



Avian Behavior, Ecology, and Evolution

Structure and function of the vocal repertoire of the Rifleman (*Acanthisitta chloris*), a member of the earliest diverging passerine suborder, Acanthisitti

Estructura y función del repertorio vocal del Acantisita Verdoso (*Acanthisitta chloris*), un miembro del suborden de paseriformes de divergencia temprana, Acanthisitti

Yen Yi Loo¹ , Ines G. Moran¹ , Ana K. Menzies¹ , Sarah Withers¹ , Margaret C. Stanley¹  and Kristal E. Cain¹ 

ABSTRACT. Birds communicate primarily using vocal signals. These signals undergo strong selection for effective transmission, which is often critical for survival. Passerines are an excellent group for studying vocal communication due to their diverse vocal repertoires, from simple calls to complex songs. However, the study of songbird calls is often overshadowed by studies of more conspicuous songs, which may bias our understanding of the true diversity of bird vocalizations. Here, we detail the vocal communication system of the Rifleman (*Acanthisitta chloris*), a New Zealand Wren (family: Acanthisittidae), a songless species from a species-poor suborder (Acanthisitti), sister to the oscine and suboscine Passerines. We describe nine adult call types and three juvenile call types, providing the most complete vocal repertoire of this species to date. Within these call types, we found variation in the spectral acoustic structure between different behavioral contexts. Furthermore, we also found negligible differences between sexes in contact calls, despite substantial size dimorphism. Using these data, we classify call types and discuss their probable function(s) based on behavioral context, such as foraging, provisioning nests, nuptial feeding, and alarm calling. Collectively, we hope that this study will provide a foundation for understanding the evolution and function of calls in Passerines and encourage more study of calls across taxa.

RESUMEN. Las aves se comunican principalmente mediante señales vocales. Estas señales se hallan sometidas a una fuerte selección para una transmisión efectiva, que suele ser crítica para la supervivencia. Los paseriformes son un grupo excelente para estudiar la comunicación vocal debido a sus diversos repertorios vocales, desde simples llamadas hasta cantos complejos. Sin embargo, el estudio de las llamadas de los paseriformes a menudo se ve eclipsado por las investigaciones sobre cantos más notables, lo cual puede sesgar nuestra comprensión acerca de la verdadera diversidad de las vocalizaciones de las aves. Aquí, detallamos el sistema de comunicación vocal del Acantisita Verdoso (*Acanthisitta chloris*), un chochín de Nueva Zelanda, especie sin cantos de un suborden pobre en especies (Acanthisitti), hermano de los subórdenes de paseriformes oscines y suboscines. Describimos nueve tipos de llamadas de adultos y tres de juveniles, proveyendo el más completo repertorio vocal de la especie al momento. Dentro de estos tipos de llamadas, encontramos variación en el espectro acústico entre diferentes contextos comportamentales. Además, también encontramos diferencias insignificantes en las llamadas de contacto entre los sexos, a pesar del sustancial dimorfismo de tamaño. Utilizando estos datos, clasificamos los tipos de llamadas y discutimos sus posibles funciones en base a contextos comportamentales tales como forrajeo, el aprovisionamiento de nidos, la alimentación nupcial y las llamadas de alarma. En conjunto, esperamos que este estudio sienta las bases para comprender la evolución y función de las llamadas en los paseriformes y promueva más estudios sobre llamadas en diversos taxones.

Key Words: *Animal communication; behavior; context; New Zealand; Passeriformes; Rifleman; vocal variability*

INTRODUCTION

Vocal communication is a primary mode of signaling among birds, and these auditory signals undergo selection for effective transmission (Janik and Slater 2000, Winkler 2001, Marler 2004a, Garcia and Favaro 2017). Among birds, songbirds (order: Passeriformes) are among the most vocally elaborate, with a high degree of variability in the complexity of their vocalizations (Robinson et al. 2019), ranging from generally simple, single note “calls” to intricately complex “songs.” Songs are defined as complex vocalizations broadcast to defend territories and attract mates and are often learned via auditory feedback (Catchpole and Slater 2008, Riebel 2016, Veit et al. 2021). Conversely, calls are typically less complex and are often used for communication within social groups, such as keeping in contact, signaling danger, or soliciting care (Kondo and Watanabe 2009, Clay et al. 2012). Calls are also often assumed to be innate due to their short duration and thus have less variation than songs (Nieder and

Mooney 2020, but see Vicario et al. 2002, Vicario 2004, Sewall 2011, Walløe et al. 2015). Vocal complexity is influenced by ecological, morphological, and social factors (Brumm et al. 2009, Soma and Garamszegi 2011, Krams et al. 2012, Fischer et al. 2017, Crouch and Mason-Gamer 2019, Yambem et al. 2020). Studying vocal complexity is important for understanding the evolutionary and ecological drivers of vocal elements, their functions, and importance to fitness (Fischer et al. 2017, Lipkind et al. 2017). Complexity can be measured in terms of song or call types, length or number of syllables, fine-scale variations in the spectral and temporal features of vocalizations, or functions of the vocalizations (Marler 2004b).

Bird calls have received substantially less attention than songs, in part due to their more cryptic nature (Marler 2004a, Benedict and Krakauer 2013, Nieder and Mooney 2020), which may lead to an incomplete picture of the breadth of vocal communication used

¹School of Biological Sciences, University of Auckland, Auckland, New Zealand

and perceived by birds (Lohr and Dooling 1999, Dooling et al. 2002, Dooling 2004, Hoeschele and Fitch 2016). Furthermore, addressing this knowledge gap is important for understanding the life history characteristics acting on the evolutionary pathways responsible for driving the variation of calls (Simpson and Vicario 1990, Marler 2004a, Loo and Cain 2021). Complexity in call communication can be investigated in the form of fine-scale, dynamic changes in pitch, call rate, amplitude, and duration (Wirthlin et al. 2019). These subtle changes may be influenced by context or social setting, as well as sex or size differences, and thus may encode rich social information about the signaller (Marler and Evans 1996, Sharp and Hatchwell 2005, Berryman 2007, Sewall 2009, Hall et al. 2013). Examples of call flexibility include variation in the intensity of begging calls used to signal hunger level (Wright and Leonard 2002), intensity or type of alarm calls used to signal danger level (Templeton et al. 2005, Suzuki 2011, 2016), and flexible advertisement calls that change depending on the relationship between the signaller and receiver (Gémard et al. 2021).

Although important for generating meaningful hypotheses in vocal communication and complexity studies (Marler 2004a, Benedict and Krakauer 2013, Petrusková et al. 2016, Loo and Cain 2021), mapping the complete call repertoire of a species is usually a secondary goal or completely ignored. As a result, the variation, context specificity, and development of calls—especially in songbirds from early diverging branches of the avian phylogeny (Loo and Cain 2021)—are poorly known, except in a few well-documented species, such as the Zebra Finch (*Taeniopygia guttata*) (Elie and Theunissen 2016, Montes-Medina et al. 2016, Gémard et al. 2021) and Black-capped Chickadee (*Poecile atricapilla*) (Templeton et al. 2005).

In this study, we quantify the vocal repertoire of the North Island Rifleman (Māori name: Titipounamu, *Acanthisitta chloris granti*), one of two extant species of New Zealand Wren (suborder: Acanthisitti), a sister group to all other passerines (Ericson et al. 2002, Robertson et al. 2007, Preston et al. 2013, Jarvis et al. 2014, Withers 2020, Withers et al. 2021). Due to its phylogenetic position, Rifleman vocal abilities and repertoire are increasingly recognized as valuable for understanding the evolution of complex vocalizations in songbirds (Suh et al. 2011, Loo and Cain 2021). Several authors have partially documented its calls using onomatopoeic names (Higgins et al. 2001, Withers 2013), although the spelling of call names may be different between authors (Vella et al. 2021). However, a complete vocal repertoire of this species has not been produced. Here, we address these issues by providing spectrograms of all Rifleman observed call types—including previously undocumented types—based on field observations and sound recordings. We match these spectrograms with their onomatopoeic call type names previously mentioned in the literature when possible. In addition, we test for spectral differences in acoustic parameters in call types used in similar vs. different contexts. In doing so, we describe the extent of call variation and differentiate call types in this species. Then we discuss the function(s) for each call type based on behavioral and social contexts. We also test for sex differences in three commonly used contact call types: chuck, pip, and zip calls.

METHODS

Study Site and Species

We conducted this study in a submontane primary forest (ca. 800 m asl) at Boundary Stream Mainland Island, Hawke's Bay, New Zealand (GPS coordinates: -39.103740545, 176.803939016). The breeding season of Rifleman is asynchronous and begins in September (austral spring) and ends in February (austral summer) (Gray 1969, Sherley 1985). They are monogamous and employ a facultative cooperative breeding strategy to increase survival rate of young birds (Sherley 1994, Preston et al. 2016). Rifleman build dome nests in secondary cavities with twigs, fine rootlets, leaf skeletons and feathers (Higgins et al. 2001). Birds were banded with two- or three-color leg bands, forming unique band combinations for field identification of individuals while recording their vocalizations and behavior.

This species is sexually dimorphic (Hunt and McLean 1993, Sherley 1993). Males are 5 g, whereas females are 7 g (Sherley 1993). From 176 adult individuals (107 males and 69 females) banded from 2018 to 2020 (excluding recaptures) for this study, males range from 5.1 to 6.7 g (mean = 5.73 ± 0.28) and females range from 5.2 to 8.5 g (mean = 6.83 ± 0.57). Males and females share territorial defence roughly equally. However, males contribute slightly more to nest building, and substantially more toward day-time incubation than females (males spend 50% more time incubating) (Cameron 1990, Sherley 1993, 1994). Despite the greater parental duties for males, there was no detectable sex difference in annual survival (Sherley 1994, Khwaja et al. 2023). Helpers at the nest are usually adult males and can be occasional helpers or regular helpers (Sherley 1985, 1990).

