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Phrase types, repertoire size and repertoire overlap in the South Island saddleback (*Philesturnus carunculatus carunculatus*)

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Abstract Males that defend territories with song benefit from sharing song types with their neighbours. Repertoire size, repertoire overlap between neighbouring birds, and song type delivery strategy were described for the South Island saddleback (*Philesturnus carunculatus carunculatus*). The song elements of 27 male South Island saddlebacks in the Ulva Island population near Stewart Island was categorised into one of 33 discrete phrase types; 10 common and 23 rare types. No stereotyped song types were found in the population. All syllables had harmonics and were simple in structure, consisting of a maximum of 2 or 3 elements. Male South Island saddlebacks had small to moderate phrase type repertoires and exhibited relatively high degrees of phrase type sharing with neighbours, which was even more prevalent when phrase cores and introductory syllables were analysed separately. Birds used a mixed-mode singing strategy, but also repeated partial and full phrases in song bouts. Compared to song studies of its North Island counterpart, the South Island saddleback had a larger phrase repertoire size, but phrase type sharing between neighbours seems to be important in both subspecies.

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INTRODUCTION

Male song is important in communication (Tobias & Seddon 2000; Enggist-Dueblin & Pfister 2002), territory defense (Catchpole & Slater 1995), male-male competition (Searcy & Andersson 1986), and plays a key role in sexual selection (Searcy & Andersson 1986). Although male song is learned in all oscine songbirds, the size and complexity of a male's song repertoire (i.e., total number of different song or phrase types) is thought to influence female mate choice (Catchpole & Slater 1995; Hasselquist *et al.* 1996; Buchanan & Catchpole 2000), as well as male-male territorial interactions (Molles & Vehrencamp 1999). In particular, song sharing with neighbouring males can play an important role in territorial interactions. For example, neighbours that shared song types had fewer aggressive interactions (Beecher & Brenowitz 2005), retained territories for longer periods (Beecher *et al.* 2000), and used these shared types in counter-singing (Catchpole & Slater 1995; Beecher *et al.* 1996). Thus repertoire overlap between neighbouring birds has been used to determine what proportion of song types two birds have in common (Molles & Vehrencamp 1999).

The New Zealand saddleback, or tieke, is a medium-sized (*ca.* 25-cm bill-tail length) forest passerine and member of the endemic wattlebird family Callaeidae of New Zealand (Heather & Robertson 1996; Hooson & Jamieson 2003a). There are currently two subspecies, the North Island (*Philesturnus carunculatus rufusater*) and the South Island saddleback (*P. c. carunculatus*) (Higgins *et al.* 2006), although recent research suggests a formal separation into two separate species would be more appropriate (Holdaway *et al.* 2001).

The vocalisations of the North Island saddleback and their role in male territorial interactions and song neighbourhoods have been studied by Jenkins (1976, 1978), Murphy (1989), and Rowe (2001). Jenkins (1976, 1978) examined 9 different song types (stereotyped sequence of phrase types) of male rhythmical songs in the North Island saddleback population on Cuvier Island, where song type repertoire sizes ranged from 1 to 4, but he reported that more song types were present on Cuvier and other islands. Current research confirms the presence of at least 39 song types in the Cuvier population (K. Parker, *pers. comm.*). Juvenile North

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Island saddleback matched their song to their neighbour's song after dispersal, and were thought to be open-ended learners (Jenkins 1976; 1978) and able to alter their repertoires after their first calendar year (Beecher & Brenowitz 2005).

The studies by Jenkins (1976, 1978) on North Island saddleback vocalisation have often been cited as a classic example of song learning (McGregor & Krebs 1982; McGregor 1989; Catchpole & Slater 1995), although his detailed research is now over 30 years old, and key advances in bird song analysis have been made with more sophisticated recording equipment and computer software. Song research using modern recording and analysing equipment is currently underway on the North Island saddleback (K. Parker, *unpubl. data*), but vocalisations of the South Island subspecies of saddleback have never been studied formally. There are significant genetic (I. Jamieson, *unpubl. data*), morphological and behavioural differences between the 2 subspecies (Holdaway *et al.* 2001; Higgins *et al.* 2006). Nevertheless, like the North Island saddleback, we expected the South Island saddleback to have a small to medium repertoire size and exhibit high levels of repertoire overlap between neighbouring birds as a result of the saddleback's relatively sedentary behaviour, and because they stay within their song neighbourhood and defend their territory with song year-round (Jenkins 1976, 1978; I. Jamieson, *unpubl. data*).

In this study we used modern song analysis software and commonly used parameters from the current bird song literature to describe the song system of the South Island saddleback. We described the main phrase types of male South Island saddlebacks, estimated repertoire size of individual birds, repertoire overlap between neighbouring birds and examined song type delivery strategy.

METHODS

Study site

Ulva Island/Te Wharawhara (46° 56′ S, 168° 08′ E) is situated in Paterson Inlet, Stewart Island. Ulva Island encompasses 259 ha, its highest point is 74 m a.s.l., and its nearest point is situated *ca.* 800 m from Stewart Island. It is covered in mostly pristine, mature podocarp forest and low coastal forest (Hooson & Jamieson 2004). In both habitat types, southern rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*) dominate, and provide important nest trees for saddlebacks (Hooson & Jamieson 2003b, 2004). Ulva Island is an 'open sanctuary' and under management by the Department of Conservation, which eradicated Norway rats (*Rattus norvegicus*) in 1996, the last remaining introduced predators of saddlebacks on Ulva Island (Beaven 2001).

