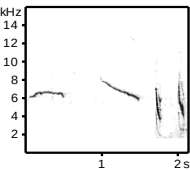


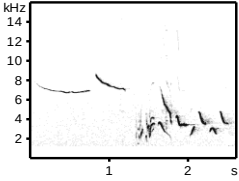
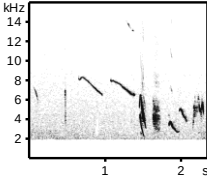
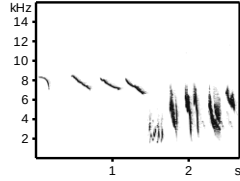
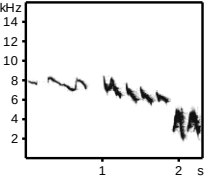
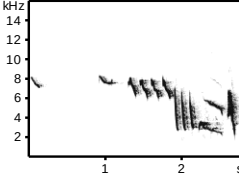
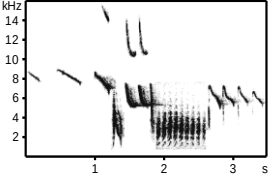
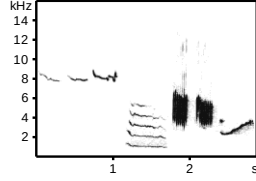
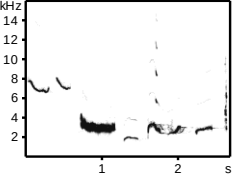
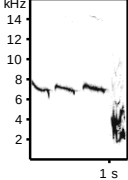
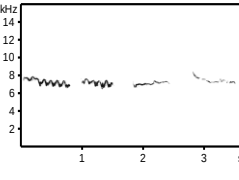
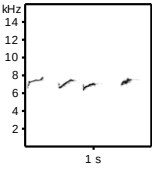
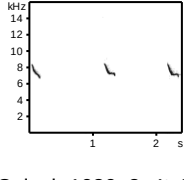
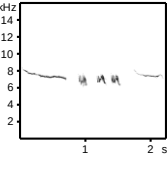
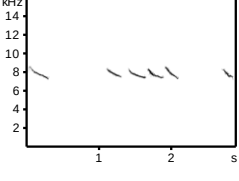
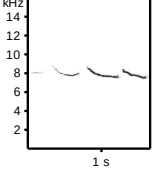
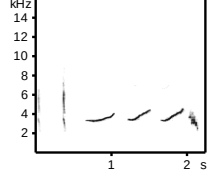
Calsab 1003_23_131to135s	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays several horizontal lines of energy, with a prominent one around 8 kHz.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Song type 438	Song type 439	Song type 440	Song type 441
 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Calsab 1008_6_38to41s	Calsab 1008_7_43to47s	Calsab 1138_31_183to186s	Calsab 1138_33_196to199s
Song type 442	Song type 443	Song type 444	Song type 445
 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Calsab 1138_34_201to205s	Calsab 1138_48_273to276s	Calsab 1008_15_79to83s	Calsab 1008_25_119to123s
Song type 446	Song type 447	Song type 448	Song type 449
 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Calsab 1008_21_106to110s	Calsab 1003_24_136to139s	Calsab 1006_1_2to5s	Calsab 1006_2_7to10s
Song type 450	Song type 451	Song type 452	Song type 453
 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Calsab 1008_17_90to92s	Calsab 1138_27_167to169s	Calsab 1002_7_44to48s	Calsab 1006W_1_3to6s
Song type 454	Song type 455	Song type 456	Song type 457
 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It displays a complex pattern of energy with multiple horizontal lines and some vertical bursts.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It shows a series of vertical lines of energy, indicating short, repeated sounds.	 A spectrogram showing frequency (kHz) on the y-axis (2 to 14) and time (s) on the x-axis (1 to 2). It features a series of vertical lines of energy, indicating short, repeated sounds.
Calsab 1003_1_19to22s	Calsab 1003_2_23to26s	Calsab 1006W_14_75to78s	Calsab 1008_4_28to31s
Song type 458	Song type 459	Song type 460	Song type 461

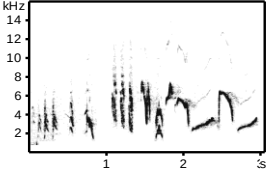
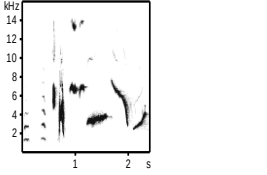
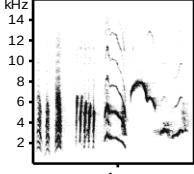
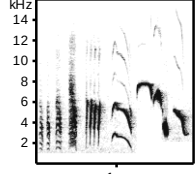
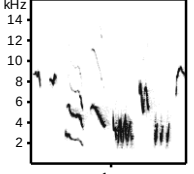
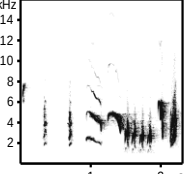
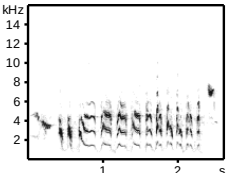
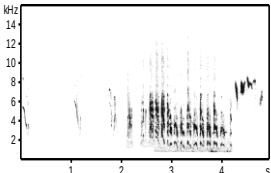
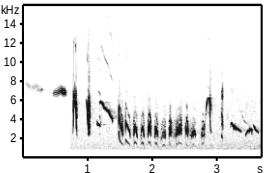
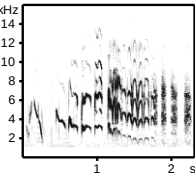
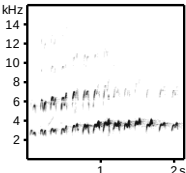
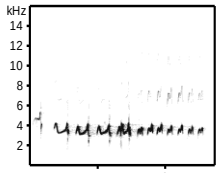
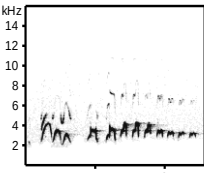
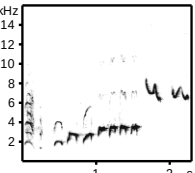
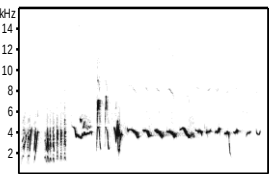
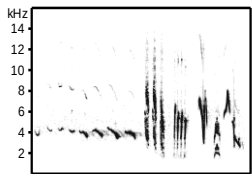
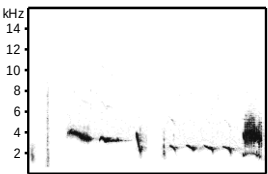


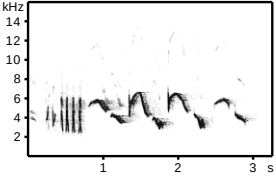
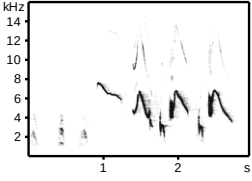
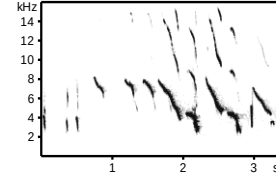
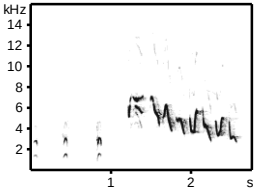
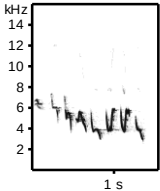
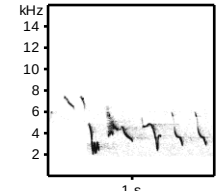
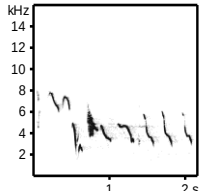
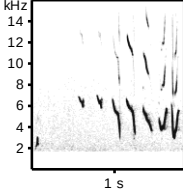
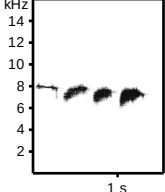
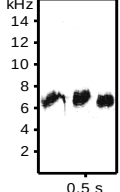
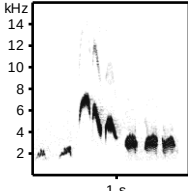
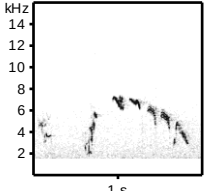
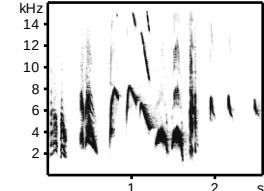
Bushmanland Arid Grassland (BAG)			
Song type 393  Calsab 1136_1_0to4s	Song type 404  Calsab 1136_2_7to12s	Song type 410  Calsab 1136_3_13to19s	Song type 412  Calsab 1136_4_22to26s
Song type 413  Calsab 1136_5_32to36s			

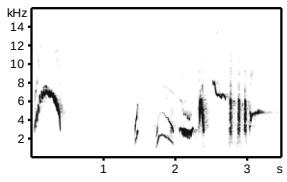
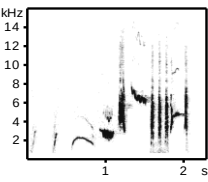
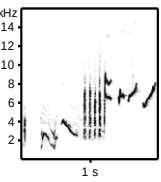
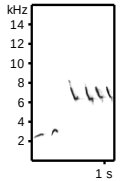
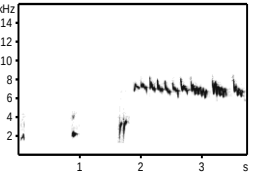
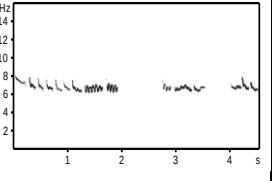
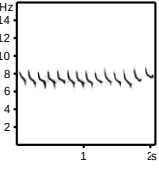
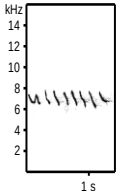
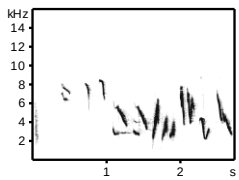
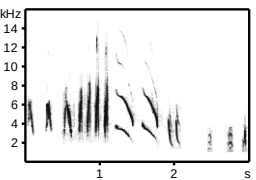
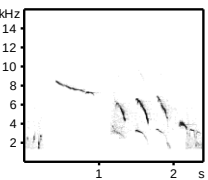
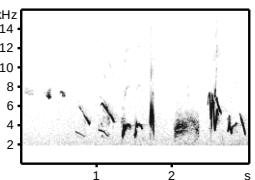
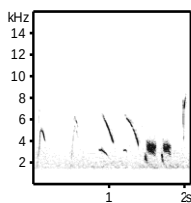
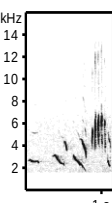
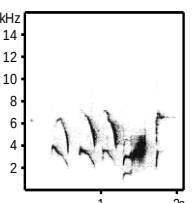
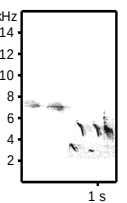
Appendix 2.3. Shared song types among Sabota larks recorded in different vegetation types. In Calsab 1045_1_6to9s (MMB1), Calsab stands for *Calendulauda sabota*, 1045 – recording identification number, 1 – strophe number, 6to9s – start and end times of the strophe within the recording, MMB1-Bird 1 from Musina Mopane Bushveld. Different codes e.g., MMB2, MGS1 etc., within a song type refers to the different individual birds that rendered a particular song type. Birds from Musina Mopane Bushveld are marked by MMB, birds from Mopane Gabbro Shrubland-MGS, Makhado Sweet Bushveld-MSB, Mopane Basalt Shrubland-MBS, Polokwane Plateau Bushveld-PPB, Roodeberg Bushveld-RB, Tsende Mopaneveld-TM, Bushmanland Basin Shrubland-BBS, Bushmanland Arid Grassland-BAG.

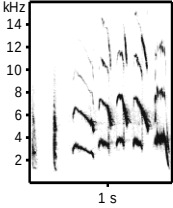
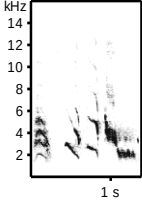
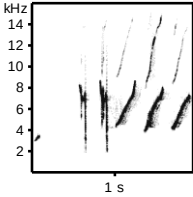
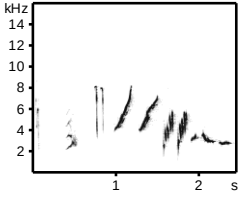
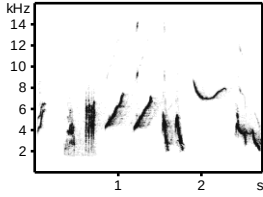
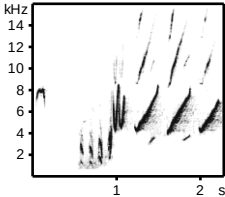
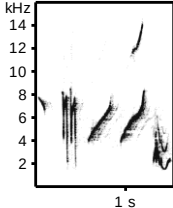
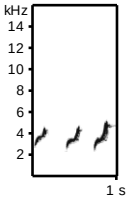
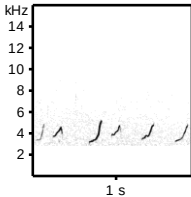
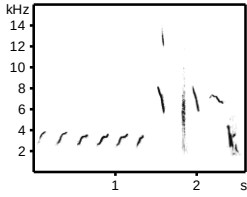
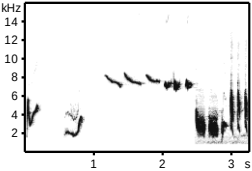
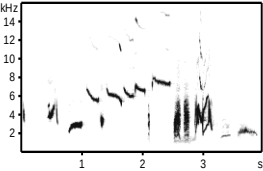
Song type 1			
 Calsab 1045_1_6to9s (MBS1)	 Calsab 1049_33_195to197s (MBS2)	 Calsab 1053_26_118to122s (MBS3)	 Calsab 1076_7_96to98s (MGS1)