Vocal Repertoire Description

Focal behavioral observations and sound recording

We observed and recorded vocalizations of wild Rifleman daily, including solitary individuals, pairs, and family groups, during the breeding season (September–February) from 2018 to 2021. Vocalizations were recorded during the day from approximately 08:00 to 18:00 h. Each observation lasted for 30 min or until we lost sight of the bird(s), whichever came first. The asynchronous breeding of Rifleman allowed us to record behaviors and vocalizations simultaneously for pre-breeding, breeding, and post-breeding stages. The breeding period of each pair from egg laying to fledging of nestlings lasted approximately 8 wks. All vocalizations recorded were naturally produced without using any playback to elicit a response. We recorded the vocalizations using Zoom H6 Handy Recorders (Zoom Corporation, Japan) and Sennheiser ME66/K6 directional microphones (Sennheiser, Germany) at a sample rate of 44,100 Hz and a bit-depth of 24-bit. Because Rifleman vocalizations are rapid, we also provided real-time dictation in each recording to identify focal individuals (either with band combinations or sex), and described the behaviors associated with vocalizations, as well as how many individuals were observed.

We followed pairs to locate their nests whenever possible, monitoring these nests daily to identify changes in breeding stage. Pairs provisioning nests are highly vigilant and easily disturbed by human observers. Thus, we recorded nest vocalizations using automated Bioacoustic Audio Recorders (BAR) fitted with

omnidirectional microphones (Frontier Lab, Australia). We scheduled the BARs to record from 1 h before sunrise to 1 h after sunset, every other day. The recording period of BARs spanned from when nests were found until when nestlings fledged. The sample rate of BAR recordings was 44,100 Hz and the bit-depth was 16-bit.

Vocal repertoire classification

We annotated the recordings and categorized the call types visually using spectrograms in Raven Pro version 1.6 (Center for Conservation Bioacoustics 2019). We only selected and filtered calls of known individuals with no overlapping calls from other individuals or species. We matched all vocalizations from the filtered recordings with behavioral and social contexts according to the “Handbook of Australian, New Zealand and Antarctic Birds” (HANZAB) wherever possible (Higgins et al. 2001). In this process, we also identified call types that were rarely or incompletely documented and provided new name classifications for them. We also documented Rifleman alarm calls in interspecific agonistic interactions using previous descriptions (Gray 1969, Sherley 1985, Higgins et al. 2001, Withers 2013). When Rifleman produced alarm calls in natural settings, we noted which predator or aggressor species were present. Here, we define predator species as species that hunt and feed on the Rifleman, such as Morepork (Ruru, *Ninox novaeseelandiae*, family: Strigidae) (Higgins et al. 2001) and Long-tailed Cuckoo (Koekoea, *Eudynamys taitensis*, family: Cuculidae) (Moran et al. 2019), and aggressor species as those that attack the Rifleman without preying upon them, such as New Zealand Bellbird (Korimako, *Anthornis melanura*, family: Meliphagidae) (Withers 2009) and Grey Warbler (Riroriro, *Gerygone igata*, family: Acanthizidae) (Loo et al. 2019).

Acoustic parameters

We conducted the following sound analyses using the R programming software version 4.0.4 (R Core Team 2021). We extracted acoustic features of each call using the “spectro_analysis” function in the “warbleR” package version 1.1.26 (Araya-Salas and Smith-Vidaurre 2017), which extracts 29 acoustic parameters (Append. 1). We used the same window length within a call type, but window length may differ between call types. To briefly summarize the acoustic features in tonal call types, we presented the frequency bandwidth (kHz), minimum and maximum frequencies (kHz), duration (sec), and peak frequency (kHz); and in broadband (noisy) call types, we presented the 90% bandwidth (kHz), first- and third-quartile frequencies (kHz), duration (sec), and peak frequency (kHz). For call types with more than one note per call bout (a phrase of notes), we also measured the call bout duration and the inter-note interval (sec). To represent the variation of all call types, the sample size used to produce these summary statistics was also reported in the results. These parameters provide an easy way to detect the calls on a spectrogram.

Context Variations in Acoustic Structure

Rifleman use some call types that are visually and acoustically similar in more than one context; in other words, they are multi-context calls. However, it is unclear whether these apparently similar calls are distinct call types. To determine whether these multi-context call types differ according to context, we compared (1) a call (zip) that is used both while foraging and feeding nestlings and (2) a call (purr) that is used both while feeding a mate

(solicitation or nuptial) and feeding nestlings. In order to identify the acoustic parameters that contribute most to the variation of these call types, we conducted a principal component analysis (PCA). We selected acoustic features with a squared cosine (\cos^2) value of more than 0.8 in the first two principal components. \cos^2 indicates the importance or quality of the variable represented in the PCA (Abdi and Williams 2010). Then, we tested context-dependent variation on these acoustic features using linear mixed-effects models (fixed effect: context, random effect: individual ID), using the “lmer” function in the “lmerTest” package version 3.1.3 (Kuznetsova et al. 2017). For the purr call only, individual IDs were not always known, thus, we tested the context differences between purr calls using t-tests for parametric variables and Wilcoxon rank test for non-parametric variables.

Sex Differences in Contact Calls

We tested for sex differences in acoustic parameters of contact calls using linear mixed-effects models (fixed effect: sex, random effect: individual ID). For this, we selected contact calls used in the same context only, i.e., chuck, pip, and zip contact calls used during foraging. We excluded nest feeding zip calls from this analysis as we found that the call structure differed according to context. We then conducted a PCA to identify the acoustic parameters that contribute most to the variation within these call types.

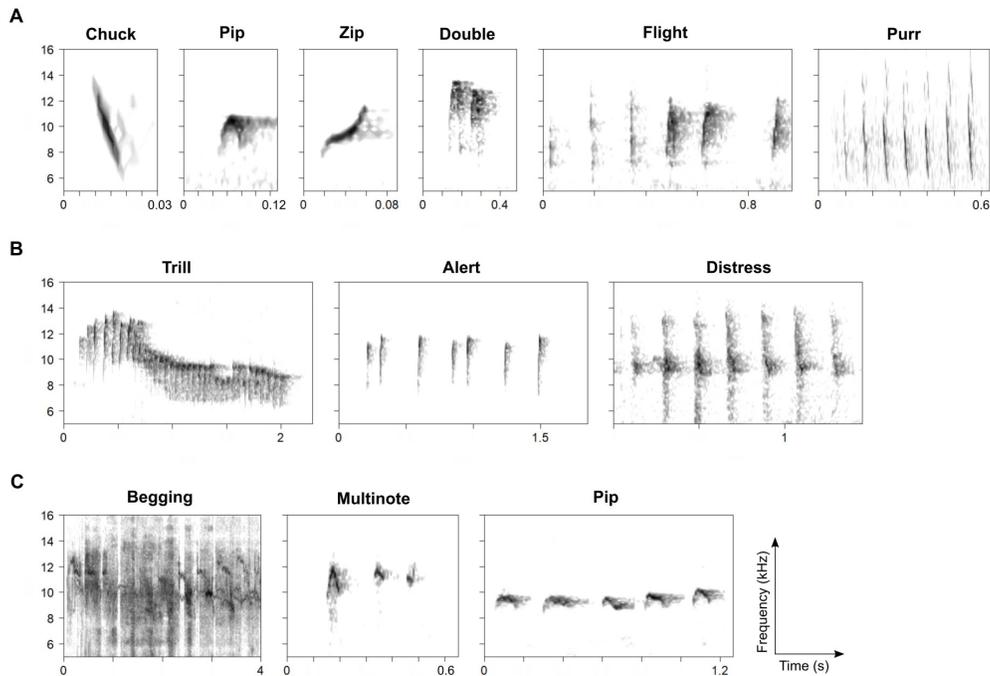
RESULTS

We identified nine call types in adults and three in juveniles that can be differentiated using behavioral context and spectrograms (Fig. 1). A total of 2,000 calls were included in the analyses. Rifleman had high-pitched calls that are produced in short bursts or pulses (Table 1). Overall, adult calls ranged from ca. 4 to ca. 13 kHz, and with each note being ca. 0.02 to ca. 0.1 sec. The lowest frequency call was the purr call, used as solicitation call at the nest. The highest frequency call was the context-generic zip call, used during foraging, flight, and nest visitation. The flight call, which is a combination of chuck, pip, and zip calls, had the broadest bandwidth in adult calls. Flight and trill calls had the longest phrase duration, and trill calls were produced with the fastest call rate.

Vocal Repertoire Description

We provided the name and context of each call type based on our observations of behavior and spectrographic visualizations, as well as previous call descriptions (Table 2). In addition, we also contributed novel spectrograms and names to multinote and purr calls. The multinote call was found only in juvenile rifleman, the purr calls were used by adults while feeding both offspring and partners. The behavioral contexts were divided into four main types based on observational data: (1) close contact interactions while foraging, (2) long-distance contact, (3) alarm toward predators, aggressors, and conspecific rivals, and (4) feeding and pair bond interactions (Table 3). Based on our results, Rifleman had four contact call types used for close-proximity communication (pip, zip, chuck, flight), one contact call used for long-distance communication (double call), three alarm calls (alert, trill, and distress), and two calls used for feeding and pair bond interactions (zip and purr). Juveniles have three call types (begging, pip, and multinote). Calls could either have single elements or multiple elements in a phrase. These phrases could also utilize elements from single calls in a combinatory way.