Study population

Thirty South Island saddlebacks were translocated from Big Island, southwest of Stewart Island, to Ulva Island in Apr 2000 (Beaven 2001). Our research group at the University of Otago has monitored the saddleback population intensively since its translocation. During each breeding season, territorial pairs were located and monitored, and offspring individually colour banded during the nestling phase. During the period of this study (2004/2005 breeding season), 98 adults and 91 jackbirds (1-year old juvenile saddlebacks) were banded, including 14 (9 female and 5 male) of the 30 original founders of the Ulva Island population (I. Jamieson, unpubl. data). In total, 46 male saddlebacks held territories during the 2004/2005 breeding season of which 44 were paired and 27 were used for this study. Of these 27 birds, 4 were founders of at least 7 years of age, 5 were 1-year old juveniles and the remaining 18 birds were between 2 and 4 years old. Sex determination of individual birds was based on observational data: only female saddlebacks incubate and males normally courtship feed females (Hooson & Jamieson 2003b).

Collection of song data

Recording saddleback vocalisations was relatively unproblematic as they spent most of their day searching for food and called constantly while feeding (Blackburn 1964; Jenkins 1976). They also defended territories year round with their song (Jenkins 1978). Male rhythmical song increased at dawn during the saddleback's breeding period (Oct – Feb) and singing rates have been shown to be unaffected by the number of territorial neighbours (Murphy 1989). Additionally, saddlebacks were very tolerant of close and continuous observation, and observer presence did not seem to affect behaviour (Blackburn 1964; Jenkins 1976).

Vocalisations of male South Island saddlebacks on Ulva Island were recorded from Oct until mid Dec 2004. All birds were followed and their vocalisations recorded during daylight hours, between 0700 – 2000 h New Zealand standard time. Saddlebacks were located by following calls or sighting birds after entering their territory. No playbacks were used to initiate calls or to locate birds at any time. Once identified by colour bands, the focal bird was followed and its calls recorded until it was out of sight or until no new phrase types were heard. All calls were recorded with a highly directional Sennheiser MKH 815T microphone (frequency response is flat within the range 50 – 20 000 Hz), covered by a Rycote windshield and wind jammer. The Sennheiser microphone was connected to a Sony TCD-D8 digital audio tape recorder, DAT (flat frequency response at 48 kHz is within the range of 20 – 22 000 Hz ± 1.0 dB). Calls were recorded at

a sample rate of 48 kHz and a resolution of 16 bits on 90- or 120-minute Sony DAT tapes. The mean distance between the microphone and the focal bird during recording was initially 2 to 5 m, which was close enough to see the colour bands without binoculars. Once the bird was identified, it was followed at a greater distance, but always remain within sight when recordings were made.

Spectrographic sound analysis

Digitising procedure

All recordings were transferred from a Sony digital audio tape recorder TCD-D10 PRO II. The audio software PEAK LE Version 1.5 (Berkley Integrated Audio Software Inc., Sausalito, U.S.A.) was used to record stereo wave files at a sample rate of 48 kHz and a resolution of 16 bits. QUICKTIME PRO (Apple Computer Inc., U.S.A.) was used to down sample all recordings from 48 kHz to 44.1 kHz, as this was the highest sample rate supported by SOUND ANALYSIS PRO 1.056 (Tchernichovski *et al.* 2000). Recordings of saddleback calls from other individuals that overlapped with calls of the focal bird were omitted. The amplitude of all calls was normalised in PEAK.

Visual classification

The bioacoustic software RAVEN 1.2.1 (Mills *et al.* 2003) was used to prepare spectrograms (spectrogram settings: Hann window, window size: 512 samples, frame overlap: 97.1%, discrete Fourier transform (DFT) size: 2084 samples) for all birds in this study. Phrase types were categorised aurally and visually on the computer monitor. Examples of spectrograms of the different phrase types were printed and displayed as references during the classification process. Classification criteria were adapted from McGregor and Krebs (1982a). Phrases consisted of an introductory syllable plus a core unit. The 3 main criteria used to classify phrase types were (in order of importance): 1) the number of syllables in a repeated unit (i.e., the core unit of the phrase), except for chatter phrase types, which were divided into short (≤5 chatter syllables after the introductory note) and long types (>5 chatter syllables); 2) frequency modulation of syllables; and 3) length of syllables. Thus, phrase types were identified by firstly considering the number of syllables in their core unit. If 2 units had the same number of syllables, the frequency modulation of syllables was compared. Differences in number and frequency modulation of syllables in a phrase generally achieved clear discrimination between phrase types. The relationships between substitutions of the introductory syllables in relation to the core unit is reflected in the naming convention (Fig. 1; see also definition of phrases). Phrase types that occurred in 20% or more of the population sampled were arbitrarily classified as common types, and phrase types that occurred in less than 20% of the population were classified as rare types (Appendix 1). Similar to Molles *et al.* (2006), we produced saturation curves, which are scatter plots of the cumulative number of units categorised versus the total number of units recorded (in chronological order), for both the number of syllables and number of phrase types recorded.

Definitions

The current bird song literature uses a variety of descriptions for the main units of bird song. For the purpose of this paper we adapted the following definitions from Catchpole and Slater (1995) and Molles *et al.* (2006), from the smallest (element) to the most inclusive (song type) unit of bird song.

ELEMENT — An element is a continuous sound and includes any accompanying harmonics. Harmonics are component frequencies that are integers of a common, fundamental frequency (Bradbury & Vehrencamp 1998). An element is the smallest unit of song (see Fig. 2).

SYLLABLE — A unit of sound, which is repeated in an unvarying manner, sometimes comprised of 2 or more elements. In the current study population only 4 of the 9 syllables categorised were comprised of more than 1 element. Several syllables make up a phrase (Fig. 2). Unlike elements, syllables could stand alone and could be used independently from each other.