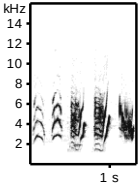
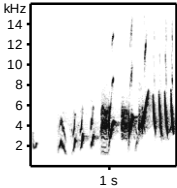
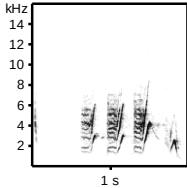
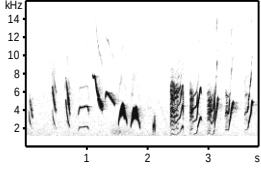
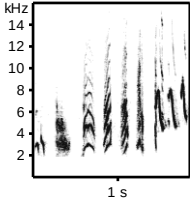
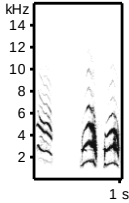
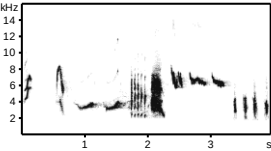
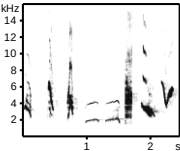
 Calsab 1079_17_112to115s (MBS8)	 Calsab 1015_36_215to218s (MBS5)	 Calsab 1046_6_37to40s (MSB2)	 Calsab 1026_7_85to88s (MSB6)
 Calsab 1002_1_3to6s (PPB1)	 Calsab 1013_8_47to51s (PPB2)	 Calsab 1017_16_162to165s (PPB4)	 Calsab 1008_27_125to129s (BBS5)
 Calsab 1036_25_143to145s (RB1)			
Song type 2			
 Calsab 1047_10_148to152s (MBS1)	 Calsab 1070_8_38to50s (MBS3)	 Calsab 1030_3_4to7s (MSB1)	 Calsab 1002_6_85to88s (MSB4)
 Calsab 1013_3_11to14s (PPB2)	 Calsab 1017_9_91to93s (PPB4)	 Calsab 1138_50_288to291s (BBS6)	
Song type 7			

 Calsab 1054_23_186to189s (MBS3)	 Calsab 1036_8_32to35s (RB1)		
Song type 9			
 Calsab 1046_4_65to67s (MBS1)	 Calsab 1053_5_18to20s (MBS3)	 Calsab 1051_18_139to141s (MSB3)	 Calsab 1002_6_30to33s (PPB1)
Song type 11			
 Calsab 1045_13_181to184s (MBS1)	 Calsab 1054_13_103to108s (MBS3)	 Calsab 1076_5_23to27s (MGS1)	 Calsab 1002_8_50to53s (BBS2)
Song type 12			
 Calsab 1045_22_261to264s (MBS1)	 Calsab 1070_3_15to18s (MBS3)	 Calsab 1004_16_166to169s (TM1)	 Calsab 1026_3_36to39s (MSB6)
Song type 17			
 Calsab 1047_5_45to50s (MBS1)	 Calsab 1054_5_35to39s (MBS3)	 Calsab 1005_3_47to50s (TM1)	
Song type 18			

 Calsab 1045_5_37to41s (MBS1)	 Calsab 1057_5_31to34s (MBS3)	 Calsab 1036_9_39to43s (RB1)	
Song type 19			
 Calsab 1045_6_52to55s (MBS1)	 Calsab 1070_18_112to114s (MBS3)	 Calsab 1007_2_24to26s (MBS2)	 Calsab 1008_1_1to3s (MBS3)
 Calsab 1015_46_271to274s (MBS5)			
Song type 25			
 Calsab 1053_16_68to70s (MBS3)	 Calsab 1036_7_29to31s (RB1)		
Song type 26			
 Calsab 1057_15_101to103s (MBS1)	 Calsab 1013_9_60to63s (MBS4)	 Calsab 1036_15_85to88s (RB1)	
Song type 32			

 Calsab 1045_26_290to294s (MBS1)	 Calsab 1054_31_240to242s (MBS3)	 Calsab 1051_23_152to155s (MSB3)	
Song type 117			
 Calsab 1002_1_41to43s (MSB4)	 Calsab 1037_6_46to50s (MSB8)	 Calsab 1013_6_28to33s (PPB2)	 Calsab 1018_1_18to21s (PPB4)
 Calsab 1027_1_160to162s (PPB5)			
Song type 23			
 Calsab 1046_1_2to6s (MSB2)	 Calsab 1051_39_227to230s (MSB3)	 Calsab 1013_1_3to6s (MBS4)	 Calsab 1015_23_126to130s (MBS5)
 Calsab 1017_1_7to9s (MBS6)	 Calsab 1079_9_65to66s	 Calsab 1005_4_63to65s (TM1)	 Calsab 1076_6_46to47 (MGS1)

 Calsab 1036_26_147to150s (RB1)	 Calsab 1021PNR_11_176to178s (PPB4)		
Song type 124			
 Calsab 1051_1_56to58s (MSB3)	 Calsab 1046_16_74to77s (MSB2)	 Calsab 1019_14_119to122s (MSB5)	 Calsab 1036_12_68to71s (RB1)
 Calsab 1019PNR_9_61to63s (PPB4)			
Song type 133			
 Calsab 1037_3_30to31s (MSB8)	 Calsab 1015_33_203to205s (MBS5)	 Calsab 1017_10_60to63s (MBS6)	
Song type 139			
 Calsab 1046_23_110to114s (MSB2)	 Calsab 1138_7_53to57s (BBS6)		

Song type 142			
 Calsab 1051_37_204to206s (MSB3)	 Calsab 1019_13_113to115s (MSB5)	 Calsab 1001_23_151to154s (MBS1)	 Calsab 1076_1_4to8s (MGS1)
Song type 143			
 Calsab 1051_34_193to195s (MSB3)	 Calsab 1036_19_112to114s (RB1)		
Song type 158			
 Calsab 1019_6_64to68s (MSB5)	 Calsab 1008_13_67to71s (BBS5)		

CHAPTER 3

Acoustic Adaptation Hypothesis – does it hold for the Sabota Lark *Calendulauda sabota*?

3.1. Introduction

Many bird species' vocalisations, both songs and calls, vary in space and time within and among species, populations, and individuals (Luther 2009, Priyadarshani *et al.* 2018). The variations range from differences in spectral (frequencies) and temporal characteristics that comprise species vocalisations (Kumar 2003). The challenge is explaining how these variations originated, their diversification, and persistence (Podos *et al.* 2004). Derryberry *et al.* (2012) maintained that “understanding the forces underlying signal evolution is an important aspect of understanding the process of species diversification”, and habitat is one such factor proposed to be imposing selection on bird vocalisations. On the other hand, Chapuis (1971) maintained the view about the influence of the dense forest environment on the evolution of the sound emissions of birds, that the species' survival requires a minimum frequency range.

Birds use their vocalisations to communicate, which refers to an association between a signaller's and a receiver's behaviour because of a signal (a specific pattern of energy transmitted between them) (Matessi *et al.* 2008). Each signal contains information which may denote the signaller's identity, behaviour, or external circumstances (Wiley and Richards 1978, Matessi *et al.* 2008). It is generally understood that avian acoustic communication has two main functions: territory defence and mate attraction (Mathevon *et al.* 2004). However, sound signals do not always reach the intended audience or rather face challenges during transmission to the receiver/s. This may result in sound signals being ineffective as auditory communication is only effective when sound signals successfully reach their intended audience (Mason and Burns 2015).

During the acoustic communication process, deterioration of sound signals is inevitable. According to Naguib and Wiley (2001), attenuation of sound signals during propagation is caused by spherical divergence (the apparent loss of energy from a wave as it spreads during transmission) and the environment. The environment causes attenuation through atmospheric absorption, stationary objects near the sound's propagation path, nonstationary turbulence in the atmosphere, and velocity gradients, including temperature and complex ground effects (Azar and Bell 2016). As a result of sound attenuation and degradation during propagation, information in a signal at the source (broadcast information) is always greater than the information obtained by the receiver (received information) (Wiley and Richards 1978). Received information depends on the receiver's ability to identify true signals instead of random perturbations of its sense organs by the background noise, distinguish among various signals, and decrypt the information contained in the signals (Wiley and Richards 1978). Several authors have suggested that distance between communicating birds is likely to be an important influence on the design of songs (Jilka and Leisler 1974; Zann 1975, Nottebohm 1975).

It is not only signallers that have to deal with challenges presented by communication constraints but also receivers (Mathevon *et al.* 2004). As a result of the modifications accumulated during propagation, a signal may be so distorted that the intended receiver fails to decrypt it, resulting in the failure of the signal affecting the intended receiver (Mason and Burns 2015). Sound signals have an active space (i.e., the maximum distance a sound signal can travel until the intended receiver detects it) (Parris and McCarthy 2013). However, the active space changes and depends on several factors which relate to the signaller (e.g., temporal and spectral characteristics, signal amplitude, spatial position), the environment (e.g., habitat structure, ambient noise, weather conditions), and the intended receiver (e.g., hearing sensitivity, spatial position) (Mathevon *et al.* 2004, Parris and McCarthy 2013). Fortunately, some of these factors can be controlled by the bird's behaviour, e.g., singing on a song post or perching to overcome ground effects, which would result in improved signal transmission (or improved signal detection for receivers), increasing the probability of being detected by the intended receiver (Morton 1975, Mathevon *et*

al. 2004, Arasco *et al.* 2022). Another way by which the signaller can control the active space of its sound signals is by choosing to sing during the times of day that are favourable for signal transmission (Aide *et al.* 2017). This is because some factors that degrade sound signals, like atmospheric turbulence, absorption, and ambient abiotic noise, can vary during the day. Along these lines, the “transmission hypothesis” proposes that the energetic singing of birds in the early hours of the day (dawn chorus) is because of minimal degradation (and thus improved propagation) of sound signals during the dawn hours (Brown and Handford 2003, Gordo *et al.* 2021).

According to Saunders and Slotow (2004), “Since birds are sensitive to signal degradation and taking into account the importance of song in determining fitness of the singer, it seems logical that natural selection would structure signals in a way to minimise degradation imposed by the environment”. Since communication involves signallers and receivers, the Sensory Drive Hypothesis (SDH) (Endler 1992) proposes that the environment imposes selection on both sensory perceptions (signal detecting capabilities) and signals (detectable features and behaviour) such that both components coevolve (Cummings and Endler 2018). This has the potential to culminate in the diversification of lineages through allopatric divergence (Sobel *et al.* 2010). Before the inception of the SDH, Morton (1975) proposed what is today known as the Acoustic Adaptation Hypothesis (AAH) (Hansen 1979), which only deals with the signalling component of the SDH (Cummings and Endler 2018). Some authors consider both hypotheses similar (Villegas *et al.* 2018), but AAH does not deal with sensory perceptions.

The AAH (Morton 1975, Hansen 1979) proposes that habitat structure imposes selection on species' vocalisations such that only those features that resist habitat-induced modification and maximise fidelity over longer distances become dominant. Therefore, selection should shape species' vocalisations to maximise transmission through their habitats. Barker (2008) identified three major approaches to studying the relationship between habitat, song structure and sound transmission: 1) by comparing song characteristics (spectral and temporal) between categories of habitats, 2) by studying sound transmission, i.e., investigating how sound propagates through the

natural environment, and 3) by investigating the relationships between habitat, song structure and song transmission in one or a few species.

The AAH predicts spectral and temporal features of species' vocalisations based on the premise that vocalisations are adapted to be less attenuated and degraded, and to travel longer distances (Azar and Bell 2016). In closed habitats that are characterised by closed canopies and dense foliage, bird vocalisations are predicted to be characterised by low frequencies (minimum, maximum, and peak/dominant frequencies), narrow frequency range or bandwidth frequency (Azar and Bell 2016), low frequency modulations (whistled or tonal), long elements separated by long inter-element intervals and fewer number of elements (Badyaev and Leaf 1997, Nemeth *et al.* 2006). On the other hand, vocalisations of birds that occur in open habitats with herbaceous coverage should produce vocalisations that have high frequencies (minimum, maximum, and peak frequencies), and a broad frequency range or broad bandwidth frequency, high frequency modulations (with trills) (Morton 1975), composed of short elements separated by short inter-element intervals and more elements (Badyaev and Leaf 1997).

Correlation has also been shown to exist between bird vocalisations and bird bill sizes. Song features like frequency modulations are affected by how fast the bill opens and closes (Ryan and Brenowitz 1985; Palacios and Tubaro 2000), and this largely depends on the size of the bill. Larger bills, necessary for feeding on food items like seeds with hard covering (Herrel *et al.* 2005; Huber and Podos 2006), open and close at slower rates than smaller bills during song delivery (Ballentine 2006). Thus, the impact of selection on bird bills as a result of diet not only affects birds' feeding skills but also indirectly affects song frequency modulation in the process (little frequency modulation in the case of large bills and rapid frequency modulations in the case of smaller bills) (Herrel *et al.* 2005; Huber and Podos 2006). Bill shape can also affect how elements are delivered within songs, with larger bills uttering elements at a slower rate (Huber and Podos 2006; Derryberry *et al.* 2012). This has been speculated to be the case in the Galapagos finches. It has been noticed that the trill rate differs among individuals with different bill sizes in the Galapagos finches, with slower-paced trills being characteristic of songs of individuals with large bills. These birds feed

mainly on seeds, and the need to extract these seeds efficiently has led to differentiation in their bill sizes (Wilkins *et al.* 2013).

Variations in the size of the syrinx (voice-producing organ in birds), which can be linked to variations in body size (Azar and Bell 2016), have also been shown to impact bird song. The larger syrinx, characteristic of birds with larger body sizes, produce lower frequency sounds than the smaller syrinx of a bird with a smaller body size (Azar and Bell 2016). This is because the larger syrinx vibrates slower than the smaller syrinx (Ryan and Brenowitz 1985; Nowicki and Marler 1988). Other factors also constrain song production, e.g., respiratory and metabolic constraints. Larger birds experience greater respiratory constraints than smaller birds (Suthers 2001) and may thus produce shorter songs. The energetic costs of uttering sounds can also have a constraining effect on the evolution of avian vocalisation. Low-pitched sounds are more expensive for the emitter than high ones (Boncoraglio and Saino 2007). Although it may be beneficial for an individual to sing loud songs that can be heard at greater distances, the constraint may be the energy required to sing such loud songs (Buskirk 1997). Morphological and metabolic constraints were found to contrast the AAH-related selective pressure (Boncoraglio and Saino 2009). In some species, habitat-dependent changes in frequency use overcome expected body size influences such that call frequency does not vary inversely in relation to body size. Thus, a bird with a smaller body size can utilise lower frequencies in its calls, rather than higher frequencies as expected, because of living in a denser habitat (Nicholls and Goldizen 2006).