Fig. 1. Vocal repertoire of the Rifleman (*Acanthisitta chloris*): (A) adult calls used in contact, pair bond, and feeding contexts, (B) alarm calls (mainly produced by adults, except for distress call, which is also produced by juveniles), (C) juvenile calls. Each call type is represented by a spectrogram of a sample, generated using the “seewave” package version 2.1.6 (Sueur et al. 2008), with x axis showing time in seconds (s) and y axis showing frequency in kilohertz (kHz).



Interspecific agonistic interactions

We found three alarm call types: distress calls were produced when in imminent danger, alert calls were produced as a low intensity alarm call, and trill calls were produced as a high intensity alarm call (Table 3). Here, we focused on the alert and trill calls as we recorded more samples of these calls (Table 4). We only observed distress calls when birds, especially juveniles, were being chased by aggressors and predators. We also observed all three alarm calls being produced in intra-specific interactions, such as in a few agonistic chasing incidents at the edge of “territories,” but these vocalizations were rarely recorded.

Alert and trill calls were produced by both males and females in the presence of other species that are aggressors (those that may chase or physically attack them) or predators (those that prey upon the eggs, nestlings, fledglings, and adults) (Table 4). Rifleman produced short alert calls for flying aggressors and predators. Sustained alert calls were the most common alarm call produced in the presence of avian and mammalian aggressors and predators, and were more variable in frequency and call rate compared with trill calls. Trill calls were more or less fixed in shape and duration, albeit with minor variations, and were produced toward fewer species. Intriguingly, in the presence of New Zealand Tomtits (*Petroica macrocephala*, family: Petroicidae) and Shining Cuckoos (*Chrysococcyx lucidus*, family: Cuculidae), Rifleman produced only trill calls, without alert calls. In one case, a male New Zealand Tomtit was observed chasing a nest-provisioning

Rifleman and attempting to take the food from its beak. Rifleman also combined alert and trill calls in agonistic interactions with avian and mammalian aggressors and predators (Table 4).

Context Variations in Acoustic Structure

Foraging and nest feeding zip calls

The zip call was used in contact interactions between individuals while foraging and when arriving at the nest to feed nestlings or exchange incubation duties (Table 3). A total of 442 calls from 37 individuals were used to test for context variations in the zip call, with 222 foraging zips from 23 individuals and 220 nest feeding zips from 16 individuals. The first four principal components contributed to 74.7% of the variation. The PCA also revealed that first-quartile frequency, mean dominant frequency, mean frequency, median frequency, minimum frequency, third-quartile frequency, and minimum dominant frequency explained the bulk of the variation in zip calls (Append. 2). Testing for context differences in zips revealed that compared with foraging zips, nest feeding zips had significantly lower first-quartile frequency, mean dominant frequency, mean frequency, median frequency, minimum frequency, third-quartile frequency, and minimum dominant frequency (Append. 3).

Nuptial and nest feeding purr calls

The purr call was used in nuptial feeding, i.e., when the male provides supplementary food to the female during egg laying, and toward nestlings when feeding at the nest (Table 3). A total of 58 calls were used to test context variation in the purr call, with 22

Table 1. Mean and standard deviation (SD) acoustic parameters in the Rifleman vocal repertoire, with number of individuals (N), number of calls analyzed or sample size (n), and number of notes in the call type (n_c). Acoustic parameters of calls with more than one n_c are measured with the whole call phrase. J = juvenile calls; min. = minimum; max. = maximum; freq. = frequency; BW = bandwidth; dur. = duration; kHz = kilohertz; s = seconds.

Call type	N	n	n _c	Mean (± SD) acoustic parameters						
				Min. freq. (kHz)	Max. freq. (kHz)	Mean peak freq. (kHz)	Freq. BW (kHz)	Note dur. (s)	Phrase dur. (s)	Call rate (note/s)
Alert	9	48	varied	7.94 ± 0.88	12.19 ± 0.61	11.048 ± 0.58	4.25 ± 2.33	-	varied	6.30 ± 3.56
Begging (J) [†]	15 [‡]	139 [#]	varied	4.69 ± 1.18	16.45 ± 0.54	9.96 ± 1.039	11.77 ± 0.90	-	3.48 ± 0.43	2.92 ± 0.35
Chuck	21	137	1	6.12 ± 0.86	12.90 ± 1.34	9.15 ± 1.22	6.78 ± 1.52	0.017 ± 0.0080	-	-
Distress [†]	5 [§]	8	varied	9.17 ± 1.38	12.46 ± 1.35	9.99 ± 1.17	3.29 ± 1.68	-	varied	5.58 ± 1.10
Double	-	12	2	6.43 ± 0.88	12.95 ± 0.90	12.00 ± 1.046	6.52 ± 1.14	-	0.17 ± 0.17	-
Flight	16 [¶]	30	2 - 6	6.18 ± 0.73	13.57 ± 1.62	9.98 ± 1.48	7.39 ± 1.76	-	0.69 ± 0.28	6.79 ± 1.65
Multinote (J)	15 [¶]	437	2 - 5	8.57 ± 0.40	11.45 ± 0.72	10.37 ± 0.57	2.88 ± 0.75	-	0.37 ± 0.80	8.34 ± 0.81
Pip	20	81	1	7.72 ± 0.94	11.23 ± 0.97	10.46 ± 0.80	3.50 ± 1.40	0.033 ± 0.011	-	-
Pip (J)	15	554	1	8.71 ± 0.38	9.84 ± 0.40	9.46 ± 0.39	1.13 ± 0.36	0.097 ± 0.029	-	-
Purr [†]	12	58	varied	4.62 ± 0.62	9.26 ± 1.39	5.80 ± 0.96	4.63 ± 1.29	-	varied	13.93 ± 2.68
Trill	18	46	12.56 ± 6.74	6.64 ± 0.65	11.26 ± 0.87	9.96 ± 1.079	4.62 ± 0.91	-	0.66 ± 0.34	18.81 ± 3.034
Zip	37	442	1	7.23 ± 0.82	13.24 ± 0.98	9.49 ± 0.73	6.013 ± 1.29	0.036 ± 0.0090	-	-

[†] First- and third-quartile frequencies are reported instead of min. and max. frequencies. Inter-quartile range is reported instead of frequency bandwidth.

[‡] Fifteen nests.

[§] Five unknown individuals.

[¶] Nine unique individuals and seven unbanded individuals.

[¶] Fifteen fledgling groups.

[#] Ten notes per sample.

nuptial feeding purrs and 36 nest feeding purrs. The first four principal components contributed to 99.68% of the variation. The PCA revealed that maximum frequency, duration, frequency bandwidth, and number of notes in a bout explained the bulk of the variation in purr calls (Append. 4). Compared with the nest feeding purr, the nuptial feeding purr had significantly higher maximum frequency, longer duration, broader frequency bandwidth, and more notes in a bout (Append. 5).

Sex Differences in Adult Foraging Contact Calls

Sex differences in chuck calls

A total of 137 calls from 21 individuals (12 males, 9 females) were used to test sex differences in the chuck contact call. In general, there was considerable similarity between male and female chuck calls. The first four principal components contributed to 78.73% of the variation (Fig. 2a; Append. 6). There were no significant differences between male and female chuck calls in the top four variables influencing the variation, mean frequency, mean dominant frequency, median frequency, and third-quartile frequency (Append. 7).

Sex differences in pip calls

A total of 81 calls from 20 individuals (13 males, 7 females) were used to test sex differences in the pip contact call. There was considerable similarity between male and female pip calls. The first four principal components contributed to 81.86% of the variation (Fig. 2b; Append. 8). There were no significant differences between male and female pip calls in the top nine variables influencing the variation, maximum dominant frequency, maximum frequency, third-quartile frequency, median time, third-quartile time, mean dominant frequency, duration, time inter-quartile range, and mean peak frequency (Append. 9).

Sex differences in zip calls

A total of 222 calls from 23 individuals (15 males, 8 females) were used to test sex differences in the zip contact call. The first four principal components contributed to 73.68% of the variation. (Fig. 2c; Append. 10). Males have significantly higher first-quartile frequency, mean dominant frequency, and median frequency than females (Append. 11).

DISCUSSION

Functions of the Rifleman Vocal Repertoire

Together, these findings represent the most comprehensive documentation of the vocal repertoire of this species to date. In total, we described nine adult call types and three juvenile call types. Rifleman have a relatively simple vocal repertoire that is functionally complex, with some calls being used in a variety of contexts and being combined in phrases. Rifleman have high-pitched and short vocalizations that are prone to signal attenuation during transmission, especially in forested habitats (Padgham 2003). Thus, contact calls may be directed toward nearby individuals, such as partners, to maintain social cohesion when foraging (Withers 2013). The chuck, pip, and zip calls may be used in combination as a cost-effective and reliable way to convey more information than each signal type alone.

The functions of the two types of Rifleman alarm calls may reflect trade-offs between motivation and locatability (Montes-Medina et al. 2016). Similar alarm calls may have different functions depending on the signal design (Tegtman and Magrath 2020). Rifleman alarm calls have a combination of wide frequency bandwidth (broadband), high call rate, and short notes. However, alarm calls are typically narrowband and high-pitched to conceal the caller from the predator while prompting conspecifics to flee, whereas mobbing calls are typically broadband and low-pitched and are hostile toward predators while providing location cues of

Table 2. Rifleman call type catalog with descriptions and contextual information extracted from the literature. Due to varying onomatopoeic names used by different authors over time to describe Rifleman calls, we have chosen one name for each call type to be used consistently in this study and referenced the origin of the name accordingly. For call types without appropriate names or descriptions, new names have been proposed in this study.