PHRASE — Stereotyped sequence of 2 or more syllables. In this study, phrase types were represented by a letter followed by a number to show the relationship between similar phrase types (i.e., A1, A2, A3; B1, B2), which often differed due to a single syllable substitution. There were 2 main classes of phrase types: stereotyped phrases, which consisted of a stereotyped core plus an introductory syllable, and 'chatter' phrases which often consisted of the chatter syllable repeated several times (Fig. 2), resulting in different core lengths. A similar vocalisation to the 'chatter' phrase exists in the North Island saddleback (Jenkins 1976). Chatter phrase types followed the same naming logic as other phrase types, but showed relations between short and long chatters. For example 'Chatter A1short' is a short type, and 'Chatter A1long' is the long type of the same chatter (see also the aforementioned 'Visual classification'). Although more common in the chatter phrases, both classes of phrases could be preceded by 1 or several 'zeet' syllables, which were also present in the North Island saddleback repertoire (Jenkins 1976).

SONG TYPE — A song type is a uniform string

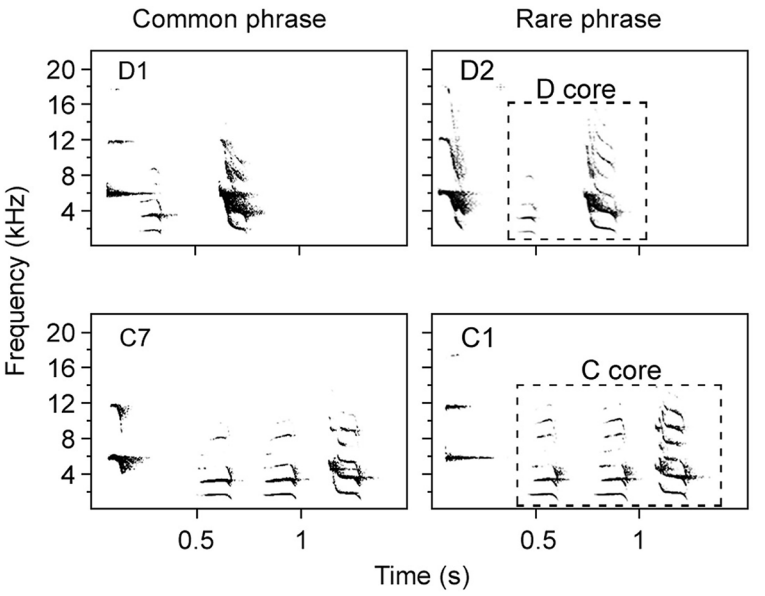

Fig. 1 Example spectrograms of common phrase types D1 (Male 3D) and C7 (Male 31A) and their related rare phrase types D2 (Male 3D) and C1 (Male 21M). Although both introductory syllables and cores of these phrase types are common in the population, particular combinations of these determine their common/rare classification.

of phrases, which follows a specific order, and in a simple case could consist of Phrases A1A1B1B1. Song types are usually stereotyped within the repertoire and can be combined with other song types in song bouts. The present study population did not exhibit any stereotyped song types, in contrast to North Island populations (Jenkins 1976; 1978).

Repertoire size

In order to determine the repertoire size of male loud calls, saturation curves for all birds used in this study were produced for both syllables and phrase types. Phrase types that were closely related were counted as separate phrases (i.e., A1 was counted as different from A2, etc.). Similar to the repertoire size analysis of the related kokako (*Callaeas cinerea*) (Molles *et al.* 2006), birds whose vocalisations were recorded extensively and that reached their phrase type asymptote after an average of 82 phrases (range 63 to 110) were selected to calculate a mean estimate at which birds reach their phrase type asymptote in relation to repertoire size. This mean percentage (78%) was used to estimate complete repertoire size of all other South Island saddlebacks recorded. Similarly, 13 birds of which more than 30 phrases were recorded and that reached their asymptote before 78% of their total sampled phrases were used for the repertoire size analysis. For these birds, repertoire sizes of phrase cores and their respective introductory syllables were also calculated. A correlation was performed in SPSS ® (Version 16.0) to investigate the relationship between age and repertoire size. Of the 13 birds used, 3 were founders of at least 7 years of age, one was a 1-year old juvenile and the remaining 10 birds were between 2 and 4 years old.

Repertoire overlap

During the 2004/2005 breeding season, most saddleback territories on Ulva Island were on the coast, and therefore, most birds had only 2 neighbours – one on either side of their territory. Only birds that had adjacent territories and completely recorded repertoires (see 'repertoire size' above) were used in the neighbour repertoire overlap analysis (7 neighbour pairs). For these birds repertoire overlap of whole phrases, their phrase cores, and respective introductory syllables were calculated. Repertoire overlap between birds was determined by $2N / (R_1 + R_2)$, where N is the number of phrase types shared by a pair of males, and R_1 and R_2 are the repertoire sizes of the 2 males (McGregor & Krebs 1982). Phrase types that were closely related were counted as separate phrases (i.e., A1 was counted as different from A2, etc.).

Digital sound analysis

The software SOUND ANALYSIS PRO 1.056 (Tchernichovski *et al.* 2000) was used to measure spectral derivatives of 6 syllables for each of 10 birds for which complete repertoires were recorded. As some birds did not have all 6 syllable types, sample sizes varied between 8 and 10 birds for a given syllable. SOUND ANALYSIS PRO (SAP) used multitaper spectral analysis to estimate spectral derivatives of sound (Tchernichovski *et al.* 2004).