Although some studies undoubtedly yielded evidence supporting the AAH, some found “mixed evidence” while others failed to support it (Mathevon *et al.* 2004, Arasco *et al.* 2022). Studies on playback transmission of natural or synthesised sounds clearly show the existence of habitat-dependent degradation patterns. Song degradation may increase when transmission occurs in habitats different from the original (Arasco *et al.* 2022), while optimal propagation is reached in each habitat only for restricted frequency ranges (Morton 1975). Conversely, observational studies where songs of species or conspecific populations from different habitats have been

compared have led to mixed results concerning the validity of the predictions of the AAH (Boncoraglio and Saino 2007).

Proposed explanations for the inconsistencies among studies are: i) a relatively broad categorisation of habitats such as 'open' versus 'closed', which oversimplifies complex habitat conditions (Hardt and Benedict 2021, Arasco *et al.* 2022), ii) prioritising one species or one call type, and iii) usage of different parameters during acoustic analyses across studies. Further complications are also brought about by other factors like phylogenetics, morphology, physiology, social system, and call or song context (Arasco *et al.* 2022). The best measurements are those consistent with previous research, such as maximum, minimum, and peak/dominant frequency (frequency of maximum amplitude), bandwidth (difference between maximum and minimum frequency), song duration, number of notes, note duration, and an indication of how slow or fast the song or call elements are repeated, such as inter-note interval (i.e., spacing between successive notes), or number of fast and slow trilled syllables (Barker 2008).

To isolate the specific effect of habitat on acoustic signals' structure, all these other confounding factors must be limited, and a proposed way to restrict them is to study acoustic communication in closely related species or conspecific populations (Arasco *et al.* 2022). Morton (1975), considering the difficulty of obtaining direct experimental evidence to support a hypothesis dealing with selective forces, partly because elements of time cannot be built into the experiment, proposed that one test of the hypothesis was to compare congeneric species of birds occupying different habitats. According to Nicholls and Goldizen (2006), several studies have found that birds from denser habitats call at lower frequencies than those from more open habitats and that temporal properties of vocalisations, such as trill rates, are influenced by habitat type as predicted. However, most of these studies have involved comparisons across different species; a within-species comparison provides a better test of the effect of habitat as it provides greater control of other factors that can influence vocalisations, such as phylogenetic history (Ryan and Brenowitz 1985) or body size (Azar and Bell 2016). Tieleman *et al.* (2002) also pointed out that one way

to reduce problems relating to differences in phylogenetic history is to compare traits among closely related species.

As evidenced by the large number of publications, most research on ecology and evolution is carried out in the Northern Hemisphere and forests habitats (Hardt and Benedict 2021). The issue comes when conclusions on research in the Northern Hemisphere are assumed to be true in the Southern Hemisphere, overlooking the unique characteristics of the Southern Hemisphere. Many aspects distinguish the Southern Hemisphere from the Northern Hemisphere, e.g., the Northern Hemisphere has more land surface. In contrast, the Southern has more ocean, contributing to their climatic differences (Chown *et al.* 2004). A Southern Hemisphere perspective must be included (Theuerkauf *et al.* 2022). Published research on birds has been primarily conducted on bird species occurring in temperate regions of the Northern Hemisphere where it is documented that typically only males sing, and this creates a bias (Wheeldon *et al.* 2022). Furthermore, most research into the AAH has been conducted on the South American temperate region bird species, with little known about the applicability of the AAH in the Afrotropics (Daniel and Blumstein 1998, Kopuchian *et al.* 2004, Derryberry *et al.* 2018).

The diversity of habitats in which the Sabota Lark *C. sabota* lives presented an opportunity to study the applicability of the AAH. This species provided a “within species” context study of an African endemic occurring in the Southern Hemisphere tropics or subtropics. In larks, singing is almost exclusively performed by males, although the female song has been recorded in the Rufous-naped Lark *Mirafraga africana* (Engelbrecht 2023). There is no unequivocal evidence that both sexes of the Sabota Lark sing, with only males that are known to sing.

Since Morton (1975) proposed the AAH, several studies on this hypothesis have shown that vegetation structure shapes bird vocalisations (Boncoraglio and Saino 2007; Tobias *et al.* 2011). These data were found through two complementary methods: i) analyses of transmitted playbacks, and ii) comparative studies of song features among species or conspecific populations. Studies on playback transmission of natural or synthesised sounds clearly show the existence of habitat-dependent degradation patterns: song degradation may increase when transmission occurs in

habitats different from the native one (Gish and Morton 1981, Nemeth *et al.* 2001), and optimal propagation is reached in each habitat only for restricted frequency ranges (Morton 1975; Wiley and Richards 1978; Wheeldon *et al.* 2022; Pandit *et al.* 2022). In this study, a comparative analyses of song features among conspecific populations of the Sabota Lark was made.

3.1.4. Aim

To investigate the relationships between habitat and the song structure of the Sabota Lark *Calendulauda sabota* by comparing the song characteristics between different types of habitats.

3.1.5. Objectives

The objectives investigated were:

- i) to determine the vegetation types associated with the localities where the songs of Sabota Larks were recorded
- ii) to find out if there are significant differences in songs of Sabota Larks that thrive in the different sampled habitats
- iii) to investigate whether the songs of the Sabota Lark could be differentiated into groups based on the types of habitats from which they were collected
- iv) to test the applicability of the AAH in songs of the Sabota Lark.

3.2. Materials and methods

3.2.1. Data collection

The vocalisations (songs) of Sabota Larks sound recordings were collected as explained in Chapter 2, item 2.2.1, Data collection, of Materials and Methods (item 2.2). What is presented in this section of the chapter was streamlined to avoid repetition of the same information and covers additional information suitable for the investigations in the context of this chapter.

3.2.2. Data analyses

Analyses of vocalisations was performed as explained in Chapter 2. In addition to what was presented in Chapter 2, items 2.2.2 - Data analyses, and item 2.2.2.1 - Spatial mapping, the quantification of vegetation in the field towards the categorisation or classification of the types of vegetation sampled in this study was beyond the scope of this study. Instead, published literature (in addition to field observation-based descriptions of the vegetation types) and the structure of vegetation were used. In addition, credible photographs from the field and those published in the literature were used to assess the type and structure of vegetation at the sampled sites. Vegetation structure was categorised visually as either open, moderately open, or moderately closed (Fig. 3.1).

Northern Cape Province



Habitat north of Pofadder,
towards Onseepkans



Keimoes region



Brandvlei region

Limpopo Province



Vachelia Savanna, Polokwane Plateau



Vachellia scrub, Polokwane Game Reserve

Broad-leaved woodlands (Kruger National Park)



Mixed *Colophospermum*-*Combretum* woodland,
Leta Region, Kruger National Park,



Open Mopani scrub, Letaba region, Kruger
National Park



Dense Mopani scrub, Letaba region, Kruger
National Park



Mixed woodland, Satara region, Kruger
National Park

Figure 3.1. Representative photographs of habitats showing vegetation at sites where songs were recorded (Photograph/s © Derek Engelbrecht).

Table 3.1. Sites from which bird song recordings were obtained. The type of vegetation and vegetation structure, number of individual birds and song recordings are shown. Vegetation types were classified and described based on vegetation shapefile obtained from the South African National Biodiversity Institute (SANBI) (SANBI 2018), Mucina and Rutherford 2006, and visual assessments. The difference between “moderately open” and “moderately closed” vegetation types is that moderately closed vegetation types have fewer open patches than moderately open sites.

Province	Recording site	Vegetation type (acronym)	Vegetation structure	Number of birds recorded	Number of recordings
Limpopo	Limpokwena Nature Reserve (LNR)	Musina Mopane Bushveld (MMB)	Moderately open	3	17
	Kruger National Park (KNP)	Tsende Mopaneveld (TM)	Moderately closed	10	3
		Mopane Basalt Shrubland (MBS)	Moderately open	8	8
		Mopane Gabbro Shrubland (MGM)	Moderately open	1	1
	Polokwane Nature Reserve (PNR)	Polokwane Plateau Bushveld (PPB)	Moderately closed	4	6
	Blouberg Nature Reserve (BNR)	Roodeberg Bushveld (RB)	Moderately closed	1	1
	De Loskop (DLK)	Makhado Sweet Bushveld (MSB)	Moderately open	6	6
	Maribana	Makhado Sweet Bushveld (MSB)	Moderately open	1	1

Northern Cape	Pofadder	Bushmanland Arid Grassland (BAG)	Open	1	1
	Kenhardt	Bushmanland Arid Grassland (BAG)	Open	1	1
	Brandvlei	Bushmanland Basin Shrubland (BBS)	Open	20	23

Table 3.2. A list of all the sites from which bird song recordings were obtained. Information on the vegetation type, structure, and song strophe is provided.

Province	Recording site	Vegetation type (acronym)	Vegetation structure	Number of birds recorded	Number of song recordings	Number of song strophes
Limpopo	Limpokwena Nature Reserve (LNR)	Musina Mopane Bushveld (MMB)	Moderately open	3	17	183
	Kruger National Park (KNP)	Tsende Mopaneveld (TM)	Moderately closed	10	3	49
		Mopane Basalt Shrubland (MBS)	Moderately open	8	8	133
		Mopane Gabbro Shrubland (MGM)	Moderately open	1	1	5
	Polokwane Nature Reserve (PNR)	Polokwane Plateau Bushveld (PPB)	Moderately closed	4	6	85
	Blouberg Nature Reserve (BNR)	Roodeberg Bushveld (RB)	Moderately closed	1	1	44
	De Loskop (DLK)	Makhado Sweet Bushveld (MSB)	Moderately open	6	6	75

	Maribana	Makhado Sweet Bushveld (MSB)	Moderately open	1	1	8
Northern Cape	Pofadder	Bushmanland Arid Grassland (BAG)	Open	1	1	8
	Kenhardt	Bushmanland Arid Grassland (BAG)	Open	1	1	2
	Brandvlei	Bushmanland Basin Shrubland (BBS)	Open	20	23	301

From each strophe, nine parameters were analysed (Table 3.3). Avisoft SAS Lab Pro (Bioacoustics sound analyses software, version 5.2.11) (Specht 2017) performs its analyses on an element basis such that all the elements in strophes were analysed for all the parameters. The software counted the number of elements per strophe to gain the parameters. It measured element duration (s), inter-element interval (s), element start time (s), element end time (s), element peak frequency (Hz), element minimum frequency (Hz), element maximum frequency (Hz), and element bandwidth frequency (Hz). The software outputs quantitative data to an MS Excel worksheet. As a result, means of parameters along each strophe were calculated using formulas in MS Excel. Element start and end time are included in element duration, hence their exclusion from the analyses. Means were calculated for each strophe's remaining seven parameters. This means the quantification associated with each of the analysed parameters henceforth represents a mean in a song strophe.

Table 3.3. Parameters of song strophes studied and their definitions.

No.	Parameter	Definition
1	Element start time (s)	The specific point at which an element in a strophe begins
2	Element end time (s)	The specific point at which an element in a strophe ends

3	Number of elements	The countable distinctive parts of a song strophe
4	Element duration (s)	The time from the start to the end of an element
5	Inter-element interval (s)	The amount of time separating individual elements
6	Element minimum frequency (Hz)	The lowest frequency in a strophe
7	Element maximum frequency (Hz)	The highest frequency in a strophe
8	Element bandwidth frequency (Hz)	The difference between maximum and minimum frequencies
9	Element peak frequency (Hz)	The frequency of the peak of greatest amplitude within the individual elements in a song strophe

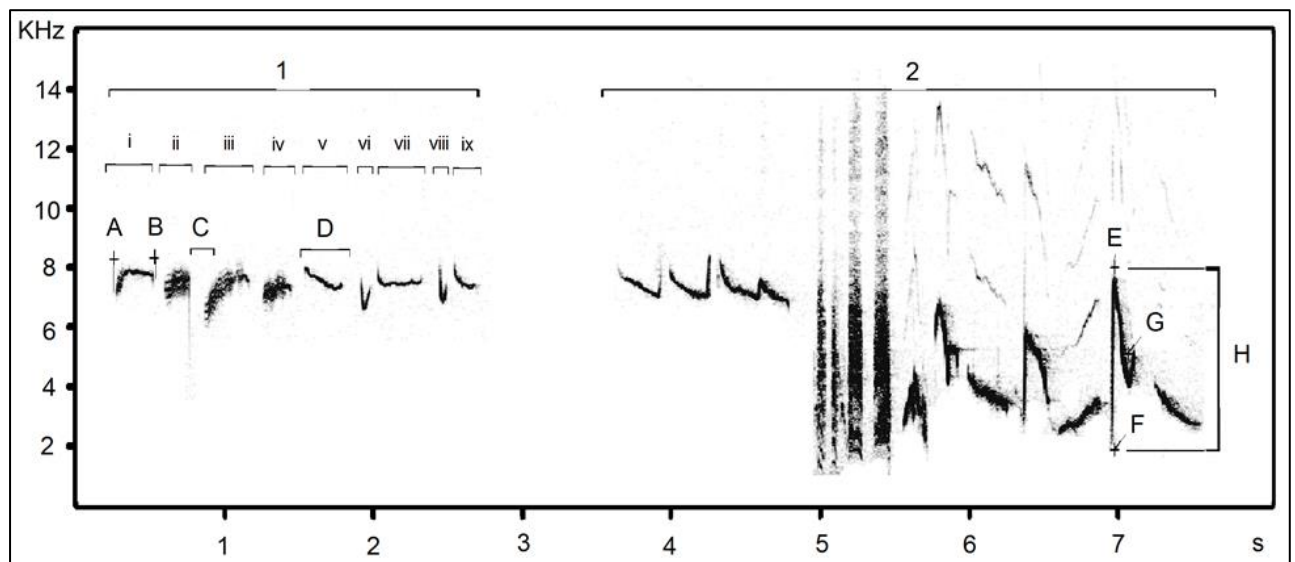


Figure 3.2. Examples of annotated spectrograms of two song strophes. 1 refers to strophe 1 (Calsab 1046_1_40to43s), 2 – strophe 2 (Calsab 1046_2_46to50s), i-ix – individual element number (e.g., i – the first element), A – element start time, B – element end time, C – inter-element interval, d – element duration, e – element maximum frequency, F – element minimum frequency, G – element peak frequency and H – element bandwidth frequency. In Calsab 1046_1_40to43s, Calsab abbreviates *Calendulauda sabota*, 1046 – field identification code of a song recording, 1 – the first strophe in a specific song recording, 40to43s – refers to the time range or block (in s - seconds) occupied by a specific strophe along the song.