Call type name	Description of call type from literature
Chuck (Withers 2013)	“Contact call” (Withers 2013)
Pip (Withers 2013)	“Contact call” (Withers 2013)
Zip (Withers 2013)	“Contact call” (Withers 2013); “single-note call, ssp, [...] when foraging together,” “cheep,” “Normally given by an adult to elicit juvenile begging” (Higgins et al. 2001); “Faint zee, when carrying food for young” (Guthrie-Smith 1914; “nest visitation call” (Withers 2013)
Double (Higgins et al. 2001)	“Uttered when pair become separated” (Sherley 1985); “punctuated call, two-syllable call tsitt, tsitt” (Sherley cited in Higgins et al. 2001); “two-note call” (Higgins et al. 2001)
Flight (Higgins et al. 2001)	“To advertise position” (Sherley 1985), “flight trill” (Sherley cited in Higgins et al. 2001); “Location Trill, a series of notes like those of Alarm Trill but spaced further apart without decrescendo” (Higgins et al. 2001)
Purr [†]	“Soft protracted chittering just before giving food to female” (Sherley 1985); “feeding call,” “solicitation chatter” (Withers 2013)
Submission [‡] (Sherley 1985)	“Uttered by female during copulation” (Sherley 1985); “submission call, monotonic sseep, sseep calls” (Higgins et al. 2001)
Alert (Withers 2013)	“Low intensity alarm call” (Sherley 1985); “staccato call” (Higgins et al. 2001); “aggressive chat,” “alert call” (Withers 2013)
Trill (Higgins et al. 2001)	“High intensity alarm call” (Sherley 1985); “scolding rattle str-r-r” (McLean 1912 cited in Higgins et al. 2001); “alarm trill, [...] decrescendo of extremely short notes run together” (Higgins et al. 2001); “alarm call” (Withers 2013)
Distress (Gray 1969)	“Alarm call, [...] loud squawks when handled” (Gray 1969)
Begging (Sherley 1985)	“Soft peeping sounds in first four days [...], older nestlings beg with call similar to Submission Call of adult (Sherley 1985); “in the first week after fledging, protracted single-note piping seeee, seeee” (Higgins et al. 2001)
Juvenile pip	“Young can give all adult calls before independence” (Higgins et al. 2001)
Multinote [†]	“Call similar to Location Trill of adults” (Higgins et al. 2001)

[†] New name of previously unnamed or undescribed calls.

[‡] The submission call was not analyzed in this study due to lack of sample size.

Table 3. The percentage of Rifleman call types used in different behavioral contexts observed and measured in this study. J = juvenile calls. Refer to Table 1 for sample sizes.

Call type	Behavioral contexts (%)						
	Contact interactions		Feeding interactions		Agonistic interactions		
	Short-distance	Long-distance	Adult-adult	Adult-young	Low intensity	High intensity	Conspecific chasing
Alert					100		?
Begging (J)			?	100			
Chuck	100						?
Distress						50	50
Double		100					
Flight	100						
Multinote (J)	100						
Pip	100						
Pip (J)	100						
Purr			37.9	62.1			
Trill						100	
Zip	50.2			49.8			

[†] “?” denote call types that are observed in the respective behavioral contexts, but sample sizes were not large enough for feature extraction and analyses. Thus, rows with “?” only indicate the presence of these calls in these contexts.

predators to conspecifics (Marler 1955, Morton 1977). Because Rifleman produce both alarm calls toward many different species (Table 4), the choice of alarm calls used may depend on whether the intruder species is an aggressor or a predator (Loo et al. 2019, Moran et al. 2019). However, this requires further research on the relationship between threat level and calling intensity (Templeton et al. 2005, Randler 2013).

The function(s) of the Rifleman double call is currently unknown, but its apparently higher amplitude, based on anecdotal field observations, may allow long-range communication and vocal recognition of individuals (Higgins et al. 2001, Withers 2013). Despite having higher frequencies than other call types in this species, which may attenuate over long distances, the Rifleman double call may be attenuation resistant, similar to the male Zebra Finch (*Taeniopygia guttata*) long-distance calls (Mouterde et al. 2014), Amazonian manatee (*Trichechus inunguis*) isolation calls (Sousa-Lima et al. 2002), and Great Tit (*Parus major*) songs (McGregor et al. 1983).

Context Variation in Acoustic Structure

Context-dependant variation in calls may be influenced by functional context, identity, breeding stage, and age (Manley 2012, Lea et al. 2020). We detected spectral structural variations that are context dependent in some Rifleman calls (e.g., nest vs. foraging zip calls, and nestling feeding vs. nuptial purr calls). Studies have shown that calls directed toward offspring are higher in frequency because they attenuate faster and thus lower the chance of revealing the nest location to potential eavesdroppers (Marler 1955). However, our results showed that the nest-associated calls of the Rifleman are lower in frequency than foraging calls. The explanation for this phenomenon remains to be tested. Khwaja et al. (2019) suggested that there may be information encoded in the Rifleman zip call that is useful in both foraging contact calls and food-offering contexts, such as the identity of the signaller. Future studies should focus on why the purr call differs between nest and nuptial feeding contexts.

Table 4. The use of alarm call types produced by Rifleman (denoted with an “X”) toward avian and mammalian aggressors and predators observed in natural conditions in this study. A_f = short alert calls for flying predators; A_s = sustained alert calls; T = trills only; AT = Combination of alert and trill calls.

Scientific name	Te reo Māori name ¹	English name	Interaction type ²	Rifleman alarm calls			
				A _f	A _s	T	AT
<i>Nestor meridionalis</i>	Kākā	-	U	X			
<i>Ninox novaeseelandiae</i>	Ruru	Morepork	P	X	X		X
<i>Falco novaeseelandiae</i>	Karearea	New Zealand Falcon	P	X			X
<i>Prothemadera novaeseelandiae</i>	Tūi	-	A	X	X		
<i>Cracticus tibicen</i>	-	Australasian Magpie	A		X		
<i>Mohoua albigilla</i>	Pōpokatea	Whitehead	A		X		
<i>Anthornis melanura</i>	Korimako	New Zealand Bellbird	A	X			X
<i>Petroica macrocephala</i>	Miromiro	New Zealand Tomtit	A				X
<i>Gerygone igata</i>	Riroriro	Grey Warbler	A		X		X
<i>Petroica australis</i>	Toutouwai	New Zealand Robin	A	X	X		X
<i>Todiramphus sanctus</i>	Kotare	Sacred Kingfisher	U		X		
<i>Eudynamis taitensis</i>	Koekoeko	Long-tailed Cuckoo	P		X		
<i>Chrysococcyx lucidus</i>	Pipiharauroa	Shining Cuckoo	A				X
<i>Callaeas wilsoni</i>	North Island Kōkako	-	U		X		
<i>Mustela erminea</i>	-	Stoat	P		X		
<i>Mustela nivalis vulgaris</i>	-	Weasel	P		X		X
<i>Rattus</i> spp.	-	Rat	P		X		X
<i>Trichosurus vulpecula</i>	-	Common brushtail possum	P		X		

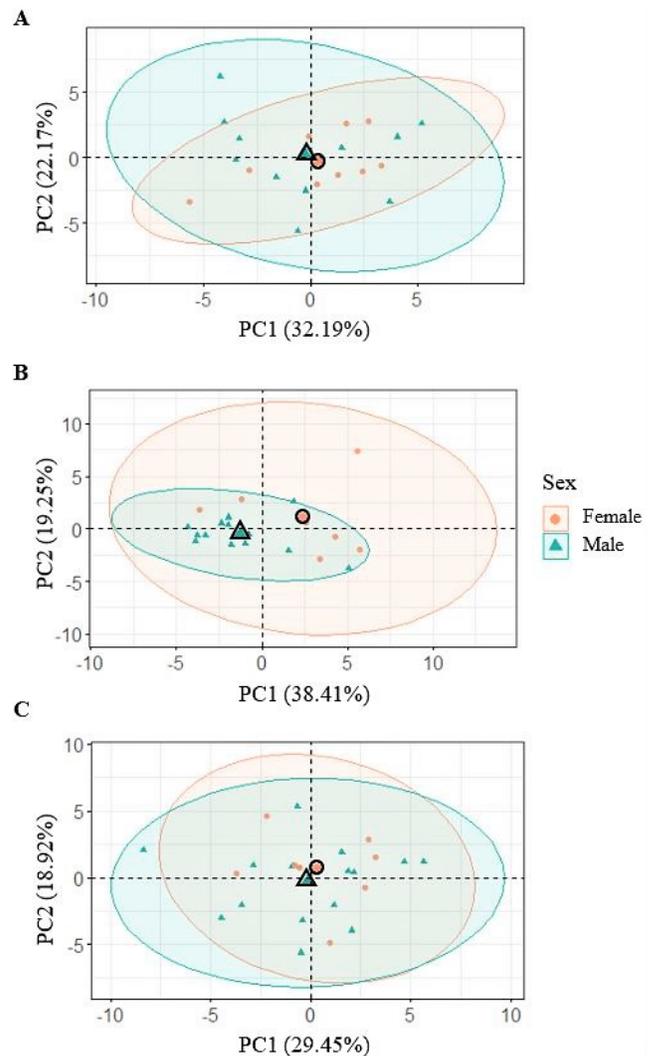
¹ There may be regional variations in te reo Māori species names (Wehi et al. 2019).
² A: aggressors; P: predators; U: unknown.