In SAP, spectral derivatives were not artificially

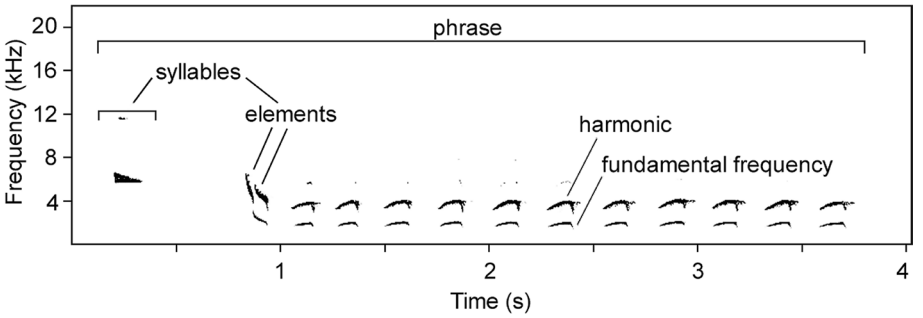

Fig. 2 Sound spectrogram of bird song units. Examples of elements, syllables and phrases are shown as defined in the current study. A harmonic frequency is an integer of its fundamental frequency (Bradbury & Vehrencamp 1998).

broadened and had the same resolution as the spectrogram (Tchernichovski *et al.* 2000). Spectral derivatives enabled more accurate measurements as they represented sound more sharply than the conventional spectrogram, especially in highly frequency-modulated fractions of syllables (Tchernichovski *et al.* 2000).

The variables used in this analysis were syllable duration, mean pitch, mean harmonic frequency, mean frequency modulation, and mean entropy. In SOUND ANALYSIS PRO 1.056 these variables were calculated as follows.

Syllable duration — The length of the syllable was defined by either semi-automatic or user-directed outlining of syllables. Both methods derived measurements only from syllables detected by the program. If semi-automatic outlining included additional segments of sound, which did not represent part of the syllable but were included as part of the syllable bout, user-directed outlining was used, which allowed the user to outline the syllable more exactly.

Mean pitch — As all saddleback syllables had harmonics, mean pitch was adjusted to measure the mean fundamental frequency of a syllable. This measure described the average of the lowest frequency of a given syllable, excluding the harmonics. Thus, it measured the frequency of the lowest component trace of a syllable.

Mean harmonic frequency — The mean frequency measure in SAP will from hereon be referred to as mean harmonic frequency. This parameter was a measure of the average peak frequency (Tchernichovski *et al.* 2004), which in the case of harmonically rich syllables, was the average of peak frequencies for all harmonics. This measure described how harmonically rich a sound was, or if there were many frequencies at once.

Mean frequency modulation— Mean frequency modulation (mean FM) calculated an absolute (unsigned) estimate of mean FM for each syllable, based on time and frequency derivatives across frequencies (Tchernichovski *et al*. 2004). This measure described how 'pure' or complex a syllable is. Pure tones had no frequency modulation, whereas complex tones had high frequency modulation.

Mean wiener entropy — Mean wiener entropy, or mean entropy, was a measure of the width and uniformity of the power spectrum, and was a pure number on a logarithmic scale between 0 and 1 in SAP. For example, white noise had an entropy value of 1 and a pure tone had an entropy value of 0 (Tchernichovski *et al.* 2004). This measure described clear or regular tones with low entropy values and tones with randomness, or irregularity with high entropy values.

All measurements were exported to Microsoft EXCEL® (version 9.0) spreadsheets. The statistical software MINITAB© (version 14.0) was used to perform principle component analysis (PCA) and discriminant function analysis (DFA). All measured parameters were used to investigate within- and between- bird variations for 6 syllable types. For within-bird variation of syllable types, measurements of all syllables of one bird were subjected to PCA and the 2 principle components with the highest eigenvalues were subjected to DFA for each bird separately. For between-bird variation of syllable types, mean measurements of all syllables (maximum of 6 syllables per bird) of all birds (8 to 10 birds per syllable) were subjected to PCA and the 2 principle components with the highest eigenvalues were subjected to DFA. PCA weighted these variables to provide maximum discrimination between categories (syllables in this case). In DFA, the proportion of syllables correctly classified to a known syllable category was estimated using cross validation, a more robust estimation of classification. SPSS® (version 10) was used to perform the remaining statistical analyses.