Out of the nine vegetation types represented in the song samples (Table 3.2), some vegetation types were underrepresented, i.e., a representative number of good-quality song strophes could not be subsampled. In contrast, the other vegetation types were appreciably represented. The underrepresented vegetation types were Mopane Gabbro Shrubland – MGS and Bushmanland Arid Grassland – BAG and were therefore removed from further analyses as their sample sizes were small. This resulted in a reduction of the total number of song strophes from 893 to 878.

Based on the circumstance mentioned above, statistical analyses were performed in two parts including: 1) an analyses of the dataset consisting of seven vegetation types (henceforth comprehensive dataset) and 2) an analyses of the dataset comprising of only the two vegetation types with the highest sampling (viz., Bushmanland Basin Shrubland – BBS and Musina Mopane Bushveld – MMB) (henceforth reduced dataset). Every territory is made up of a mosaic of open and denser patches, and it is also dynamic, e.g., it might be considerably thicker in summer when all the trees are in full bloom of leaves. Because of the variation within territories, we had to make a subjective judgment and label a territory according to the "mean" degree of openness or closedness. We reduced the observer effect by having only one person assign a territory to a vegetation type, thereby reducing inter-observer variability in such subjective assessments. All analyses were performed in R (version 4.2.3) (R Core Team 2023). The data were tested for normality or normal distribution prior to univariate multivariate statistical analyses, and when the data failed the normality test, they were log-transformed.

One-way Analyses of Variance (ANOVA)

The Analyses of Variance (ANOVA) determines whether three or more groups are statistically different from each other, i.e., it is applied to test the means of more than two groups (Langer *et al.* 2020). In this study, ANOVA was used to compare the means of song parameters of song strophes from the comprehensive dataset to determine if there were significant differences in line with the predictions in Table 3.4. For post-hoc analyses, a review of 10 papers by Ruxton and Beauchamp (2008) showed that multiple comparisons of variables were generally not planned and that

some papers did post-hoc analyses without mentioning the method used. Others mentioned it but without justification for using the chosen technique. They showed that there is not much in the literature for non-statisticians in terms of the criterion to be used when selecting a method for post-hoc analyses in terms of advantages and limitations in multiple comparisons of variables. This is the gap that Ruxton and Beauchamp (2008) set out to fill, and, among others, for unplanned nonparametric tests, they recommended the Games-Howell test as one of the preferred methods. This approach was common even in recent publications (Midway *et al.* 2020). In this study, whenever statistically significant differences between group means were found, the nonparametric Games-Howell post-hoc test was performed because of its non-assumptive nature and non-reliance on equal variances and sample sizes.

Although AAH generalises its predictions mainly between vocal signals in open and closed habitats, the predictions of this study were justified by the fact that vegetation types that were categorised as having “moderately closed” and “moderately open” structures had more trees than those that were categorised as having an open structure (of which were open fields consisting of shrubs, and completely treeless). These study predictions are outlined in Table 3.4, which includes the general AAH predictions of vocal parameters of songs from open vs. closed habitats, and predictions of vocal parameters of songs from “moderately closed” and “moderately open” relative to those of songs from “open” vegetation structure. It does not include predictions of vocal parameters of the Sabota Lark songs from “moderately closed” relative to “moderately open” because differences between the two vegetation structures were based only on subjective visual assessments. Nevertheless, efforts were made in the analyses to investigate the differences or similarities in vocal parameters of songs from “moderately closed” in comparison with songs from “moderately open”, as this had the potential to assist in concluding whether “moderately closed” and “moderately open” habitat types were different or not.

Table 3.4. General predictions of the Acoustic Adaptation Hypothesis (AAH) on vocal signals of birds living in open habitats compared with those living in closed habitats, and predicted outcomes of vocal signals in the songs of Sabota Larks.

Song parameters	General AAH predictions		Predicted Sabota Lark song parameters		
	Open	Closed	Open	Moderately open	Moderately closed
Minimum frequency	Higher	Lower	Higher	Lower	Lower
Maximum frequency	Higher	Lower	Higher	Lower	Lower
Bandwidth frequency	Broader	Narrower	Broader	Narrower	Narrower
Peak frequency	Higher	Lower	Higher	Lower	Lower
Inter-element interval	Shorter	Longer	Shorter	Longer	Longer
Element duration	Shorter	Longer	Shorter	Longer	Longer
Number of elements per strophe	More	Fewer	More	Fewer	Fewer

T-test

The t-test is a method that determines whether two populations are statistically different from each other, i.e., it compares or analyses two data groups or population samples. The t-test is a ratio that quantifies how significant the difference is between the means of two groups while taking their variance or distribution into account (Wadhwa and Marappa-Ganeshan 2023). The t-test was used to test for any statistically significant differences in songs associated with the means of the two vegetation types with the largest sample sizes, i.e., Bushmanland Basin Shrubland-BBS and Musina Mopane Bushveld-MMB.

Principal Component Analyses (PCA)

Principal Component Analyses (PCA) was performed on the dataset with seven vegetation types. It is a popular technique for analysing large datasets containing many dimensions or features (song strophe variables) per observation (vegetation types). It can increase the interpretability of data while preserving the maximum amount of information and enabling the visualisation of multidimensional data, which explains most of the variance (Jolliffe and Cadima 2016).

Linear Discriminant Analyses (LDA)

Linear Discriminant Analyses (LDA) or Discriminant Function Analyses (DFA) is a method closely related to PCA. They both look for linear combinations of variables that best explain the data. This method attempts to model the difference between the classes of data. Thus, it finds linear combinations of dimensions or features that characterise or separate two or more classes of objects or events. Linear Discriminant analyses was used to investigate whether songs recorded from the sites defined by different vegetation types could be classified based on the parameters analysed or not. This is also in relation to the vegetation structure (open vs. closed).

LDA is sensitive to the ratio of sample size versus the number of predictor variables, with some studies suggesting a ratio of 20 observations per predictor variable (minimum size recommended being five observations per predictor variable) (Meloun and Militky 2011). According to Meloun and Militky (2011), "when using discriminant analyses, a question of interest is whether some subset of the original variables could provide a classification rule equal to the rule based on using all available variables". Therefore, to test how the "classification rule" of using some subset of the original variables compares with that of using all the variables, linear discriminant analyses was performed using or informed by 1) principal component data and 2) using a comprehensive dataset. This was also done to address the issue of a skewed strophe sample size in the comprehensive dataset, in particular, small song strophe sample sizes in some collection sites, as these are standard methods to solve issues about small sample sizes (Tharwat *et al.* 2017).

3.3. Results

3.3.1 Spatial mapping – vegetation and songs

Figure 2.1 shows that the birds recorded in the four sites in the Limpopo Province were inhabiting nine vegetation types within two bioregions (Mopane-mp and Central Bushveld-cb) of the Savanna biome. Limpokwena Nature Reserve (LNR) and Kruger National Park (KNP) fall within the Mopane (mp) bioregion while Maribana, De Loskop (DLK), Blouberg Nature Reserve (BNR), and Polokwane Nature Reserve (PNR) fall within the Central Bushveld (cb) bioregion. In LNR, the vegetation type is Musina Mopane Bushveld (MMB). At the same time, in KNP, the birds were recorded in three vegetation types: Mopane Basalt Shrubland (MBS), Mopane Gabbro Shrubland (MGS), and Tsende Mopaneveld (TM). Regarding the sites in the Central Bushveld-cb bioregion, the PNR vegetation type is Polokwane Plateau Bushveld (PPB), for BNR, is Roodeberg Bushveld (RB), while in DLK and Maribana, the birds were recorded in Makhado Sweet Bushveld (MSB). In the Northern Cape Province, the recorded birds were inhabiting two types of vegetation: Bushmanland Arid Grassland (BAG) and Bushmanland Basin Shrubland (BBS) that are classified in the Bushmanland-b bioregion of the Nama-Karoo biome (Tables 3.1, 3.2).

3.3.2. Statistical outcomes – comprehensive dataset

3.3.2.1. *Univariate analyses-based outcomes*

As already mentioned in Table 3.4 (under Materials and Methods), predictions were made only for vocal parameters of songs from the “moderately closed” and “moderately open” relative to those of songs from the “Open”. No predictions were made about how vocal parameters of “moderately closed” songs would differ from those of “moderately open” habitats. Therefore, the ANOVA results (Table 3.5) were tailored to complement the structure of the predictions with the focus being on 1) how mean song parameters of songs from moderately open compared with those of songs from open (Table 3.6), 2) how means of song parameters of songs from moderately closed compare with those of songs from the open (Table 3.7), and 3) how means of

song parameters of songs from moderately open compared with those of songs from moderately closed (Table 3.8). Although the F-tests (Table 3.5) showed that there were significant differences ($p < 0.05$) in the means of song strophe parameters among the vegetation types, indicating that variances between vegetation types were not equal, this did not mean all the differences in Tables 3.6 and 3.7 were statistically significant.

When comparing the songs of Sabota Larks from the BBS (open) habitats to the two other habitat categories, songs from the open habitats were, on mean, consistently characterised by fewer elements per strophe (6.56), lower minimum frequency (2602.48 Hz), lower maximum frequency (4437.09 Hz), broad bandwidth frequency (1830.28 Hz), lower peak frequency (3472.61 Hz), and shorter inter-element interval (0.17 s) (see Tables 3.6 and 3.7). The lower minimum frequency, lower maximum frequency, and lower peak frequency were contrary to the study predictions, while broad bandwidth frequency and shorter inter-element interval were in line with the predictions. BBS songs had the highest mean bandwidth frequency (viz., 1830.28 Hz) compared with songs from the other vegetation types. In all the other six vegetation types, the bandwidth frequency was within the range of 1300–1600 Hz (cf. Tables 3.6 and 3.7, Fig. 3.3F), minimum frequency > 3300 Hz (as opposed to 2602.48 Hz in BBS songs, Fig. 3.3D), maximum frequency > 4800 Hz (4437.09 Hz in BBS songs, Fig. 3.3E), and peak frequency > 4100 Hz (3472.61 Hz in BBS songs, Fig. 3.3G). The duration of elements (i.e., element duration) in songs from BBS was, on average, longer than that of songs from moderately close vegetation types (Table 3.6, Fig. 3.3A), but when compared with that of songs from moderately open (Table 3.7), the results were inconclusive. This was also true of the number of elements; fewer in songs from BBS but more in songs from moderately close vegetation types (Table 3.6, Fig. 3.3B), but inconclusive compared with songs from moderately open (Table 3.7).

Table 3.5. ANOVA test results, means and standard deviations of song strophes parameters in each vegetation type. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld.

Mean (Standard deviation)							
Vegetation type	Element duration (s)	Elements per strophe	Inter-element interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
BBS	0.15 (0.06)	6.56 (5.60)	0.17 (0.10)	2602.48 (733.07)	4437.09 (1097.19)	1830.28 (1293.74)	3472.61 (726.53)
MSB	0.11 (0.04)	10.63 (5.36)	0.18 (0.07)	4335.31 (1159.91)	5751.28 (856.36)	1411.16 (720.12)	5002.71 (964.53)
MBS	0.11 (0.04)	9.35 (3.86)	0.21 (0.05)	3903.06 (691.99)	5374.89 (687.23)	1467.44 (666.69)	4602.17 (632.73)
MMB	0.12 (0.06)	10.57 (4.92)	0.20 (0.08)	4286.80 (1363.39)	5824.51 (1079.24)	1532.97 (973.85)	5059.09 (1125.61)
PPB	0.16 (0.08)	5.37 (5.34)	0.21 (0.13)	4570.58 (1421.10)	5909.83 (1268.24)	1334.31 (879.97)	5169.08 (1303.72)
RB	0.14 (0.06)	9.43 (5.01)	0.21 (0.09)	4431.68 (1127.13)	5933.72 (742.62)	1497.52 (771.20)	5116.95 (874.05)
TM	0.12 (0.04)	8.00 (3.42)	0.19 (0.05)	3357.93 (612.30)	4894.17 (653.32)	1531.77 (601.19)	4183.33 (615.45)
ANOVA F-statistic	16.38***	19.67***	6.05***	106.28***	53.27***	3.93***	101***
*** $p < 0.001$; ** $p < 0.05$							

The means of the frequency parameters of songs from the open vegetation type (Bushmanland Basin Shrubland-BBS) were either lower or higher (narrower or broader, respectively, for bandwidth frequency) relative to those of songs from the moderately open vegetation types (Musina Mopane Bushveld-MMB, Makhado Sweet Bushveld-MSB, Mopane Basalt Shrubland-MBS). The means of the time-based

parameters of songs from the open vegetation types were longer or shorter than those of the moderately open vegetation types (Table 3.6).

Table 3.6. Comparison of means of song parameters from open vs. moderately open habitats. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld.

Song parameters	Predicted Sabota Lark song parameters		Outcomes (mean)			
	Open	Moderately open	Open	Moderately open		
			BBS	MMB	MSB	MBS
Minimum frequency (Hz)	Higher	Lower	Lower (2602.48)	Higher (4286.80)	Higher (4335.310)	Higher (3903.06)
Maximum frequency (Hz)	Higher	Lower	Lower (4437.09)	Higher (5824.51)	Higher (5751.28)	Higher (5374.89)
Bandwidth frequency (Hz)	Broader	Narrower	Broader (1830.28)	Narrower (1532.97)	Narrower (1411.16)	Narrower (1467.44)
Peak frequency (Hz)	Higher	Lower	Lower (3472.61)	Higher (5059.09)	Higher (5002.71)	Higher (4602.17)
Inter-element interval (s)	Shorter	Longer	Shorter (0.17)	Longer (0.20)	Longer (0.18)	Longer (0.21)
Element duration (s)	Shorter	Longer	Longer (0.15)	Shorter (0.12)	Shorter (0.11)	Shorter (0.11)
Number of elements per strophe	More	Fewer	Fewer (6.56)	More (9.35)	More (10.63)	More (10.57)

The means of the frequency parameters of songs from the open vegetation type (Bushmanland Basin Shrubland-BBS) were either lower or higher (narrower or broader, respectively, for bandwidth frequency) relative to those of songs from the moderately closed vegetation types (Polokwane Plateau Bushveld-PPB, Roodeberg Bushveld-RB, Tsende Mopaneveld-TM.) The means of the time-based parameters of songs from the open vegetation types were longer or shorter relative to those of songs from the moderately closed vegetation types (Table 3.7).