Based on these spectral acoustic variations, we suggest that apparently similar call types used in different contexts may in fact represent cryptic call types that are modified for different functions (Platzen 2004, Magrath et al. 2007, Götze et al. 2020). Spotted Crane (*Porzana porzana*) also use their small call repertoire in diverse behavioral contexts, such as territory defence and individual recognition (Rek 2015). Furthermore, flexible signals may be an evolutionarily stable strategy due to the need to navigate changing resources and social environments (Seyfarth and Cheney 2017, Smith 2017), and this is especially relevant for cooperative breeding species, such as the Rifleman (Sherley 1994, Preston et al. 2016, Yambem et al. 2020). Thus, we suggest that classification of call types would benefit from studying spectral variation in animal signals that are used in different behavioral contexts (Faure and Barclay 1994, Bermejo and Omedes 1999, Wong et al. 1999, Schwartz et al. 2007).

Sex differences in Adult Contact Calls

Sex differences in calls can indicate sex roles and functions of call types (Gahr 2007). However, whereas functional sex differences in songs are found in a wide array of songbird species, the hypotheses on the mechanisms of sex differences in calls are inconclusive and require further research (Arnold 1997, Riebel 2016, Webb et al. 2021, but see Amy et al. 2018). In adult Rifleman, the level of sex-specific acoustic variation in contact calls depended on the call type—we detected sex differences in zip calls but not in chuck and pip calls. The strong similarity in the spectral acoustic structures of male and female Rifleman calls, despite the

Fig. 2. Principal component analysis of male and female (A) chuck, (B) pip, and (C) zip contact calls. Principal components 1 (PC1) and 2 (PC2) and their percentage contributions to the variance in the data are represented in the x and y axes, respectively. Solid circle symbols represent individual means of the female calls, and triangle symbols represent individual means of the male calls. Larger symbols represent the mean of each sex category. Ellipses encompass 95% of the group samples.



significant size dimorphism, might indicate that the calls are not sex specific and serve similar functions. This similarity may also be due to their monogamous and cooperative breeding strategy with mainly close-range communication required (Gray 1969, Sherley 1994, Withers 2020). In contrast, the detectable sex difference in the zip call may provide some insight into its function. Previous researchers working on the same and a different population of Rifleman have speculated that this call is important as an individual signature (Khawaja et al. 2019, Moran 2021). If so, conveying sex might be an important part of that call’s

function. To test this hypothesis, future studies could use vocal playback techniques to determine whether Rifleman have sex-specific responses to male/female calls. However, little is known about the structure and size of syrinxes in this species, and it possible that the syrinx size is not different between sexes despite substantial differences in body size.

Implications and Future Directions

The vocal repertoire of the Rifleman provided in this paper serves as a basis for future research to explore its vocal behavior and communication system. In addition, an increased understanding of vocal variation and alarm call behaviors may also be helpful in conservation biology, where predation is a crucial driver of population decline (Lewis et al. 2021). This comprehensive vocal repertoire description of a passerine, from a suborder that diverged from all other passerines before the oscines/suboscine split, allows us to explore variation and evolution of avian vocal behaviors and development, including the evolution of vocal learning in the avian phylogeny. Analyzing the context- and sex-dependent variation of calls can also inform our understanding of the communicative function(s) of call types and provide comparisons across species. Furthermore, the observed variability in some call types suggests that some calls may be learned or influenced by social and developmental factors, and thus warrants more in-depth analyses (Lotem and Biran-Yoeli 2014). Our research identifies several additional questions worthy of study. For example, could the lack of sex differences in some contact calls in this species, despite their size dimorphism, be attributed to shared responsibility in territory defence? Why do birds need more than one type of contact call? Why are some call types used in contact interactions, but not in other contexts? Why are there sex differences in some calls but not others (Morton 1975, Robinson et al. 2019)? The relationship between vocal diversity and context specificity of vocalizations provides fertile ground for expanding our understanding of the depth of animal communication. Similar research in other species is needed for global comparisons in the evolution of calls and songs.

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Data Availability:

Data/code available on request because of privacy/ethical restrictions. The data/code that support the findings of this study are available on request from the corresponding author, YYL. None of the data/code are publicly available because of indigenous

people's data sovereignty, e.g., recordings of sacred species. Animal ethics approval for this research study was granted by University of Auckland Animal Ethics Committee (approval number: 001866).

LITERATURE CITED

- Abdi, H., and L. J. Williams. 2010. Principal component analysis. Wiley Interdisciplinary Reviews: Computational Statistics 2 (4):433-459. <https://doi.org/10.1002/wics.101>
- Amy, M., P. Salvin, and G. Leboucher. 2018. Chapter Six. The functions of female calls in birds. *Advances in the Study of Behavior* 50:243-271. <https://doi.org/10.1111/2041-210X.12624>
- Arnold, A. P. 1997. Sexual differentiation of the Zebra Finch song system: positive evidence, negative evidence, null hypotheses, and a paradigm shift. *Journal of Neurobiology* 33(5):572-584. <https://doi.org/10.1159/000021717>
- Berryman, A. 2007. Song sharing and repertoire change as indicators of social structure in the Noisy Scrub-bird. Dissertation. Murdoch University, Murdoch, Australia. <https://doi.org/10.1017/CBO9780511754791>
- Center for Conservation Bioacoustics. 2019. Raven Pro: interactive sound analysis software. <http://ravensoundsoftware.com>
- Clay, Z., C. L. Smith, and D. T. Blumstein. 2012. Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour* 83(2):323-330. <https://doi.org/10.1016/j.anbehav.2011.12.008>
- Crouch, N. M. A., and R. J. Mason-Gamer. 2019. Identifying ecological drivers of interspecific variation in song complexity in songbirds (Passeriformes, Passeri). *Journal of Avian Biology* 50 (3):1-14. <https://doi.org/10.1111/jav.02020>
- Dooling, R. J. 2004. Chapter 7. Audition: can birds hear everything they sing? Pages 206-225 in P. Marler and H. Slabbekoorn, editors. *Nature's music: the science of birdsong*. Academic Press, Cambridge, Massachusetts, USA. <https://doi.org/10.1121/1.1494447>
- Elie, J. E., and F. E. Theunissen. 2016. The vocal repertoire of the domesticated Zebra Finch: a data-driven approach to decipher the information-bearing acoustic features of communication signals. *Animal Cognition* 19(2):285-315. <https://doi.org/10.1007/s10071-015-0933-6>
- Ericson, P. G. P., L. Christidis, A. Cooper, M. Irestedt, J. Jackson, U. S. Johansson, and J. A. Norman. 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceedings of the Royal Society of London B* 269:235-241. <https://doi.org/10.1098/rspb.2001.1877>
- Faure, P. A., and R. M. R. Barclay. 1994. Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. *Journal of Comparative Physiology A* 174:651-660. <https://doi.org/10.1007/BF00217386>
- Fischer, J., P. Wadewitz, and K. Hammerschmidt. 2017. Structural variability and communicative complexity in acoustic communication. *Animal Behaviour* 134:229-237. <https://doi.org/10.1016/j.anbehav.2016.06.012>