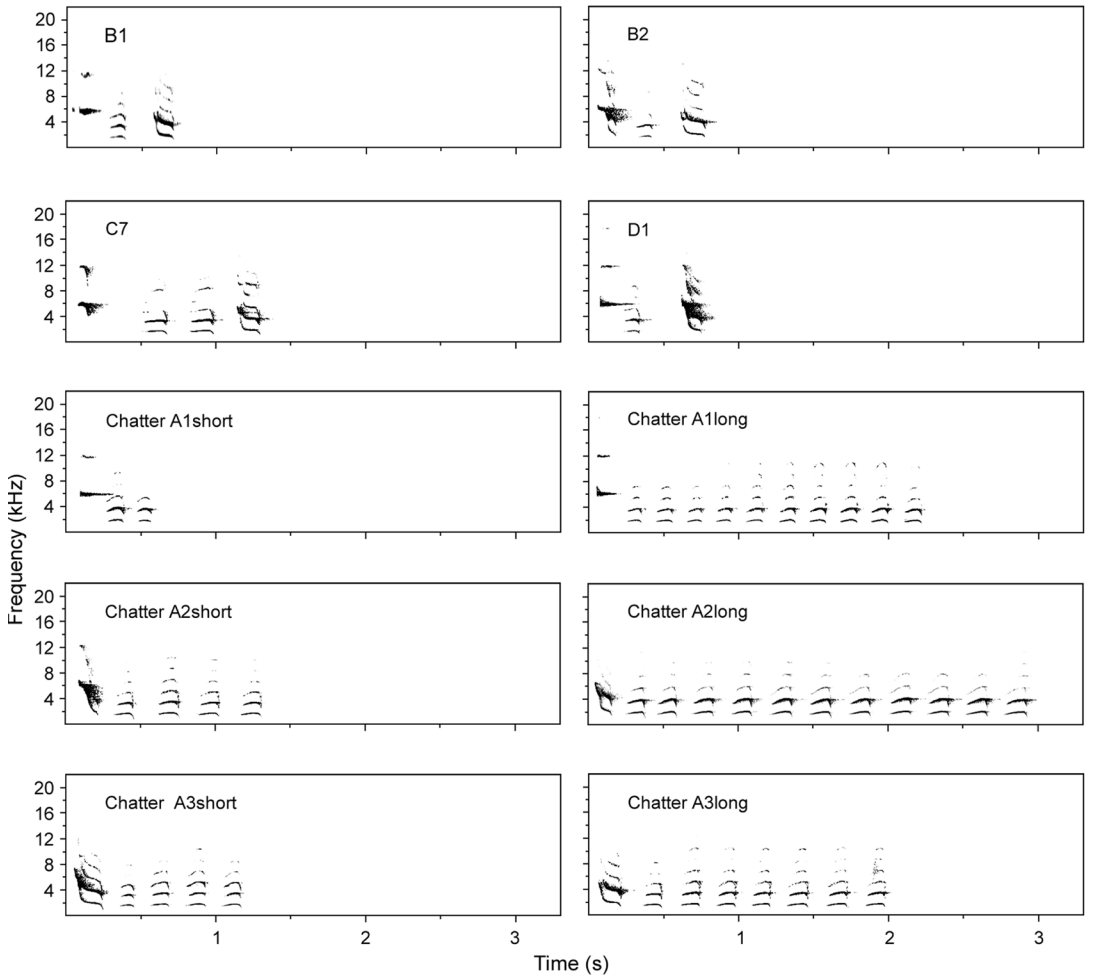

Fig. 3 Spectrograms of common phrase types in a population of South Island saddleback on Ulva Island. Examples of phrase types that originate from a single bird are: Chatters A1short and A1long (Bird 26B); Chatters A2 and A3 short and long (Bird 16K).

Means are displayed as ± 1 standard deviation unless stated otherwise.

RESULTS

Syllable and phrase types

The songs of male South Island saddlebacks in the Ulva Island population were assigned as one of 33 discrete phrase types; 10 were relatively common (Fig. 3) and 23 were rare (Appendix 2). The classification of common and rare phrase types is shown in Appendix A. Chatter phrases were the most common phrase types within the population and within a single-bird's repertoire (Fig. 4). Rare phrase types were usually minor variations of common phrase types, such as a single syllable substitution to a phrase core (Fig. 1).

A mean of 7.77 ± 3.42 phrase types (n = 13, range = 3 - 14), and 6.46 ± 1.61 syllable types (n = 13, range = 4 - 9) were recorded for any one bird. Syllables in the song of South Island saddlebacks were very simple. The most complex syllables had only 2 or 3 elements. In fact, many single elements were considered syllables, because they were used independently, such that phrase types could be defined as consisting of several single elements. Single syllables were discrete and generally did not overlap. All South Island saddleback syllables had multiple accompanying harmonics. Except for 3 syllables, the amplitude of the 1st harmonic was consistently higher than that of the fundamental frequency (Ludwig 2007). The chatter phrases of South Island saddlebacks were similar in structure

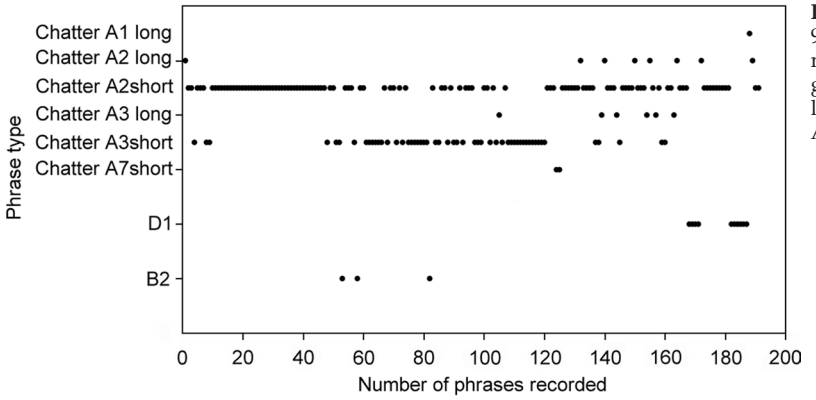

Fig. 4 Phrase types used by Male 9G, the most extensively recorded male in the current study. The graph shows the most frequently sung phrase types (Chatters A2short and A3short).

to that of the North Island saddlebacks described by Jenkins (1976, 1978). Chatter phrases had 1 introductory syllable, which preceded multiple chatter syllables (usually the same syllable repeated multiple times, see Fig. 2). Short chatter phrase types had 5 or fewer chatter syllables, whereas long chatter phrase types had 6 or more chatter syllables. Chatter phrases were sometimes introduced by a 'zeet' syllable. Chatters A1 and A2 short and long were the most frequently sung chatter types in the Ulva Island population (Appendix 1) and in a single bird's repertoire (Fig. 4).

Phrase type delivery

Unlike the North Island saddleback (Jenkins 1976, 1978), male South Island saddleback did not seem to use consecutive phrases in a stereotyped manner to form song types, termed 'distinct patterns of male rhythmical song' by Jenkins (1978). Instead, South Island saddlebacks used phrase types as the largest unit in a song composition. Both bout singing, where partial and full phrases were repeated, and mixed-mode singing, using a variety of phrases in a more or less random order, were used.

Individual South Island saddlebacks showed variability during phrase type delivery by singing starts of various phrase types at any given time and adding new endings to phrase types, most commonly to chatter phrases (Ludwig 2007). These phrase types were not categorised as new phrases, as they were rare and clearly part of a singing bout of the same phrase types, often appearing as a precursor or in addition to the phrase core.