Table 3.7. Outcomes of comparisons of song parameters means between songs from BSS and songs from moderately closed vegetation types (viz. PPB, RB, TM). BBS abbreviates Bushmanland Basin Shrubland, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld.

Song parameters	Predicted Sabota Lark song parameters		Outcomes			
	Open	Moderately closed	Open	Moderately closed		
			BBS	PPB	RB	TM
Minimum frequency (Hz)	Higher	Lower	Lower (2602.48)	Higher (4570.58)	Higher (4431.68)	Higher (3357.93)
Maximum frequency (Hz)	Higher	Lower	Lower (4437.09)	Higher (5909.83)	Higher (5933.72)	Higher (4894.17)
Bandwidth frequency (Hz)	Broader	Narrower	Broader (1830.28)	Narrower (1334.31)	Narrower (1497.52)	Narrower (1531.77)
Peak frequency (Hz)	Higher	Lower	Lower (3472.61)	Higher (5169.08)	Higher (5116.95)	Higher (4183.33)
Inter-element interval (s)	Shorter	Longer	Shorter (0.17)	Longer (0.21)	Longer (0.21)	Longer (0.19)
Element duration (s)	Shorter	Longer	0.15	0.16	0.16	0.12
Elements per strophe	More	Fewer	6.56	5.37	9.43	8.00

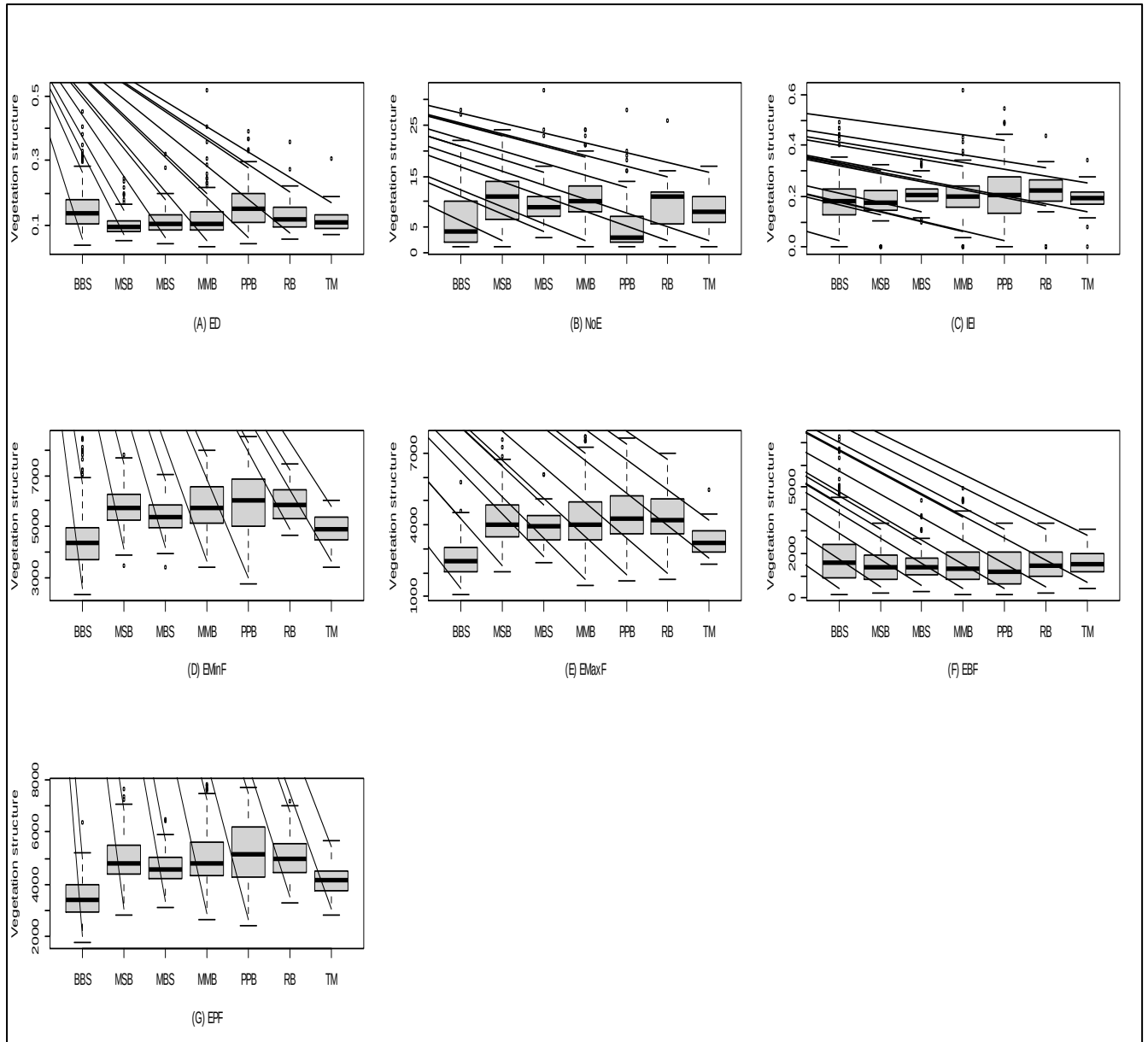


Figure 3.3. Box-and-whisker plots summarising the song parameters (A–G) of the Sabota Lark analysed in this study according to vegetation type. A – song strophe mean (ssa) element duration (ED), B – ssa number of elements (NoE), C – ssa inter-element-interval (IEI), D – ssa element minimum frequency (EMinF), E – ssa element maximum frequency (EMaxF), F – ssa element bandwidth frequency (EBF), and G – ssa element peak frequency (EPF). Vegetation types are: Bushmanland Basin Shrubland-BBS, Makhado Sweet Bushveld-MSB, Mopane Basalt Shrubland-MBS, Musina Mopane Bushveld-MMB, Polokwane Plateau Bushveld-PPB, Roodeberg Bushveld-RB, and Tsende Mopaneveld-TM.

Since statistically significant ANOVA results do not identify the pairs of means that are significantly different, post-hoc tests were performed to aid with this. A nonparametric Games-Howell test was performed to determine or identify the pairs of vegetation types that differ in relation to the parameters of the songs recorded from the studied vegetation types (Tables 3.8a-e).

Again, the results were tailored to complement the structure of the predictions with the focus being on 1) how the means of song parameters of songs from moderately open habitat types compare with those of songs from open habitat types (Table 3.8a), 2) how means of song parameters of songs from moderately closed habitats compared with those of songs from the open habitats (Table 3.8b), 3) how means of song parameters of songs from moderately open habitats compared with those of songs from moderately closed habitats (Table 3.8c), 4) how means of song parameters of songs from moderately open habitat types compared among the moderately open habitat types (Table 3.8d), and 5) how means of song parameters of songs from moderately closed habitat types compared among the moderately closed habitat types (Table 3.8e).

The significant differences in means of inter-element interval of songs in the pairs MMB:BBS and MBS:BBS, supported the prediction of shorter inter-element interval in songs from BBS as opposed to longer inter-element interval in songs from moderately open vegetation types. For bandwidth frequency, significant difference was found in means of bandwidth frequencies of songs only in the pair PPB:BBS. This supported the prediction of broad bandwidth frequency in BBS as opposed to narrow bandwidth frequency in PPB. Element duration was significantly different only in the pair TM:BBS, contrary to the predictions. Minimum, maximum, and peak frequencies were highly significantly different in all three vegetation type pairs, contrary to the predictions. Differences in elements per strophe were statistically significant only in the pairs TM:BBS and RB:BBS, with songs from BBS having fewer number of elements per strophe.

Table 3.8(a-e). Post-hoc test results using nonparametric Games-Howell test to determine the vegetation types that differ significantly in song parameters of songs. (a) Open (i.e., BBS) vs. Moderately open (MBS, MSB, and MMB). (b) Open (BBS) vs. Moderately closed (RB, TM, PPB). (c) Moderately open (MBS, MSB, and MMB) vs. Moderately closed (RB, TM, PPB). (d) Within-group comparisons – Moderately open (i.e., MBS vs. MSB vs. MMB). (e) Within group comparisons – Moderately closed (RB vs. TM vs. PPB) (Lee and Lee 2018). BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld.

(a)	Difference between group means (T-statistic)							
	Pairs of vegetation types	Element duration (s)	No of elements per strophe	Inter-element Interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
1	MMB:BBS	0.42 (4.40)***	-0.87 (10.29)***	-0.36 (3.91)**	-1.37 (17.24)***	-1.20 (14.30)***	0.22 (2.29)	-1.42 (18.54)***
2	MBS:BBS	0.61 (7.32)***	-0.81 (10.82)***	-0.45 (5.70)***	-1.20 (18.95)***	-0.90 (11.84)***	0.12 (1.36)	-1.12 (17.17)***
3	MSB:BBS	0.72 (7.53)***	-0.82 (7.10)***	-0.11 (0.99)	-1.445 (16.00)***	-1.17 (12.64)***	0.27 (2.29)	-1.40 (15.23)***
Key: *** $p < 0.001$; ** $p < 0.05$								

(b)	Difference between group means (T-statistic)							
	Pairs of vegetation types	Element duration (s)	No of elements per strophe	Inter-element Interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
1	TM:BBS	0.50 (4.35)***	-0.58 (5.28)***	-0.27 (2.51)	-0.78 (9.30)***	-0.50 (4.87)***	0.05 (0.43)	-0.75 (7.91)***
2	RB:BBS	0.22 (1.39)	-0.64 (4.11)**	-0.48 (2.93)	-1.51 (12.76)***	-1.32 (13.35)***	0.20 (1.25)	-1.50 (14.12)***
3	PPB:BBS	-0.23 (1.59)	0.23 (1.79)	-0.38 (2.23)	-1.55 (14.58)***	-1.23 (9.97)***	0.54 (3.61)**	-1.47 (12.47)***
Key: *** $p < 0.001$; ** $p < 0.05$								

(c)	Difference between group means (T-statistic)							
	Pairs of vegetation types	Element duration (s)	No of elements per strophe	Inter-element Interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
1	MMB:PPB	0.65 (4.32)***	-1.10 (8.76)***	0.03 (0.16)	0.18 (1.56)	0.03 (0.23)	-0.32 (2.04)	0.05 (0.37)
2	MMB:RB	0.21 (1.30)	-0.22 (1.47)	0.13 (0.77)	0.14 (1.11)	0.12 (1.22)	0.03 (0.16)	0.08 (0.71)
3	MMB:TM	-0.08 (0.63)	-0.29 (2.76)	-0.09 (0.85)	-0.59 (6.17)***	-0.70 (6.81)***	0.17 (1.37)	-0.67 (6.58)***
4	MSB:PPB	0.95 (6.29)***	-1.05 (7.10)***	0.27 (1.53)	0.10 (0.84)	0.06 (0.43)	-0.27 (1.56)	0.07 (0.50)
5	MSB:RB	-0.50 (3.13)**	0.18 (1.02)	-0.37 (2.16)	-0.06 (0.48)	-0.15 (1.39)	-0.08 (0.44)	-0.10 (0.82)
6	MSB:TM	-0.22 (1.76)	0.24 (1.83)	-0.16 (1.34)	0.67 (6.35)***	0.67 (6.11)***	-0.22 (1.55)	0.65 (5.71)***
7	MBS:PPB	0.84 (5.85)***	-1.05 (8.75)***	-0.07 (0.44)	0.35 (3.33)**	0.33 (2.78)	-0.43 (2.86)	0.35 (3.00)
8	MBS:RB	0.40 (2.57)	-0.17 (1.15)	0.03 (0.17)	0.31 (2.64)	0.421 (4.545)***	-0.081 (0.521)	0.385 (3.643)**
9	MBS:TM	0.12 (0.96)	-0.23 (2.41)	-0.19 (1.99)	-0.42 (5.07)***	-0.40 (4.14)**	0.07 (0.56)	-0.37 (3.92)**
Key: *** $p < 0.001$; ** $p < 0.05$								

(d)	Difference between group means (T-statistic)							
	Pairs of vegetation types	Element duration (s)	No of elements per strophe	Inter-element Interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
1	MMB:MBS	-0.19 (1.98)	-0.05 (0.82)	0.10 (1.31)	-0.17 (2.18)	-0.30 (3.93)**	0.12 (1.13)	-0.30 (4.02)***
2	MMB:MSB	-0.29 (2.80)	-0.05 (0.45)	-0.25 (2.36)	0.08 (0.75)	-0.03 (0.29)	-0.05 (0.40)	-0.02 (0.23)
3	MBS:MSB	-0.107 (1.146)	0.01 (0.05)	-0.35 (3.62)**	0.25 (2.76)	0.27 (3.17)**	-0.16 (1.34)	0.28 (3.11)**
Key: *** $p < 0.001$; ** $p < 0.05$								

(e)	Difference between group means (T-statistic)							
	Pairs of vegetation types	Element duration (s)	No of elements per strophe	Inter-element Interval (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Bandwidth frequency (Hz)	Peak frequency (Hz)
1	TM:RB	0.29 (1.65)	0.06 (0.37)	0.21 (1.24)	0.73 (5.63)***	0.82 (7.11)***	-0.15 (0.83)	0.75 (5.97)***

2	TM:PPB	0.73 (4.46)***	-0.82 (5.65)***	0.12 (0.64)	0.77 (6.48)***	0.73 (5.32)***	-0.49 (2.89)	0.72 (5.29)***
3	RB:PPB	0.44 (2.29)	-0.88 (4.81)***	-0.10 (0.45)	0.04 (0.28)	-0.09 (0.69)	-0.345 (1.727)	-0.03 (0.24)
Key: *** $p < 0.001$; ** $p < 0.05$								

3.3.2.2. Multivariate analyses-based outcomes – comprehensive dataset

A summary of the Principal Component Analyses (PCA) results is presented in Table 3.6. The principal components (PCs) were arranged in descending order of the standard deviations. Since the data have been standardised and centred, the standard deviations are equal to the eigenvalues. The proportion of variance represents the actual variance explained by each component. In this case, the first principal component, PC1, contributed 39.5% of the variation, PC2 contributed 29.5%, and PC3 contributed 14.3%. PC1, PC2, and PC3 contributed 83.3% of the explained variation. This means the first three (3) components accounted for 83.3% of the variation. The use of all seven PCs would explain 100% of the variation. However, the essence of PCA is to use as few components as possible while still accounting for high explanatory variation.