- Gahr, M. 2007. Sexual differentiation of the vocal control system of birds. *Advances in Genetics* 59:67-105. [https://doi.org/10.1016/S0065-2660\(07\)59003-6](https://doi.org/10.1016/S0065-2660(07)59003-6)
- Garcia, M., and L. Favaro 2017. Animal vocal communication: function, structures, and production mechanisms. *Current Zoology* 63(4):417-419. <https://doi.org/10.1093/cz/zox040>
- Gémard, C., V. Planas-Bielsa, F. Bonadonna, and T. Aubin. 2021. Contextual variations in calls of two nonoscine birds: the Blue Petrel *Halobaena caerulea* and the Antarctic Prion *Pachyptila desolata*. *Behavioral Ecology* 32(4):1-11. <https://doi.org/10.1093/beheco/arab020>
- Götze, S., A. Denzinger, and H. U. Schnitzler. 2020. High frequency social calls indicate food source defense in foraging common pipistrelle bats. *Scientific Reports* 10(1):1-9. <https://doi.org/10.1038/s41598-020-62743-z>
- Gray, R. S. 1969. Breeding biology of Rifleman at Dunedin. *Notornis* 16:5-22.
- Guthrie-Smith, H. 1914. Mutton birds and other birds. Whitcome and Tombs Ltd., Christchurch, New Zealand.
- Hall, M. L., S. A. Kingma, and A. Peters. 2013. Male songbird indicates body size with low-pitched advertising songs. *PLoS ONE* 8(2):1-5. <https://doi.org/10.1371/journal.pone.0056717>
- Higgins, P. J., J. M. Peter, and W. K. Steele. 2001. *Acanthisitta chloris*, Rifleman. Pages 51-55, 58-76 in P. J. Higgins, J. M. Peter, and W. K. Steele, editors. *Handbook of Australian, New Zealand and Antarctic Birds*. Volume. 5. Oxford University Press, Melbourne, Australia.
- Hoeschele, M., and W. T. Fitch. 2016. Phonological perception by birds: Budgerigars can perceive lexical stress. *Animal Cognition* 19(3):643-654. <https://doi.org/10.1007/s10071-016-0968-3>
- Hunt, G. R., and I. G. McLean. 1993. The ecomorphology of sexual dimorphism in the New Zealand Rifleman *Acanthisitta chloris*. *Emu* 93(2):71-78. <https://doi.org/10.1071/MU9930071>
- Janik, V. M., and P. J. B. Slater. 2000. The different roles of social learning in vocal communication. *Animal Behaviour* 60(1):1-11. <https://doi.org/10.1006/anbe.2000.1410>
- Jarvis, E. D., C. Ye, S. Liang, Z. Yan, M. L. Zepeda, P. F. Campos, A. Missael, V. Velazquez, J. A. Samaniego, M. Avila-arcos, et al. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346(6215):1126-1138. <https://doi.org/10.1126/science.1253451>
- Khwaja, N., J. V. Briskie, and B. J. Hatchwell. 2019. Individuality, kin similarity and experimental playback of contact calls in cooperatively breeding Riflemen. *New Zealand Journal of Zoology* 46(4):334-347. <https://doi.org/10.1080/03014223.2019.1587477>
- Khwaja, N., S. A. J. Preston, B. J. Hatchwell, and J. V. Briskie. 2023. Recruitment, survival and breeding success in a declining Rifleman population. *New Zealand Journal of Ecology* 47(1):3507. <https://doi.org/10.20417/nzjecol.47.3507>
- Kondo, N., and S. Watanabe. 2009. Contact calls: information and social function. *Japanese Psychological Research* 51(3):197-208. <https://doi.org/10.1111/j.1468-5884.2009.00399.x>
- Krams, I., T. Krama, T. M. Freeberg, C. Kullberg, and J. R. Lucas. 2012. Linking social complexity and vocal complexity: a parid perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1597):1879-1891. <https://doi.org/10.1098/rstb.2011.0222>
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82(13):1-26. <https://doi.org/10.3758/s13420-020-00421-w>
- Lewis, R. N., L. J. Williams, and R. T. Gilman. 2021. The uses and implications of avian vocalizations for conservation planning. *Conservation Biology* 35(1):50-63. <https://doi.org/10.1111/cobi.13465>
- Lipkind, D., A. T. Zai, A. Hanuschkin, G. F. Marcus, O. Tchernichovski, and R. H. R. Hahnloser. 2017. Songbirds work around computational complexity by learning song vocabulary independently of sequence. *Nature Communications* 8(1). <https://doi.org/10.1038/s41467-017-01436-0>
- Lohr, B., and R. J. Dooling. 1999. Detection of changes in timbre and harmonicity in complex sounds by Zebra Finches (*Taeniopygia guttata*) and Budgerigars (*Melopsittacus undulatus*). *Journal of Comparative Psychology* 112(1):36-47. <https://doi.org/10.1037/0735-7036.112.1.36>
- Loo, Y. Y., and K. E. Cain. 2021. A call to expand avian vocal development research. *Frontiers in Ecology and Evolution* 9(757972):1-8. <https://doi.org/10.3389/fevo.2021.757972>
- Loo, Y. Y., I. G. Moran, and K. E. Cain. 2019. Grey Warbler (*Gerygone igata*) aggressive behaviour towards Rifleman (*Acanthisitta chloris*) fledglings. *Notornis* 66(3):174-177.
- Lotem, A., and I. Biran-Yoeli. 2014. Evolution of learning and levels of selection: a lesson from avian parent-offspring communication. *Theoretical Population Biology* 91:58-74. <https://doi.org/10.1016/j.tpb.2013.10.003>
- Magrath, R. D., B. Pitcher, and A. H. Dalziell. 2007. How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator. *Animal Behaviour* 74:1117-1129. <https://doi.org/10.1016/j.anbehav.2007.01.025>
- Manley, G. A. 2012. Vertebrate hearing: origin, evolution and functions. Pages 23-40 in F. G. Barth, P. Giampieri-Duetsch, and H.-D. Klein, editors. *Sensory perception: mind and matter*. Springer, Vienna, Austria and New York, New York, USA. https://doi.org/10.1007/978-3-211-99751-2_2
- Marler, P. 1955. Characteristics of some animal calls. *Nature* 176:6-8. <https://doi.org/10.1038/176006a0>
- Marler, P. 2004a. Bird calls: a cornucopia for communication. Pages 132-177 in P. Marler and H. Slabekoor, editors. *Nature's music: the science of birdsong*. Elsevier, Academic Press, New York, New York, USA. <https://doi.org/10.1016/B978-012473070-0/50008-6>
- Marler, P. 2004b. Science and birdsong: the good old days. Pages 1-38 in P. Marler and H. Slabekoor, editors. *Nature's music: the science of birdsong*. Elsevier, Academic Press, New York, New York, USA. <https://doi.org/10.1016/B978-012473070-0/50004-9>

- Marler, P., and C. Evans. 1996. Bird calls: just emotional displays or something more? *Ibis* 138(1):26-33. <https://doi.org/10.1111/j.1474-919x.1996.tb04310.x>
- McGregor, P. K., J. R. Krebs, and L. M. Ratcliffe. 1983. The reaction of Great Tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk* 100(4):898-906. <https://doi.org/10.1093/auk/100.4.898>
- Montes-Medina, A. C., A. Salinas-Melgoza, and K. Renton. 2016. Contextual flexibility in the vocal repertoire of an Amazon Parrot. *Frontiers in Zoology* 13(1):1-13. <https://doi.org/10.1186/s12983-016-0169-6>
- Moran, I. G. 2021. The evolutionary roots of vocal learning: exploring vocal learning abilities in assumed vocal non-learners in birds. Dissertation, University of Auckland. Auckland, New Zealand.
- Moran, I. G., Y. Y. Loo, and K. E. Cain. 2019. Long-tailed Cuckoo (*Eudynamis taitensis*) predation on Rifleman (*Acanthisitta chloris*) nestlings. *Notornis* 66(2):103-107.
- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *The American Naturalist* 109(965):17-34. <https://doi.org/10.1086/282971>
- Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist* 111(981):855-869. <https://doi.org/10.1086/283219>
- Mouterde, S. C., F. E. Theunissen, J. W. Elie, C. Vignal, and N. Mathevon. 2014. Acoustic communication and sound degradation: how do the individual signatures of male and female Zebra Finch calls transmit over distance? *PLoS ONE* 9(7). <https://doi.org/10.1371/journal.pone.0102842>
- Nieder, A., and R. Mooney. 2020. The neurobiology of innate, volitional and learned vocalizations in mammals and birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375(1789). <https://doi.org/10.1098/rstb.2019.0054>
- Padgham, M. 2003. Reverberation and frequency attenuation in forests—implications for acoustic communication in animals. *Journal of the Acoustical Society of America* 115(1):402-410. <https://doi.org/10.1121/1.1629304>
- Petrusková, T., I. Pišvejcová, A. Kinštová, T. Brinke, and A. Petrusek. 2016. Repertoire-based individual acoustic monitoring of a migratory passerine bird with complex song as an efficient tool for tracking territorial dynamics and annual return rates. *Methods in Ecology and Evolution* 7(3):274-284. <https://doi.org/10.1111/2041-210X.12496>
- Platzen, D. 2004. Parent-nestling vocal interactions in the White-browed Scrubwren. Dissertation. Australian National University, Canberra, Australia.
- Preston, S. A. J., J. V. Briskie, and B. J. Hatchwell. 2016. Adult helpers increase the recruitment of closely related offspring in the cooperatively breeding Rifleman. *Behavioral Ecology* 27(6):1617-1626. <https://doi.org/10.1093/beheco/aru087>
- Preston, S. A. J., D. A. Dawson, G. J. Horsburgh, and B. J. Hatchwell. 2013. Characterisation of microsatellite loci in the Rifleman (*Acanthisitta chloris*, Acanthisittidae, AVES) and their predicted genome locations. *Conservation Genetics Resources* 5(2):555-560. <https://doi.org/10.1007/s12686-012-9851-y>
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org>
- Randler, C. 2013. Alarm calls of the Cyprus Wheatear *Oenanthe cypriaca*—one for nest defence, one for parent–offspring communication? *Acta Ethologica* 16:91-96. <https://doi.org/10.1007/s10211-012-0141-1>
- Ręk, P. 2015. High functional complexity despite an extremely small repertoire of calls in the Spotted Crake (*Porzana porzana*). *Auk* 132(3):613-623. <https://doi.org/10.1642/AUK-14-267.1>
- Riebel, K. 2016. Understanding sex differences in form and function of bird song: the importance of studying song learning processes. *Frontiers in Ecology and Evolution* 4:62. <https://doi.org/10.3389/fevo.2016.00062>
- Robertson, C. J. R., P. Hyvönen, M. J. Fraser, and C. R. Pickard. 2007. Atlas of bird distribution in New Zealand 1999–2004. WEBATLAS, Ornithological Society of New Zealand Inc. https://nzbirdsonline.org.nz/sites/all/files/Maps_for_website_6MAR09_237.pdf
- Robinson, C. M., K. T. Snyder, and N. Creanza. 2019. Correlated evolution between repertoire size and song plasticity predicts that sexual selection on song promotes open-ended learning. *eLife* 8:1-26. <https://doi.org/10.7554/eLife.44454>
- Schwartz, C., J. Tressler, H. Keller, M. Vanzant, S. Ezell, and M. Smotherman. 2007. The tiny difference between foraging and communication buzzes uttered by the Mexican free-tailed bat, *Tadarida brasiliensis*. *Journal of Comparative Physiology A* 193:853-863. <https://doi.org/10.1007/s00359-007-0237-7>
- Sewall, K. B. 2009. Limited adult vocal learning maintains call dialects but permits pair-distinctive calls in Red Crossbills. *Animal Behaviour* 77(5):1303-1311. <http://dx.doi.org/10.1016/j.anbehav.2009.01.033>
- Sewall, K. B. 2011. Early learning of discrete call variants in red crossbills: implications for reliable signaling. *Behavioral Ecology and Sociobiology* 65(2):157-166. <https://doi.org/10.1007/s00265-010-1022-0>
- Seyfarth, R. M., and D. L. Cheney. 2017. The origin of meaning in animal signals. *Animal Behaviour* 124:339-346. <https://dx.doi.org/10.1016/j.anbehav.2016.05.020>
- Sharp, S. P., and B. J. Hatchwell. 2005. Individuality in the contact calls of cooperatively breeding Long-tailed Tits (*Aegithalos caudatus*). *Behaviour* 142(11/12):1559-1575. <https://doi.org/10.1163/156853905774831918>
- Sherley, G. H. 1985. The breeding system of the South Island Rifleman (*Acanthisitta chloris*) at Kowhai Bush, Kaikoura, New Zealand. Dissertation, University of Canterbury, Christchurch, New Zealand.
- Sherley, G. H. 1990. Co-operative breeding in Riflemen (*Acanthisitta chloris*) benefits to parents, offspring and helpers. *Behaviour* 112(1/2):1-22. <https://doi.org/10.1163/156853990X00653>