Repertoire size

A total of 9,602 syllables (range: 54 - 1023) and 1,775 phrases (range: 10 - 214) were recorded from 27 male South Island saddlebacks. For the 13 birds for which full repertoires were recorded, a total of 5741 syllables (mean = 442; range = 138-951) and 1079 phrases (mean = 83; range = 31-214) were recorded. Male South Island saddlebacks had a mean syllable repertoire size of 6.46 ± 1.61 (range = 4-9, n = 13) and a mean phrase type repertoire size of 7.77 ± 3.42 (range = 3-14, n = 13). For these birds, mean repertoire sizes of phrase cores and their introductory syllables were 4.46 ± 1.27 (range = 3-7, n = 13) and 6.54 ± 1.51 (range = 4-9, n = 13), respectively. There was no correlation between repertoire size and age ($r^2 = 0.003$, df = 12, P = 0.85).

Repertoire overlap

The mean repertoire overlap of neighbouring males that had both reached their phrase repertoire asymptotes was significantly greater than males where at least 1 of the pair was recorded less often (mean = 0.65 ± 0.18; n = 7 and 0.41 ± 0.14; n = 21, respectively; t = 3.24, df = 24, P = 0.003), and therefore pairs with males recorded less were omitted from the analysis. The repertoire overlap analysis was thus limited to 7 neighbour-neighbour pairs, for which there were the most extensive recordings. The mean phrase repertoire overlap between neighbours was 0.65 ± 0.18 (range = 0.50-0.94). The mean phrase core repertoire overlap and their respective introductory syllables repertoire overlap between neighbours was 0.75 ± 0.16 (range = 0.57-1.0) and 0.82 ± 0.13 (range = 0.60-1.00), respectively.

Digital sound analysis

Syllable types generally separated along the first principal component for within-bird comparisons, with some overlap (see example in Fig. 5). Mean measurements of the 'zeet' (Syllable 1) and 'chatter' syllables (Syllable 4) always separated well within- and between- birds, while other syllables showed more overlap in PCA (Figs. 5 and 6). All dependent variables played an important role in explaining the variation in the data, with the first 3 principle components explaining 93.1% of the variation in the syllable types used among individual birds. This was confirmed by cross validation, where all 3 factors (PC1 – PC3) assigned syllables correctly 78.2% of the time, and PC1 alone 65.5% of the time.

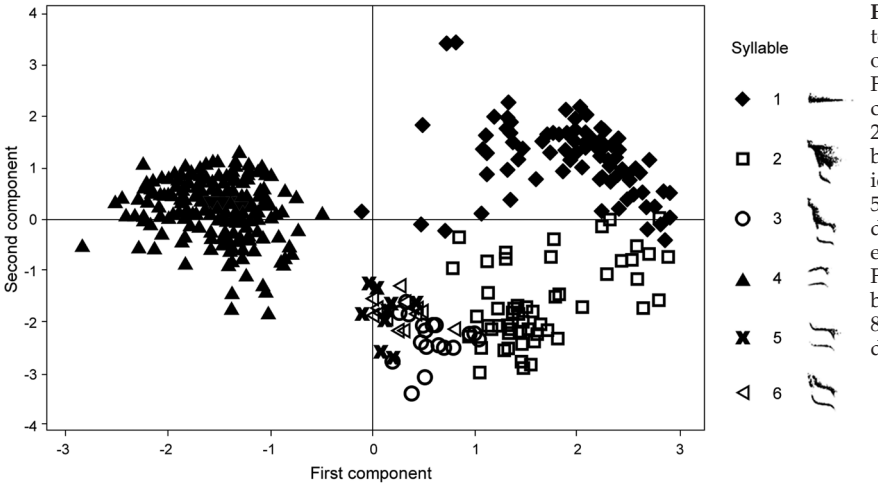

Fig. 5 Example of PCA clusters for within-bird variation of syllable types (Bird 13D). For this bird, the first principle component (PC1, EV = 2.83) was largely influenced by pitch and mean harmonic frequency and explained 56.6% of the variation in the data, while PC2 was influenced by syllable duration, FM, and entropy and combined with PC1 explained 88.2% of the variation in the data.

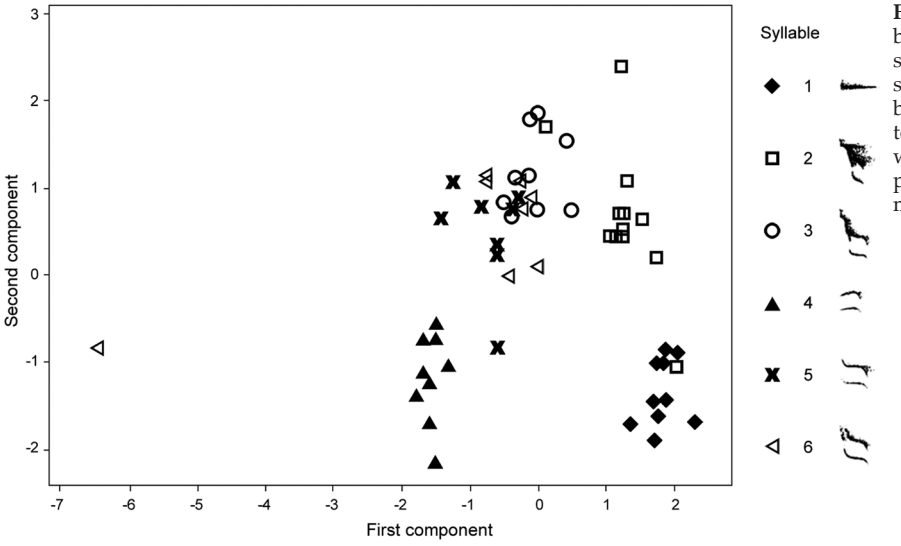

Fig. 6 PCA clusters for between-bird variation of syllable types. Note the separation between Syllables 1 ('zeet') and 4 (chatter) along PC1, which was largely influenced by pitch, FM and mean harmonic frequency.