Table 3.9. Principal Component Analyses (PCA) of multiple song variables showing the proportion of variance represented in each principal component (PC).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.66	1.44	1.00	0.89	0.51	0.28	0.21
Proportion of variance	0.40	0.30	0.14	0.11	0.04	0.01	0.01
Cumulative Proportion	0.40	0.69	0.83	0.95	0.98	0.99	1.00

From the Scree plot (Fig. 3.4a), only three of the seven components had eigenvalues ≥ 1 . Discarding any component with eigenvalues less than 1 is preferable, as such components would account for less than a distinct explanatory variable. The Scree plot, therefore, suggested that only three components can be used. The cumulative variance plot (Fig. 3.4b) showed that the three components explained 83.3% of the variation.

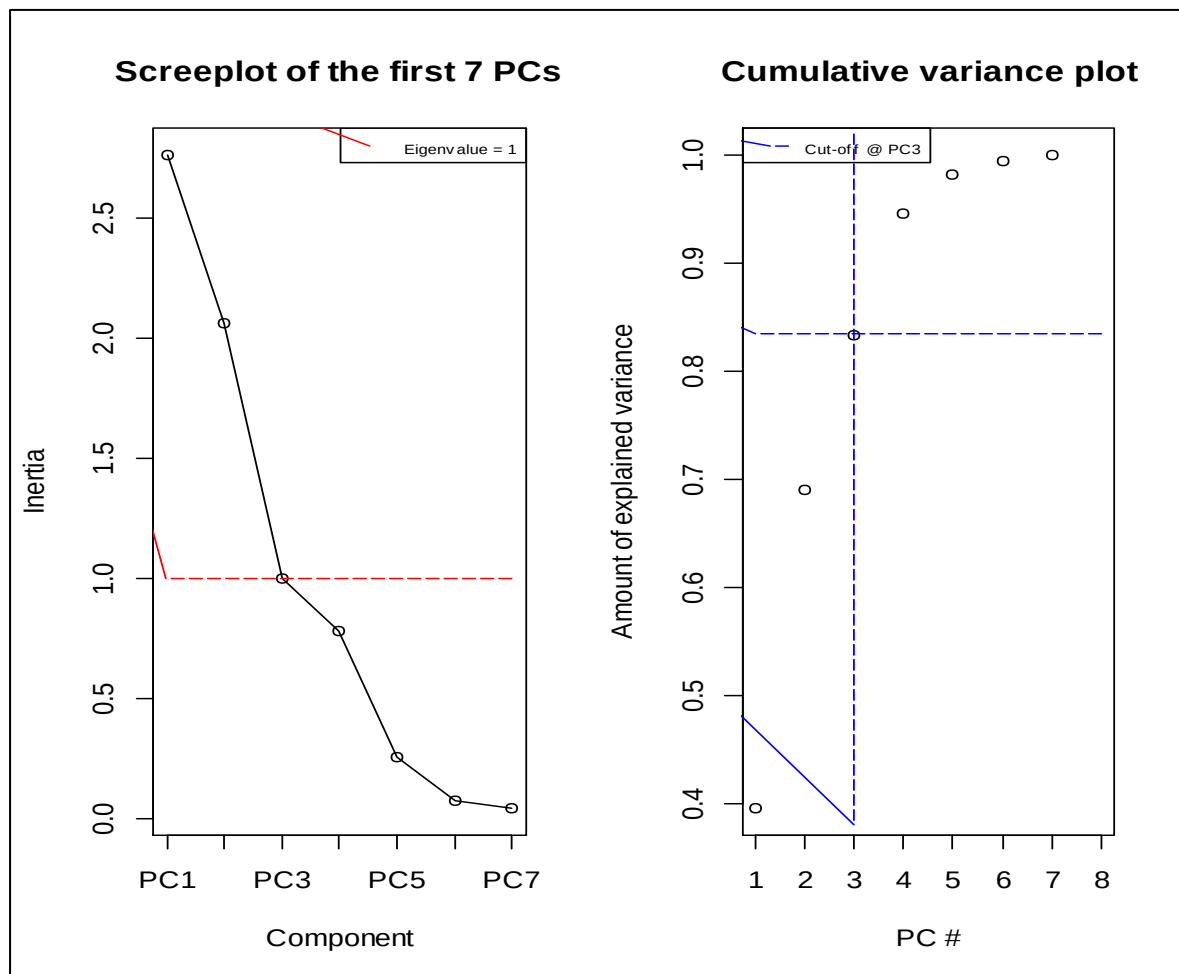


Figure 3.4(a). A Scree plot showing eigenvalues for each individual principal component. (b) Cumulative variance plot showing the total percentage of variance explained against the number of principal components.

The 2D PCA plot (Fig. 3.5) showed that the Sabota Lark songs could not be grouped accurately according to habitats using the first two components. These first two principal components accounted for 69% of the song variation between the vegetation types; PC1 explained 39.5% of the variation, and PC2 explained 29.5%. The points representing the songs from all the vegetation types were clustered together, concentrated at the centre of the coordinate axis, and there was no clear separation, indicating a high level of similarity in songs from the different vegetation

types. The coefficients of linear discriminants of the original variables from which the principal components (PCs) were generated are shown in Table 3.7.

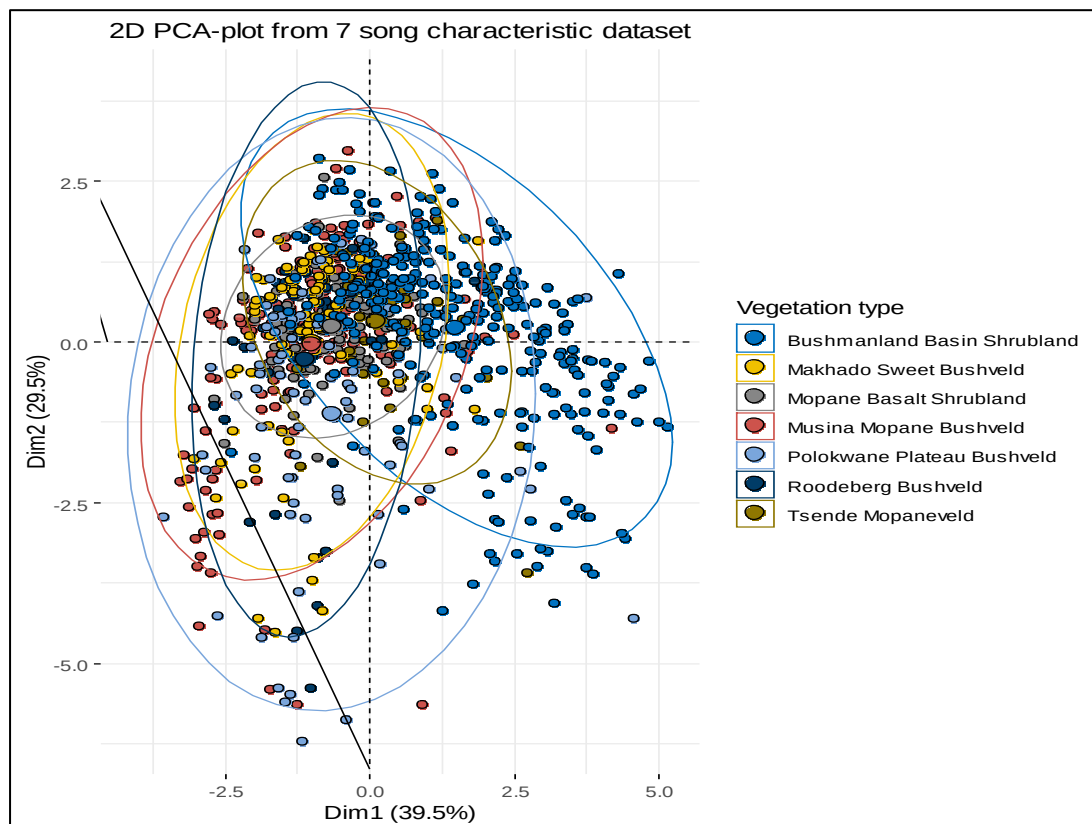


Figure 3.5. Basic two-dimensional Principal Component Analyses plot (2D PCA-plot) showing clustering of songs from the seven vegetation types across seven song feature datasets.

Table 3.10. Coefficients of linear discriminants of the original variables from which the principal components (PCs) are constructed. There is only one discriminant function as the maximum number of discriminant functions equals the number of group categories (which is two, i.e., BBS vs. MMB) minus one.

	LD1	LD2	LD3
PC1	-0.80	0.11	0.04
PC2	-0.18	-0.68	-0.17
PC3	-0.03	0.27	-0.96

Linear Discriminant Analyses (LDA) on Principal Components (PCs)

The evaluation of the LDA-PC model (Tables 3.8-3.10) has returned low predictive accuracy in classifying song strophes according to habitat type, meaning that the model did not allow accurate classification. This was especially true of the vegetation types with low sampling, as reflected in the sensitivity of the evaluation methods, which was low for these vegetation types. Only the song strophes from BBS and MMB were correctly classified with a high percentage as belonging to their respective vegetation types, e.g., in the resubstitution error (Table 8), 85% of the song strophes in BBS were correctly classified as belonging to BBS while 73% in MMB were correctly classified as belonging to MMB.

Table 3.11. Outcomes of the evaluation of the accuracy of the Linear Discriminant Analyses (LDA) on Principal Components (PCs) (LDA-PC) model by Resubstitution error. Generally, the larger the training set, the better the classifier. The larger the test data, the more accurate the predictive accuracy or error estimation is. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MMB	PPB	RB	TM
Accuracy	0.47						
Kappa	0.28						
McNemar's Test P-Value	NA						
Sensitivity	0.85	0.00	0.03	0.73	0.22	0.00	0.00
Pos Pred Value (Precision)	0.66	NaN	0.15	0.32	0.40	NaN	NaN

Table 3.12. Outcomes of the evaluation of the accuracy of the Linear Discriminant Analyses (LDA) on Principal Components (PCs) (LDA-PC) model by Jackknife. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane

Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MM	PPB	RB	TM
Accuracy	0.47						
Kappa	0.28						
McNemar's Test P-Value	NA						
Sensitivity	0.85	0.00	0.03	0.71	0.22	0.00	0.00
Pos Pred Value (Precision)	0.66	NaN	0.15	0.31	0.38	NaN	NaN

Table 3.13. Outcomes of the evaluation of the accuracy of the Linear Discriminant Analyses (LDA) on Principal Components (PCs) (LDA-PC) model by 5-fold cross-validation. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MMB	PPB	RB	TM
Accuracy	0.46						
Kappa	0.27						
McNemar's Test P-Value	NA						
Sensitivity	0.95	0.00	0.00	0.78	0.00	0.00	0.00
Pos Pred Value (Precision)	0.69	NaN	NaN	0.32	NaN	NaN	NaN

Linear Discriminant Analyses (LDA) on a comprehensive dataset

The evaluation of the Linear Discriminant Analyses (LDA) based on the comprehensive dataset model (Tables 3.12-3.14) yielded results that were similar to the evaluation results of the LDA-PC model when using the comprehensive dataset in the analyses. The evaluation methods indicated low predictive accuracy in classifying song strophes to the vegetation type they were collected in, meaning that the training data did not allow accurate classification. This was especially true of the vegetation types with low sampling, as reflected in the sensitivity of the evaluation methods, which was low for these vegetation types. Only songs from BBS and MMB were correctly

classified with a high percentage as belonging to their respective vegetation types, e.g., in the Resubstitution error (Table 17), 84% of the songs in BBS are correctly classified as belonging to BBS while 71% in MMB were correctly classified as belonging to MMB. The standardised coefficient for minimum frequency in the discriminant function (DF) 1 is greater in magnitude than the coefficients for the other six variables (Table 3.14). Therefore, the minimum frequency had the most discriminating ability in DF1. However, generally, it was observed that several variables have high values for the other five discriminant functions (DF2-5). It remains unclear whether the variables that specifically stand out as having the classification power in each function.

Table 3.14. Coefficients of song strophe parameters on each of the six discriminant functions. There are only six discriminant functions; the maximum number equals the number of group categories (seven vegetation types) minus one.

Data	Vegetation type	Discriminant functions and Standardised coefficients					
		First	Second	Third	Fourth	Fifth	Sixth
All seven vegetation types	Element duration	-0.23	-0.04	0.74	-0.90	0.03	-0.62
	No of elements	0.14	-1.25	0.84	-0.44	0.17	-0.09
	Inter-element interval	-0.04	0.52	-0.30	-0.54	0.15	0.78
	Minimum frequency	1.15	0.42	-1.36	-0.30	1.43	-1.25
	Maximum frequency	-0.10	0.29	1.98	1.01	2.13	0.87
	Bandwidth frequency	0.29	0.16	-1.33	-0.92	-0.07	-1.53
	Peak frequency	0.40	-0.18	-0.64	-0.64	-3.37	-0.09

Table 3.15. Outcomes of evaluating the Linear Discriminant Analyses (LDA) accuracy on comprehensive data model by Resubstitution Error. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MMB	PPB	RB	TM
Accuracy	0.52						

Kappa	0.36						
McNemar's Test P-Value	NA						
Sensitivity	0.84	0.00	0.23	0.71	0.53	0.00	0.00
Pos Pred Value (Precision)	0.71	0.00	0.43	0.35	0.54	NaN	NaN

Table 3.16. Outcomes of the evaluation of accuracy of the Linear Discriminant Analyses (LDA) on comprehensive data model by Jack knife. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MMB	PPB	RB	TM
Accuracy	0.51						
Kappa	0.35						
McNemar's Test P-Value	NA						
Sensitivity	0.83	0.00	0.20	0.69	0.52	0.00	0.00
Pos Pred Value (Precision)	0.70	0.00	0.39	0.34	0.52	NaN	NaN

Table 3.17. Outcomes of the evaluation of accuracy of the Linear Discriminant Analyses (LDA) on comprehensive data model by Cross validation. BBS abbreviates Bushmanland Basin Shrubland, MSB – Makhado Sweet Bushveld, MBS – Mopane Basalt Shrubland, MMB – Musina Mopane Bushveld, PPB – Polokwane Plateau Bushveld, RB – Roodeberg Bushveld, TM – Tsende Mopaneveld, NaN – not a number, NA – not available.