- Sherley, G. H. 1993. Parental investment, size sexual dimorphism, and sex ratio in the Rifleman (*Acanthisitta chloris*). New Zealand Journal of Zoology 20(3):211-217. <https://doi.org/10.1080/0301-4223.1993.10422862>
- Sherley, G. H. 1994. Cooperative parental care; contribution of the male Rifleman (*Acanthisitta chloris*) to the breeding effort. Notornis 41:71-81. http://notornis.osnz.org.nz/system/files/Notornis_41_1_71.pdf
- Simpson, H. B., and D. S. Vicario. 1990. Brain pathways for learned and unlearned vocalizations differ in Zebra Finches. Journal of Neuroscience 10(5):1541-1556. <https://doi.org/10.1523/jneurosci.10-05-01541.1990>
- Smith, C. L. 2017. Referential signalling in birds: the past, present and future. Animal Behaviour. 124:315-323. <http://dx.doi.org/10.1016/j.anbehav.2016.08.015>
- Soma, M., and L. Z. Garamszegi. 2011. Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. Behavioral Ecology 22(2):363-371. <https://doi.org/10.1093/beheco/arq219>
- Sousa-Lima, R. S., A. P. Paglia, and G. A. B. da Fonseca. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). Animal Behaviour 63(2):301-310. <https://doi.org/10.1006/anbe.2001.1873>
- Suh, A., M. Paus, M. Kiefmann, G. Churakov, F. A. Franke, J. Brosius, J. O. Kriegs, and J. Schmitz. 2011. Mesozoic retroposons reveal parrots as the closest living relatives of passerine birds. Nature Communications 2(443). <https://doi.org/10.1038/ncomms1448>
- Suzuki, T. N. 2011. Parental alarm calls warn nestlings about different predatory threats. Current Biology 21(1):R15-R16. <https://doi.org/10.1016/j.cub.2010.11.027>
- Suzuki, T. N. 2016. Semantic communication in birds: evidence from field research over the past two decades. Ecological Research 31(3):307-319. <https://doi.org/10.1007/s11284-016-1339-x>
- Tegtman, N. T., and R. D. Magrath. 2020. Discriminating between similar alarm calls of contrasting function. Philosophical Transactions of the Royal Society of London B: Biological Sciences 375(1802):20190474. <https://doi.org/10.1098/rstb.2019.0474>
- Templeton, C. N., E. Greene, and K. Davis. 2005. Allometry of alarm calls: Black-capped Chickadees encode information about predator size. Science 5730:1934-1937. <https://doi.org/10.1126/science.1108841>
- Veit, L., L. Y. Tian, C. J. M. Hernandez, and M. S. Brainard. 2021. Songbirds can learn flexible contextual control over syllable sequencing. eLife 10:e61610. <https://doi.org/10.7554/eLife.61610>
- Vella, K., D. Johnson, and P. Roe. 2021. Describing the sounds of nature: using onomatopoeia to classify bird calls for citizen science. PLoS ONE 16(5):e0250363. <https://doi.org/10.1371/journal.pone.0250363>
- Vicario, D. S. 2004. Using learned calls to study sensory-motor integration in songbirds. Annals of the New York Academy of Sciences 1016:246-62. <https://doi.org/10.1196/annals.1298.040>
- Vicario, D. S., J. N. Raksin, N. H. Naqvi, N. Thande, and H. B. Simpson. 2002. The relationship between perception and production in songbird vocal imitation: what learned calls can teach us. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 188(11-12):897-908. <https://doi.org/10.1007/s00359-002-0354-2>
- Walløe, S., H. Thomsen, T. J. Balsby, and T. Dabelsteen. 2015. Differences in short-term vocal learning in parrots, a comparative study. Behaviour 152(11):1433-1461. <https://doi.org/10.1163/15-68539X-00003286>
- Webb, W. H., M. M. Roper, M. D. Pawley, Y. Fukuzawa, and D. H. Brunton. 2021. Sexually distinct song cultures in a songbird metapopulation. Frontiers in Ecology and Evolution 9:755633. <https://doi.org/10.3389/fevo.2021.755633>
- Wehi, P. M., L. Carter, T. W. Harawira, G. Fitzgerald, K. Lloyd, H. Whaanga, and C. J. Macleod. 2019. Enhancing awareness and adoption of cultural values through use of Maori bird names in science communication and environmental reporting. New Zealand Journal of Ecology 43(3):1-9. <https://doi.org/10.20417/nzjecol.43.35>
- Winkler, H. 2001. The ecology of avian acoustical signals. Pages 79-104 in F. G. Barth and A. Schmid, editors. Ecology of sensing. Springer, Berlin, Heidelberg, Germany. https://doi.org/10.1007/978-3-662-22644-5_5
- Wirthlin, M., E. F. Chang, M. Knörnschild, L. A. Krubitzer, C. V. Mello, C. T. Miller, A. R. Pfenning, S. C. Vernes, O. Tchernichovski, and M. M. Yartsev. 2019. A modular approach to vocal learning: disentangling the diversity of a complex behavioral trait. Neuron 104(1):87-99. <https://doi.org/10.1016/j.neuron.2019.09.036>
- Withers, S. J. 2009. Observations of Bellbird (*Anthornis melanura*) aggression toward North Island Rifleman (*Acanthisitta chloris granti*) in a translocated population. Notornis 56(1):44-45.
- Withers, S. J. 2013. Population variation of the North Island Rifleman (*Acanthisitta chloris granti*): implications for conservation management. Dissertation, University of Auckland, Auckland, New Zealand. <https://researchspace.auckland.ac.nz/handle/2292/20613>
- Withers, S. J. 2020. Rifleman. New Zealand Birds Online. <http://nzbirdsonline.org.nz/species/rifleman>
- Withers, S. J., S. Parsons, M. E. Hauber, A. Kendrick, and S. D. Lavery. 2021. Genetic divergence between isolated populations of the North Island New Zealand Rifleman (*Acanthisitta chloris granti*) implicates ancient biogeographic impacts rather than recent habitat fragmentation. Ecology and Evolution 11(11):5998-6014. <https://doi.org/10.1002/ece3.7358>
- Wong, J., P. D. Stewart, and D. W. Macdonald. 1999. Vocal repertoire in the European badger (*Meles meles*): structure, context, and function. Journal of Mammalogy 80(2):570-588. <https://doi.org/10.2307/1383302>
- Wright, J., and M. L. Leonard. 2002. The evolution of nestling begging: competition, cooperation and communication. Kluwer Academic Press, Dordrecht, The Netherlands. <https://doi.org/10.1007/0-306-47660-6>

Yambem, S. D., S. Choroi, and M. Jain. 2020. Structural and functional complexity of vocalizations in a cooperatively breeding passerine. bioRxiv, preprint. <https://doi.org/10.1101/2020.04.23.056879>

Appendix 1

Table A1. Acoustic parameters as defined in warbleR package version 1.1.26 (Araya-Salas & Smith-Vidaurre, 2017).

Acoustic parameter (unit)	Definitions
bottom.freq (kHz)	Bottom frequency limit of selection.
duration (s)	Length of signal.
entropy	Spectrographic entropy. Product of time and spectral entropy sp.ent * time.ent.
freq.IQR (kHz)	Interquartile frequency range. Frequency range between 'freq.Q25' and 'freq.Q75'.
freq.median (kHz)	Median frequency. The frequency at which the signal is divided in two frequency intervals of equal energy.
freq.Q25 (kHz)	First quartile frequency. The frequency at which the signal is divided in two frequency intervals of 25% and 75% energy respectively.
freq.Q75 (kHz)	Third quartile frequency. The frequency at which the signal is divided in two frequency intervals of 75% and 25% energy respectively.
kurt	Kurtosis. Peakedness of the spectrum.
meandom	Average of dominant frequency measured across the acoustic signal.
meanfreq (kHz)	Mean frequency. Mean of frequency spectrum (i.e. weighted average of frequency by amplitude within supplied band pass).
mindom	Minimum of dominant frequency measured across the acoustic signal.
sd (kHz)	Standard deviation of frequency.
sfm	Spectral flatness. Similar to sp.ent Pure tone ~ 0; noisy ~ 1.
skew	skewness. Asymmetry of the spectrum.
sp.ent	Spectral entropy. Energy distribution of the frequency spectrum. Pure tone ~ 0; noisy ~ 1.
time.ent	Time entropy. Energy distribution on the time envelope. Pure tone ~ 0; noisy ~ 1.
time.IQR (s)	Interquartile time range. Time range between 'time.Q25' and 'time.Q75'.
time.median (s)	Median time. The time at which the signal is divided in two time intervals of equal energy.
time.Q25 (s)	First quartile time. The time at which the signal is divided in two time intervals of 25% and 75% energy, respectively.
time.Q75 (s)	Third quartile time. The time at which the signal is divided in two time intervals of 75% and 25% energy, respectively.
top.freq (kHz)	Top frequency limit of selection.

Appendix 2

Table A2. Principal component analysis results illustrating the contribution of acoustic features in the first four principal components to the context variation of zip calls, sorted in decreasing order according to the total squared cosine (\cos^2) score of the first two principal components (values more than 0.8 in bold).