DISCUSSION

The results of our study showed that phrases of male South Island saddleback could be categorised as one of 33 discrete types. All syllables had harmonics and were simple in structure, consisting of maximally 2 to 3 elements. Most syllables separated well within and between birds in digital sound analyses, which supports the current classification used. Although partial and full phrases were repeated in a song bout, no stereotyped song types were found, and phrases were often used in a unique sequence, indicating that the South Island saddleback used mixed-mode singing with intermittent bout singing. Compared to other species (see Catchpole & Slater 1995; Bradbury & Vehrencamp 1998), male South Island saddleback had a small to moderate phrase type repertoire (mean = 7.77) and exhibited a relatively high degree of phrase type sharing with neighbours (mean phrase repertoire overlap = 0.65), which was even more prevalent in shared phrase core and introductory syllable repertoire overlap between neighbours (mean = 0.75 and 0.82, respectively). On average, saddlebacks had more introductory syllable types in their repertoire than phrase cores, which suggests that birds use the same phrase cores and add different introductory syllables to create new phrases.

The latter result suggests that phrase type sharing in the South Island saddleback is as important as it is in the North Island subspecies, particularly because individuals of both subspecies defend their territory with their song year-round (Jenkins 1976; 1978; I. Jamieson *pers. obs.*). Territories that become available are usually filled quickly

by males that are likely to bring new phrases into the song neighbourhood. Males that adjust their song repertoire so that overlap with neighbours is maintained could be at an advantage and therefore benefit from the development of a song neighbourhood. Variation of repertoire overlap in the current study was relatively low between neighbouring birds (0.65 ± 0.18), which could suggest an optimal level of phrase type sharing that may be maintained across seasons. This requires further study.

Open-ended learners are birds that can alter repertoire composition across seasons and throughout their life. The South Island saddleback may be an open-ended learner, similar to its North Island counterpart (Jenkins 1976, 1978). In the study population, 33 phrase types were recorded, while the average male phrase type repertoire size was only 7.77 (range 3 to 14). Because the study population had more phrase types than were recorded from a single bird, there is a high probability that a newly settled yearling, for example, would encounter unknown phrase types to those heard in its parental neighbourhood. Studies on song learning in saddlebacks need to examine whether yearlings add to their original (parental) repertoire or delete unused phrase types at the same rate as they pick up new ones. Longitudinal data on repertoire sizes of individual birds could clarify if repertoire sizes change with age. Given the difference in delayed plumage maturation between the 2 subspecies, it would be interesting to examine if there are differences in the patterns of song behaviour between age groups within a subspecies.

Phrase type delivery of South Island saddlebacks could be studied more closely to see whether it varies as a function of agonistic context. The banded wren (*Thryothorus pleurostictus*) was also classified as mixed-mode (serial) singer, which can use repetition of the same song types (Molles & Vehrencamp 1999). Molles and Vehrencamp (1999) found that singing mode changed depending on the context. Birds used faster, high-diversity singing with high switching mode (ability to change from one song type to another) in non-aggressive contexts and low-diversity, repetitive singing in more aggressive contexts. While it was noted during this study that South Island saddlebacks increased bout singing when agitated, this needs to be investigated more formally. It might be useful to examine switching rate and song type diversity in aggressive versus non-aggressive interactions of individual birds, similar to Molles and Vehrencamp's (1999) study. Chatter phrases might be of particular relevance for such a study. While South Island saddlebacks used quiet vocalisations including creeks and whistles during close-range territory disputes (K. Ludwig, *pers. obs*.), chatter phrase types were the most common phrase type in a single bird's repertoire and could be important in everyday territory maintenance. Territorial males often responded to their neighbours with bout singing of chatter phrase types (K. Ludwig, *pers. obs*.). Furthermore, a given chatter phrase could be viewed as a simplified bout singing of syllables. This bout singing strategy is particularly powerful in long chatter phrase types. The longest chatter phrase recorded in this study consisted of 38 chatter syllables. If bout singing of chatter phrases was predominantly used in territorial interactions, this singing strategy would be consistent with the observation that bout singing species use their song type repertoires in male-male interactions and countersinging (Bradbury & Vehrencamp 1998).

While these results were consistent with research on North Island saddleback where chatter phrases were the most common saddleback vocalisation, Jenkins (1976, 1978) did not speculate on the function of this phrase type in territory maintenance. A formal comparison of phrase types, morphology and DNA, and how these relate to the status of North and South Island saddlebacks as a single species is currently underway (K. Parker, *pers. comm*.). We examine elsewhere whether there is sufficient overlap in song between fathers and their sons to serve as an inbreeding avoidance mechanism (K. Ludwig, *unpubl. data*).