	BBS	MSB	MBS	MMB	PPB	RB	TM
Accuracy	0.55						
Kappa	0.39						

McNemar's Test P-Value	NA						
Sensitivity	0.90	0.00	0.31	0.69	0.41	0.00	0.00
Pos Pred Value (Precision)	0.70	NaN	0.42	0.40	0.50	NaN	NaN

3.3.3. Statistical outcomes – reduced dataset with two vegetation types with the highest sampling size (BBS vs. MMB)

3.3.3.1. Univariate Analyses-based outcomes

The t-test (Table 3.15) on the reduced dataset indicated statistically significant differences in the means of all song strophe parameters between BBS songs and MMB songs, with MMB songs having the highest means in all the parameters except in bandwidth frequency (Fig. 3.6F) and element duration (Fig. 3.6A). Broad bandwidth frequency in songs from BBS supported the prediction of broad bandwidth frequency in open habitat songs. Shorter element duration in BBS songs also supported the prediction of short elements in open habitats. Low minimum, maximum, and peak frequencies in BBS (open habitat) songs contradicted the study predictions.

Table 3.18. Outcomes of the T-test, showing song parameters that are significantly different between songs of Sabota Larks from Musina Mopane Bushveld – MMB and Bushmanland Basin Shrubland – BBS.

	Vegetation types				
Song parameters	BBS	MMB	df	T	p-value
	Means				
Element duration	0.15	0.12	482.00	4.18	< 0.001.
No of elements	6.56	10.57	422.13	-8.24	< 0.001.
Inter-element interval	0.17	0.20	461.69	-3.64	< 0.001.
Element minimum frequency	2602.48	4286.80	246.97	-15.41	< 0.001.
Element maximum frequency	4437.09	5824.51	482.00	-13.57	< 0.001.
Element bandwidth frequency	1830.28	1532.97	460.48	2.87	< 0.001.
Element peak frequency	3472.61	5059.09	275.16	-17.03	< 0.001.

Key: *** $p < 0.001$; ** $p < 0.05$

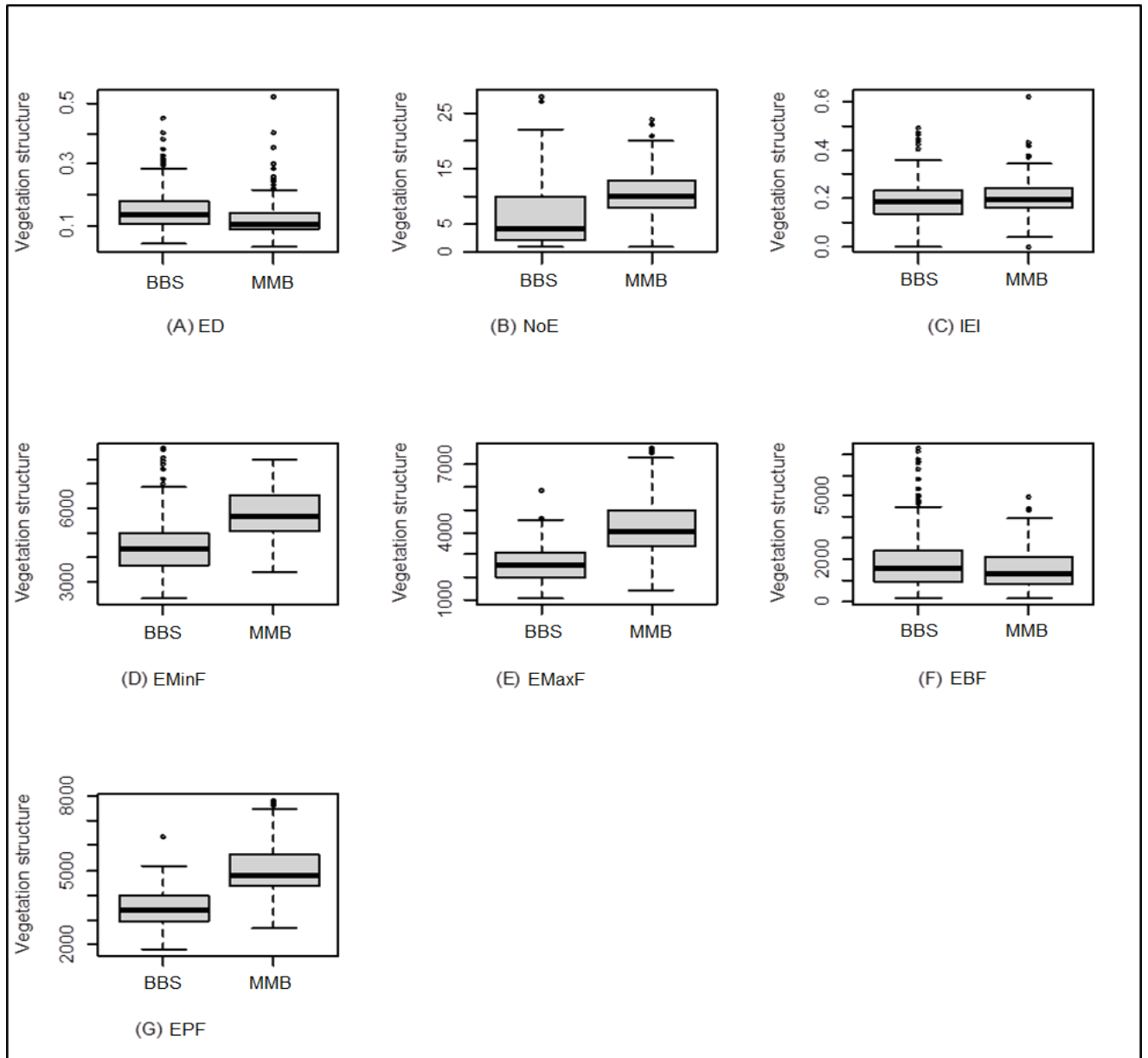


Figure 3.6. Box-and-whisker plots of the means of song parameters of the Sabota Lark in two structurally different habitat types, open (Bushmanland Basin Shrubland – BBS) and moderately open (Musina Mopane Bushveld – MMB). A – song strophe mean (ssa) element duration (ED), B – ssa number of elements (NoE), C – ssa inter-element-interval (IEI), D – ssa element minimum frequency (EMinF), E – ssa element

maximum frequency (EMaxF), F – ssa element bandwidth frequency (EBF), and G – ssa element peak frequency (EPF).

3.3.3.2. Multivariate-based outcomes – reduced dataset with two vegetation types with the highest sampling size (BBS vs. MMB)

In the summary of the PCA results (Table 3.16) the principal components were arranged in descending order of the standard deviations. Since the data has been standardised and centred, the standard deviations are equal to the eigenvalues. The proportion of variance represents the actual variance explained by each component. In this case, the first principal component, PC1, contributed 43.4% of the variation, PC2 contributed 25.9%, and PC3 contributed 15.3%. PC1, PC2, and PC3 contributed 84.6% of the explained variation. This means the first three components accounted for 84.6% of the variation. Usage of all seven PCs would explain 100% of the variation, but the essence of PCA is to use as few components as possible while still accounting for high explanatory variation.

Table 3.19. Principal component analyses (PCA) of multiple song variables of the Sabota Lark songs showing the proportion of variance represented in each principal component (PC).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.74	1.35	1.03	0.85	0.48	0.29	0.22
Proportion of variance	1.74	0.26	0.15	0.10	0.03	0.01	0.01
Cumulative Proportion	0.43	0.69	0.85	0.95	0.98	0.99	1.00

From the Scree plot (Fig. 3.7a), only three of the seven components had eigenvalues greater or equal to one (1). Since it is preferable to discard any component with eigenvalues < 1 , as such components would account for less than a distinct explanatory variable, the scree plot suggested that only three components can be used. The cumulative variance plot (Fig. 3.7(b)) showed that the three components explained 84.6% of the variation.

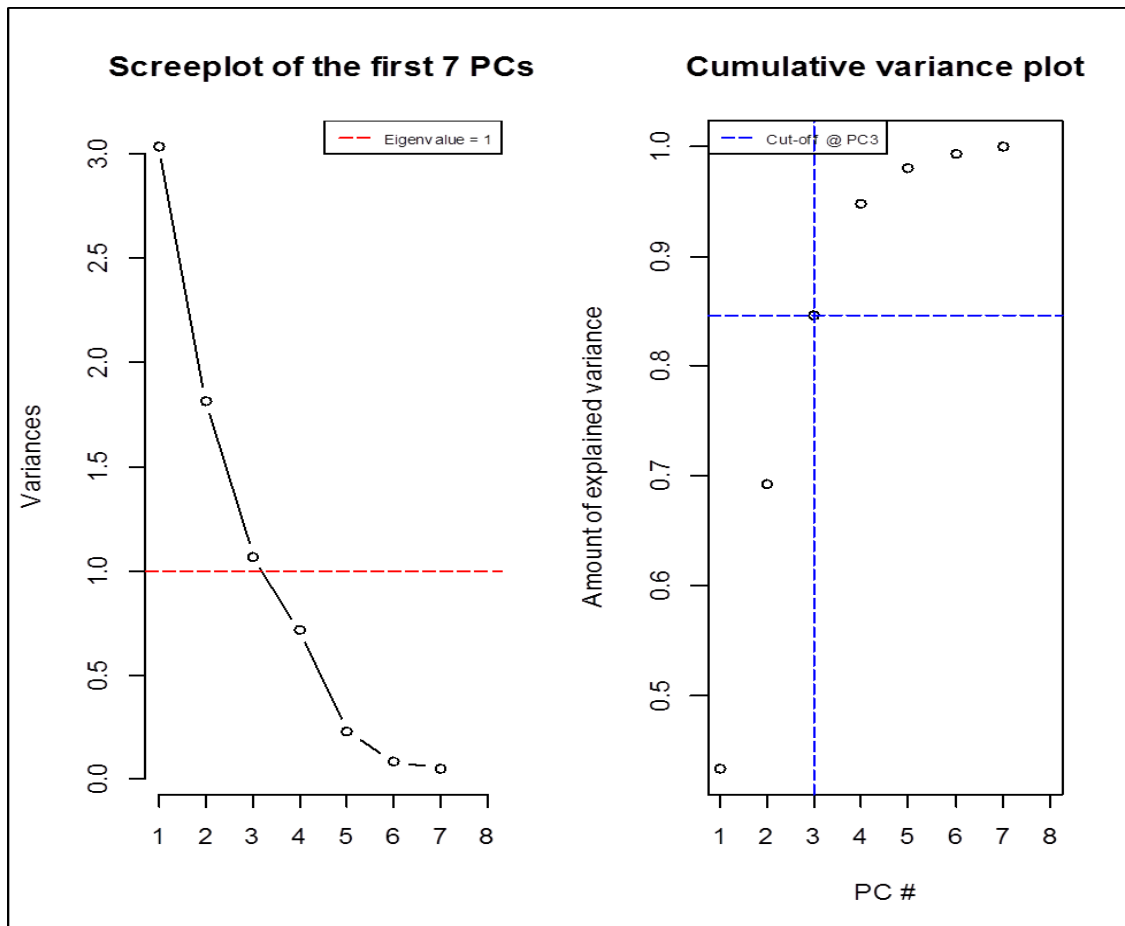


Figure 3.7. (a). A scree plot showing eigenvalues for each individual principal component. (b) Cumulative variance plot showing the total percentage of variance explained against the number of principal components.

The 2D PCA plot (Fig. 3.8) indicated some overlap between Nama-Karoo and Savanna-type habitats but with an appreciable level of separation. As shown in the PCA results, the first two principal components accounted for 69.3% of the vocalisation variation between the vegetation types; specifically, PC1 explained 43.4% of the variation, and PC2 explained 25.9% of the variation. The points representing the vocalisations from both vegetation types were more widely scattered and covered a larger coordinate axis area, just in different directions and quadrants. As much as this result indicated a high diversity of songs in both vegetation types, there was also a level of similarity in vocalisations, represented by the concentration of points from both vegetation types in the top left quadrant to the centre of the coordinate axis.

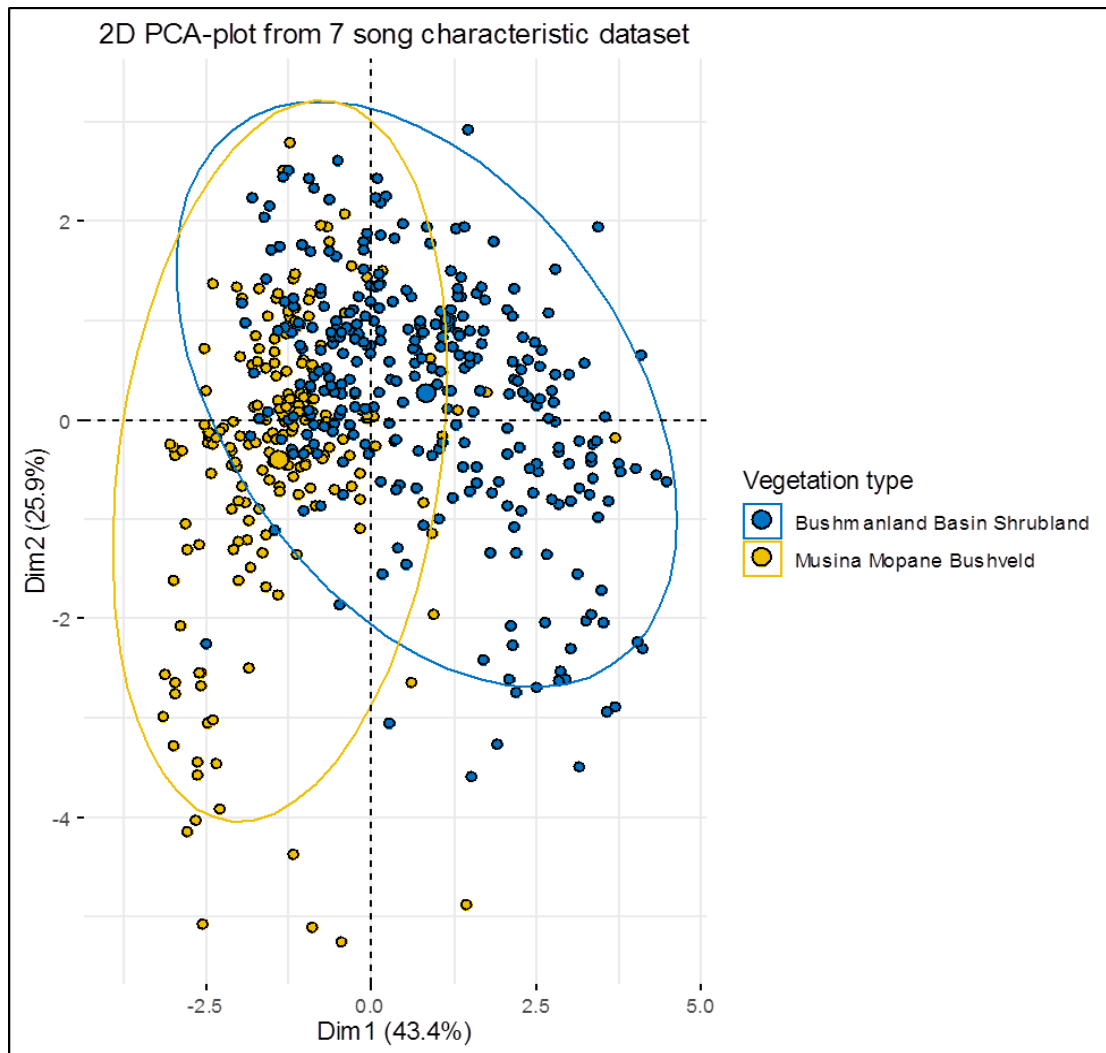


Figure 3.8. Basic two-dimensional principal component analyses plot (2D PCA-plot) showing clustering/differentiation of song strophes from Bushmanland Basin Shrubland (BBS) and Musina Mopane Bushveld (MMB) vegetation types across the seven-song strophe feature dataset.