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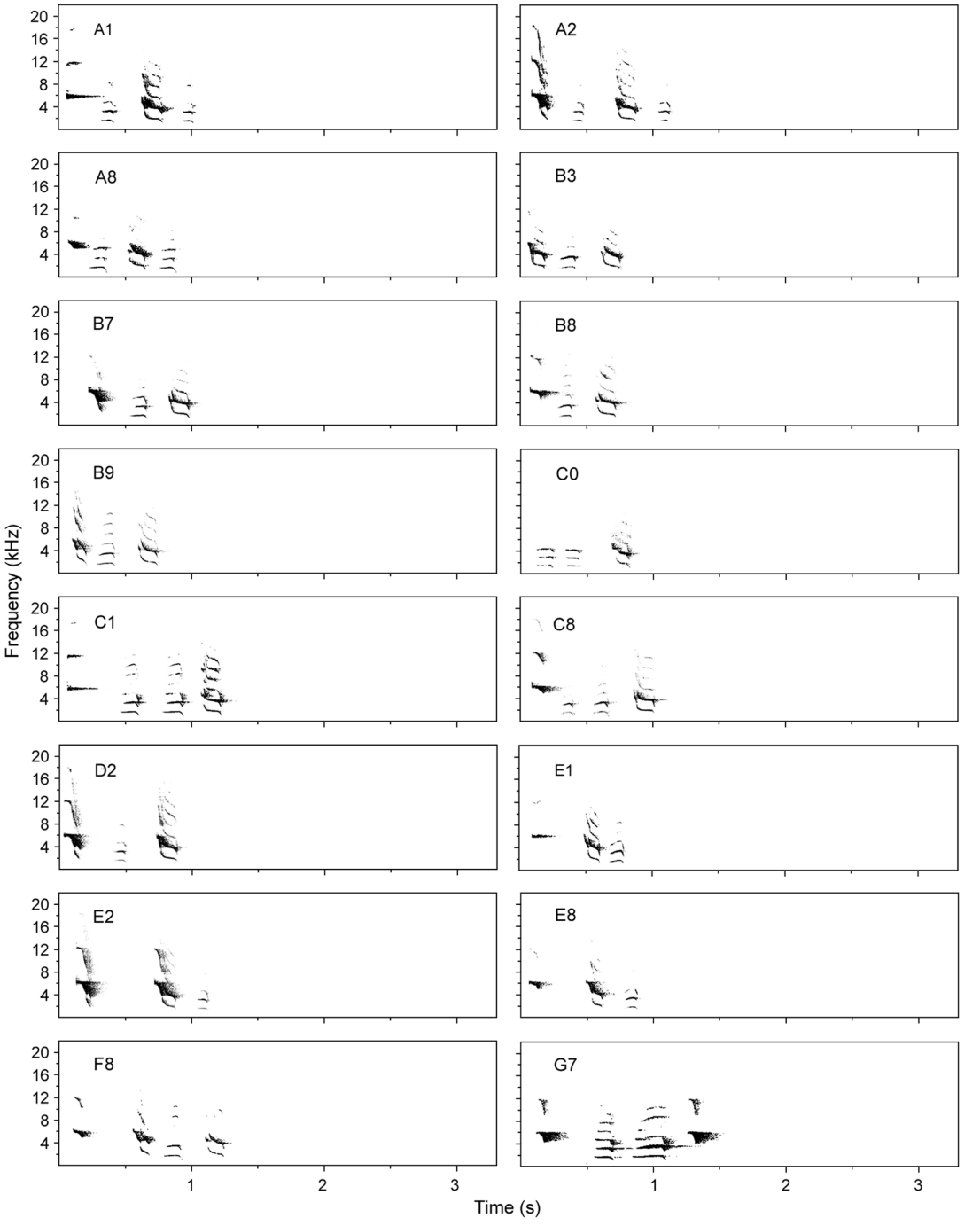
Appendix 1 Common (bold) and rare phrase types in a population of male South Island saddlebacks on Ulva Island, New Zealand. Phrase types were arbitrarily classified as common if they occurred in more than 20% of both bird groups shown below, they were otherwise classified as rare. Numbers in brackets show birds that have that phrase type.

Phrase type	Percent occurrence in population (*n*=27)	Percent occurrence in birds with full repertoires (*n*=14)	Classification
A1	19 (5)	31 (4)	rare
A2	4 (1)	8 (1)	rare
A8	7 (2)	8 (1)	rare
B1	**29 (8)**	**23 (3)**	**common**
B2	**33 (9)**	**38 (5)**	**common**
B3	7 (2)	15 (2)	rare
B7	15 (4)	15 (2)	rare
B8	4 (1)	8 (1)	rare
B9	4 (1)	0 (0)	rare
C0	4 (1)	8 (1)	rare
C1	26 (7)	8 (1)	rare
C7	**30 (8)**	**31 (4)**	**common**
C8	4 (1)	0 (0)	rare
D1	**33 (9)**	**23 (3)**	**common**
D2	4 (1)	8 (1)	rare
E1	4 (1)	0 (0)	rare
E2	19 (5)	38 (5)	rare
E8	19 (5)	15 (2)	rare
F8	4 (1)	0 (0)	rare
G7	4 (1)	8 (1)	rare
Chatter A1short	**30 (8)**	**38 (5)**	**common**
Chatter A1long	**33 (9)**	**31 (4)**	**common**
Chatter A2short	**81 (22)**	**85 (11)**	**common**
Chatter A2long	**44 (12)**	**54 (7)**	**common**
Chatter A3short	**85 (23)**	**92 (12)**	**common**
Chatter A3long	**78 (21)**	**92 (12)**	**common**
Chatter A7short	19 (5)	15 (2)	rare
Chatter A7long	4 (1)	8 (1)	rare
Chatter A8short	11 (3)	8 (1)	rare
Chatter A9short	15 (4)	23 (3)	rare
Chatter B5short	11 (3)	15 (2)	rare
Chatter C4short	11 (3)	23 (3)	rare
Chatter C5long	4 (1)	8 (1)	rare

Appendix 2 Spectrograms of rare phrases found in a population of South Island saddleback on Ulva Island. Examples of phrase types that originate from a single bird are: A1, D2, E2 (Bird 3D); E1 and E8 (Bird 4E); B7, B8, Chatters A7 long and A8 short (Bird 13D); B9 and F8 (Bird 16J); C1 and Chatter A7 short (Bird 21M); C0, Chatters C4 short and C5 long (Bird 28I); and G7 and Chatter B5 short (Bird 32C).



Appendix 2 (continued) Spectrograms of rare phrases found in a population of South Island saddleback on Ulva Island. Examples of phrase types that originate from a single bird are: A1, D2, E2 (Bird 3D); E1 and E8 (Bird 4E); B7, B8, Chatters A7 long and A8 short (Bird 13D); B9 and F8 (Bird 16J); C1 and Chatter A7 short (Bird 21M); C0, Chatters C4 short and C5 long (Bird 28I); and G7 and Chatter B5 short (Bird 32C).