Linear Discriminant Analyses (LDA) on Principal Components (PCs)

The evaluation results of the Linear Discriminant Analyses based on principal components (LDA-PC model) (Table 3.17) yielded higher predictive accuracy and sensitivity when using BBS and MMB than when using all seven (7) vegetation types, some of which are not well-represented in sampling. The evaluation methods (Table 3.18) indicated high predictive accuracy in classifying vocalisations to the vegetation type in which they were collected, meaning that the training data allowed for accurate

classification of songs. All three evaluation methods indicated that more than 75% of the vocalisations from BBS and MMB were correctly classified as belonging to their respective vegetation types.

Table 3.20. Coefficients of principal components constructed from the raw dataset. There is only one discriminant function as the maximum number of discriminant functions equals the number of group categories (which is two, i.e., BBS vs. MMB) minus one.

PCs	LD1
PC1	-0.80
PC2	-0.18
PC3	-0.03

Table 3.21. Outcomes of the evaluation of accuracy of the Linear Discriminant Analyses (LDA) on Principal components (PCs) model by Resubstitution error, Jackknife, and Cross validation. The PCs were generated from the dataset comprised of the two-vegetation types.

	Resubstitution error	Jackknife	Cross validation
Accuracy	0.85	0.84	0.78
Kappa	0.67	0.65	0.52
McNemar's Test P-Value	0.25	0.31	0.19
Sensitivity	0.89	0.89	0.88
Pos Pred Value (Precision)	0.86	0.86	0.79

Positive Class: Bushmanland Basin Shrubland in all the models

Linear Discriminant Analyses (LDA) on a comprehensive dataset

As expected, the evaluation results of the LDA-comprehensive data model (Table 3.19) indicated higher predictive accuracy and sensitivity than in the LDA-PC model. The PCA neglects some discriminant information, which may reduce the classification performance (Tharwat *et al.* 2017). The Linear Discriminant Analyses evaluation results based on comprehensive data (Table 3.20) yielded higher predictive

accuracy and sensitivity than in the LDA-PC model (Table 3.19) when using BBS and MMB. This was expected since PCA neglects some discriminant information, which may reduce the classification performance (Tharwat *et al.* 2017). The evaluation methods indicate high predictive accuracy in classifying vocalisations to their vegetation collection types, meaning that the training data allowed for the accurate classification of songs. All three evaluation methods indicated that more than 85% of the vocalisations from BBS and MMB were correctly classified as belonging to their respective vegetation types. Similarly, minimum frequency has the highest standard coefficient value (table 3.22), as observed in Linear Discriminant Analyses (LDA) on a comprehensive dataset in Table 3.14. Thus, it has the most discriminating ability.

Table 3.22. Coefficients of song parameters in the First discriminant function. There is only one discriminant function as the maximum number of discriminant functions equals the number of group categories (which is two, i.e., BBS vs. MMB) minus one.

Vegetation types	Song parameters	First discriminant function and standardised coefficients
BBS: MMB	Element duration	-0.16
	Elements per strophe	0.32
	IE Interval	-0.31
	Minimum frequency	0.78
	Maximum frequency	0.14
	Bandwidth frequency	0.02
	Peak frequency	0.52

Table 3.23. Outcomes of the evaluation of accuracy of the Linear Discriminant Analyses (LDA) on comprehensive data model (i.e., LDA-comprehensive data model) by Resubstitution error, Jackknife, and Cross validation.

	Resubstitution error	Jackknife	Cross validation
Accuracy	0.86	0.86	0.92
Kappa	0.70	0.70	0.82
McNemar's Test P-Value	0.72	0.81	0.72

Sensitivity	0.89	0.89	0.95
Pos Pred Value (Precision)	0.88	0.88	0.92

Positive Class: Bushmanland Basin Shrubland in all the models

3.4. Discussion

This study focused on an intraspecific comparative analyses of the relationship between the categories of habitats and song characteristics (frequency and temporal) of Sabota Larks inhabiting the habitats. Seven song parameters were used to test predictions of the AAH in seven vegetation types with different structures: one open (BBS), three moderately closed (TM, RB, PPB), and three moderately open (MMB, MBS, MSB). Only bandwidth frequency and inter-element interval predictions were supported, albeit not strongly. Although some of the findings of this study support the predictions regarding habitat structure, others contradicted the predictions.

These inconclusive findings may be attributed to a couple of factors. There is an inherent difficulty in reducing a singing male's territory to one of two habitat types: moderately open or moderately closed, as any territory constitutes a mosaic of open and less open patches. Sabota Larks occupy territories ranging in size from 2-4 ha (Dean 2005, GD Engelbrecht pers. comm.), which makes assigning such a large area to a "single unit" problematic. However, despite being subjective, care was taken to ensure that the visual assessment of vegetation structure was based on the "mean" of a vegetation type and that the criteria used in the decision were consistent across vegetation types. Larks avoid "closed" habitats, and the decision to assign a habitat type to a moderately open or moderately closed category was based on whether a habitat type leans toward the more open or more closed end of the spectrum of vegetation structure. For example, the Bushmanland Basin Shrubland (BBS) is clearly more open than bushveld and woodland habitats. The former is an open environment with grasses and shrubs, almost entirely treeless. At the same time, the bushveld and woodland habitat types are characterised by scattered trees varying in density but with no continuous canopy between trees.

The results showed that songs from MBS and TM significantly differed from each other and from songs from RB, PPB, MMB and MSB, mainly in minimum,

maximum, and peak frequencies. The TM songs had the lowest mean in all three parameters (NB. MMB, MBS, and MSB were categorised as having moderately open vegetation structures, and TM, PPB, and RB were moderately closed). On the contrary, songs from RB, PPB, MMB and MSB were not significantly different, on average, in five song parameters. This means that the song parameters of Sabota Larks from the moderately closed vegetation types analysed in this study are similar to those of Sabota Larks from the moderately open vegetation types. This may be because of similarity in habitat acoustics in the two habitat types, or it could be attributed to the small sample sizes of song strophes of birds recorded from some vegetation types. Since Sabota Larks are territorial, it cannot be ignored that some of the vegetation types are small patches, increasing the likelihood of individual birds wandering in multiple vegetation types. This means that numerous vegetation types may be imposing selection on the vocalisations of individual birds. This may again suggest that the vegetation types that individuals were recorded in may not best represent the habitat that may be imposing selection pressure on their songs, as it is typical of some species to reside in multiple habitat types for different purposes, e.g., breeding in closed or dense habitats and foraging in the open. However, 'dense', as used here in the context of lark ecology, cannot be equated with overstorey canopy closure as is typically used in literature (Hesselbarth *et al.* 2018).

Although contrary to this study's predictions, the high minimum, maximum, and peak frequencies and a greater number of elements per strophe in the Sabota Lark songs from the Savanna vegetation types (both moderately open and moderately closed) may reflect acoustic adaptations or adjustments. The Savanna vegetation types have greater avian species richness than the Karoo. Aide *et al.* (2017) have shown that an increase in the richness of acoustically active species is associated with a proportional increase in the total acoustic space use (ASU). Keeping in mind that the acoustic space in any given environment is a limited resource used by all vocal species living there, increasing the number of acoustically active species implies increased biotic noise (i.e., background noise) and interference of signals. This comes with costs like a lack of responses to appropriate signals, which could risk finding a mate or confronting an intruder. However, individuals can compensate for interference from

background noise by adjusting their signalling behaviour. Such adjustments can range from increasing signal amplitude, changing when (time) and where (space) the singing occurs, to increasing the rate of signal redundancy (Brumm and Slabbekoorn 2005; Wiley 2006). The high minimum, maximum, and peak frequencies and a greater number of elements per strophe in the Sabota Lark songs from the Savanna vegetation types may be an adjustment to increased acoustic space use because of increased acoustic competitors. This may enable individuals to communicate better.

One should also keep in mind that the Savanna biome is like a transition between grasslands and forests, mostly dominated by trees and grasses that are intolerant of shades but tolerant of fires, which limits their cover to an open state (Mucina and Rutherford 2006, Baudena *et al.* 2015). Furthermore, deciduous habitats, e.g., broad-leaved Savanna, differ over seasons. The loss of leaves in winter presents near-open habitat conditions, while the regrowth of leaves in summer presents some denseness. It may be that sound transmits differently when the deciduous habitats are leafed out in summer versus when bare in winter, and this may be influencing the propagation of songs of birds living there, as has been observed with the song of the great tit *Parus major* (Blumenrath and Dabelsteen 2004). This could also explain the lack of a significant difference in bandwidth frequency and the inter-element interval between songs that were recorded in moderately closed and open vegetation type songs, as birds in the broad-leaved Savanna may be spending a considerable part of their annual cycle in near-open (if not open) habitat conditions rather than near-closed habitats.

The results of these studies revealed, contrary to what was expected, that songs of Sabota Larks from the Karoo had on average, lower minimum, maximum, and peak frequencies than those of Sabota Larks in the savanna. Although contrary to what was expected, these characteristics may be acoustic adaptations to selective forces other than habitat vegetation. On average, there were no significant differences in five parameters of songs of Sabota Larks from moderately open and moderately closed, which may imply similar habitat conditions. Future studies are therefore recommended to perform quantitative analyses of vegetation, collect larger representative samples across study sites, and complete sound transmission tests.

CHAPTER 4

Conclusions, recommendations, and future prospects

Research on animal communication systems is necessary as its findings can, not only broaden our knowledge in general but, can also inform decision making in matters concerning conservation. However, this aspect has been given much attention mainly in bird species in the northern hemisphere (Hardt and Benedict 2021). In the present study, the evolution and range of acoustic communication in the Sabota Lark *Calendulauda sabota* (Alaudidae), especially in terms of song composition and influence of habitat types on song, were investigated. This makes an important contribution to our knowledge of the evolution and range of acoustic communication in southern hemisphere species.

The Sabota Lark emerged as a species that shows considerable variation in songs rendered across and within individual birds (CHAPTER 2). These variations were also encountered across different habitat types and within each unique habitat. Nordby *et al.* (2002) concluded that “one of the main difficulties in identifying a species as either an age-limited or open-ended song learner is the labour-intensive method of documenting full song repertoires, especially in species with multiple song types. It is even more difficult, or perhaps impossible, to document within-song type variation fully for a species”. In this study, considering the number of songs recorded in each unique habitat during breeding seasons and considering the study limitations mentioned in Chapter 1, Sabota Lark, nevertheless, emerged as a species with many unique song types and song strophes.

Furthermore, this species explores both types of presentation or singing styles: some individuals repeat song types at least twice before switching to another song type, hence the “eventual variety” style of song presentation or singing; the other birds render song types once, and never twice in succession, and this is known as “immediate” variety which means that they switch straight to new song types without having to repeat song types. Songs can be delivered as homogenous sequences, i.e.,

singing one song type several times before switching to another, which is rendered a couple of times before switching to another, and so on. These sequences of song types are called bouts. In this study, bout singing was observed in a vocal recording of only one individual Sabota Lark (Chapter 2, Fig. 2.3b). The level of complexity of songs in Sabota Larks is noteworthy. This is evidenced by large numbers of song strophes and song types collected from songs of the Sabota Larks analysed. One song type is rarely rendered a couple of times in succession without some variation in element structure and/or syllable composition.

Although there are mixed results regarding the extent to which the different types of habitats influence the songs of Sabota Lark, there are findings that are somewhat robust about the applicability of the Acoustic Adaptation Hypothesis (CHAPTER 3). The use of broad bandwidth frequency by Sabota larks that occupy habitats with an open vegetation structure and the observation of short inter-element intervals support the Acoustic Adaptation Hypothesis (AAH), which posits a correlation between bird vocalisations and habitat structure. While habitat type and structure may play a role in shaping the Sabota Lark songs, it is essential that large sample sizes with at least equal or unskewed proportions across habitats are analysed, and the vegetation structure should be quantified in more detail. This study has revealed that there could be more beyond what is considered 'similar' vegetation structure, with particular reference to habitat types that have open vegetation structures yet are significantly different.

Scientists must continue to improve their understanding of the role of habitat in shaping the evolution of bird songs, especially studying species of birds that occur in different biogeographic realms that will present different types of habitats. This is notwithstanding the notion that no single selective force can be treated as the sole driver of the evolution of bird vocalisations. Instead, various selective forces coupled with the limitations of the vocal systems to evolve, all contribute toward the evolution of bird vocal systems. There is no doubt that the AAH holds, in part, with regard to the songs of Sabota Larks, and this undeniably follows similar findings in other studies of the AAH in avian species. Therefore, there is a need for further research to understand the extent to which vegetation type and structure influence avian vocalisations.

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