Acoustic features	Loadings				Cos ²		
	PC1	PC2	PC3	PC4	PC1	PC2	Total
freq.Q25	-0.2263	-0.2549	-0.1079	-0.0758	0.5343	0.3750	0.9093
meandom	-0.2684	-0.1603	-0.0976	-0.0855	0.7517	0.1484	0.9001
meanfreq	-0.2739	-0.1331	-0.1442	-0.0449	0.7825	0.1022	0.8847
freq.median	-0.2646	-0.1584	-0.1277	-0.0865	0.7305	0.1448	0.8753
bottom.freq	-0.2348	-0.2122	0.0802	0.0450	0.5752	0.2598	0.8350
freq.Q75	-0.2814	-0.0317	-0.1610	-0.0563	0.8258	0.0058	0.8316
mindom	-0.1634	-0.3031	0.0466	-0.0542	0.2784	0.5302	0.8086
sp.ent	-0.1716	0.2816	0.0545	-0.0213	0.3072	0.4575	0.7647
freq.IQR	-0.1196	0.3255	-0.1004	0.0212	0.1491	0.6114	0.7605
sd	-0.0894	0.3321	-0.1442	0.1722	0.0834	0.6366	0.7200
entropy	-0.2261	0.1698	0.0593	0.2334	0.5333	0.1664	0.6996
sfm	-0.1971	0.2091	0.1199	0.1563	0.4054	0.2524	0.6577
meanpeakf	-0.2076	-0.1868	-0.1205	-0.0994	0.4498	0.2014	0.6512
maxdom	-0.2361	0.0742	-0.1912	-0.0465	0.5815	0.0318	0.6133
time.IQR	0.2325	-0.0707	-0.1573	-0.0579	0.5640	0.0288	0.5929
startdom	-0.1610	-0.2242	-0.0207	0.1872	0.2706	0.2901	0.5607
dfrange	-0.1119	0.2622	-0.2051	-0.0080	0.1306	0.3966	0.5272
duration	0.2125	-0.0753	-0.3008	0.0107	0.4713	0.0327	0.5041
time.Q75	0.2119	-0.0749	-0.3284	-0.0131	0.4684	0.0324	0.5008
time.ent	-0.1971	0.0520	0.0385	0.3289	0.4053	0.0156	0.4208
bandwidth	0.0922	0.2225	-0.3134	0.0234	0.0886	0.2856	0.3742
skew	0.0993	-0.2046	-0.1094	0.3347	0.1030	0.2415	0.3445
dfslope	-0.0875	0.1985	-0.0007	-0.3686	0.0798	0.2273	0.3072
enddom	-0.1681	0.0287	-0.1929	-0.3333	0.2950	0.0047	0.2997
kurt	0.0879	-0.1777	-0.1000	0.3338	0.0806	0.1822	0.2628
time.median	0.1440	-0.0621	-0.3690	0.0222	0.2164	0.0223	0.2387
modindx	-0.1426	0.0346	-0.0434	0.4685	0.2122	0.0069	0.2191
top.freq	-0.0746	0.1156	-0.3452	0.0684	0.0581	0.0771	0.1352
time.Q25	0.0078	-0.0219	-0.3505	0.0720	0.0006	0.0028	0.0034
Standard deviation	3.2299	2.4022	1.7881	1.5042			
Proportion of Variance	0.3597	0.1990	0.1103	0.0780			
Cumulative Proportion	0.3597	0.5587	0.6690	0.7470			
Eigenvalue	10.4324	5.7704	3.1974	2.2627			

Appendix 3

Table A3. Linear mixed-effects model results showed significant difference in acoustic parameters between foraging and nest feeding zip calls.

Acoustic parameters and contexts	Linear mixed effects model statistics		
	Coefficient	Confidence interval	<i>P</i>
First-quartile frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.495	0.092	0.000***
Mean dominant frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.723	0.087	0.000***
Mean frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.668	0.081	0.000***
Median frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.678	0.087	0.000***
Minimum frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.804	0.113	0.000***
Third-quartile frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.848	0.088	0.000***
Minimum dominant frequency			
Foraging zip (reference)	-	-	-
Nest feeding zip	-0.242	0.115	0.0377*

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Appendix 4

Table A4. Principal component analysis results illustrating the contribution of acoustic features in the first four principal components to the context variation of purr calls, sorted in decreasing order according to the total squared cosine (\cos^2) score of the first two principal components (values more than 0.8 in bold).

Acoustic features	Loadings				Cos ²		
	PC1	PC2	PC3	PC4	PC1	PC2	Total
top.freq	-0.3930	0.6012	0.0293	-0.0086	0.4196	0.5795	0.9990
duration	-0.5300	-0.3619	0.0254	0.1602	0.7628	0.2100	0.9728
bw	-0.3803	0.5194	-0.4061	-0.0331	0.3928	0.4326	0.8254
num_notes	-0.4971	-0.3052	0.0276	0.5317	0.6711	0.1494	0.8205
call_rate	0.4069	0.2770	-0.0926	0.8295	0.4496	0.1230	0.5726
bottom.freq	-0.0860	0.2606	0.9079	0.0495	0.0201	0.1089	0.1289
Standard deviation	1.6480	1.2662	1.0271	0.7786			
Proportion of Variance	0.4527	0.2672	0.1758	0.1011			
Cumulative Proportion	0.4527	0.7199	0.8957	0.9968			
Eigenvalue	2.7160	1.6033	1.0550	0.6063			

Appendix 5

Table A5. Linear mixed-effects model results showed significant difference in acoustic parameters between nuptial feeding and nest feeding purr calls.

Acoustic parameters and contexts	Model type	Model results		
		Statistics	d.f.	<i>P</i>
Maximum frequency	t-test			
Nuptial feeding purr (reference)		-	-	-
Nest feeding purr		-5.202	34.333	0.000**
Duration	Wilcoxon rank test			
Nuptial feeding purr (reference)		-	-	-
Nest feeding purr		236	-	0.00978***
Frequency bandwidth	Wilcoxon rank test			
Nuptial feeding purr (reference)		-	-	-
Nest feeding purr		201	-	0.001827**
Number of notes in call bout	Wilcoxon rank test			
Nuptial feeding purr (reference)		-	-	-
Nest feeding purr		192	-	0.000***

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Appendix 6

Table A6. Principal component analysis results illustrating the contribution of acoustic features in the first four principal components to the sex variation of chuck calls, sorted in decreasing order according to the total squared cosine (\cos^2) score of the first two principal components (values more than 0.8 in bold).

Acoustic features	Loadings				Cos ²		
	PC1	PC2	PC3	PC4	PC1	PC2	Total
meanfreq	0.2559	0.2281	-0.0100	-0.0921	0.6110	0.3346	0.9456
meandom	0.2205	0.2676	-0.0254	-0.0150	0.4537	0.4605	0.9142
freq.median	0.2435	0.2360	-0.0088	-0.1224	0.5535	0.3582	0.9117
freq.Q75	0.2797	0.1510	-0.0971	-0.1125	0.7301	0.1467	0.8767
freq.Q25	0.1822	0.2960	0.0932	-0.0891	0.3098	0.5634	0.8731
maxdom	0.2830	0.0778	-0.1348	0.1032	0.7477	0.0389	0.7866
mindom	0.0540	0.3216	0.1566	-0.0554	0.0272	0.6653	0.6925
meanpeakf	0.2071	0.2095	-0.0454	-0.0323	0.4003	0.2823	0.6826
top.freq	0.2664	0.0398	-0.1713	0.1517	0.6623	0.0102	0.6725
time.Q75	0.1974	-0.2058	0.2554	0.0094	0.3638	0.2723	0.6361
time.IQR	0.1902	-0.2101	0.2370	0.0013	0.3378	0.2840	0.6218
entropy	0.2085	-0.1825	-0.0763	-0.0762	0.4057	0.2141	0.6198
duration	0.1924	-0.2057	0.2572	0.0341	0.3456	0.2720	0.6176
time.median	0.1910	-0.2019	0.2544	0.0071	0.3406	0.2621	0.6027
dfrange	0.2105	-0.1437	-0.2200	0.1260	0.4136	0.1327	0.5464
sd	0.2012	-0.1569	-0.2749	0.0711	0.3780	0.1583	0.5362
time.Q25	0.1853	-0.1796	0.2500	0.0177	0.3203	0.2074	0.5277
time.ent	0.2005	-0.1450	-0.0130	0.0853	0.3753	0.1353	0.5106
bottom.freq	0.0928	0.2522	0.2206	-0.2183	0.0805	0.4090	0.4895
freq.IQR	0.1831	-0.1625	-0.2705	-0.0527	0.3131	0.1697	0.4828
modindx	0.1606	-0.1868	0.2834	-0.0801	0.2406	0.2243	0.4649
enddom	0.1473	0.1957	0.1200	-0.0340	0.2025	0.2462	0.4487
bw	0.1820	-0.1076	-0.2757	0.2571	0.3091	0.0745	0.3836
sp.ent	0.1199	-0.1714	-0.1851	-0.4011	0.1343	0.1888	0.3231
startdom	0.0651	0.1621	-0.1084	0.2895	0.0395	0.1690	0.2085
sfm	0.0747	-0.1244	-0.1546	-0.4321	0.0521	0.0996	0.1516
kurt	0.1157	0.0120	0.1976	0.2798	0.1249	0.0009	0.1259
skew	0.0724	0.0560	0.1910	0.4085	0.0489	0.0202	0.0691
dfslope	0.0362	-0.0684	0.1555	-0.2858	0.0122	0.0301	0.0423
Standard deviation	3.0551	2.5358	2.1989	1.4935			
Proportion of Variance	0.3219	0.2217	0.1667	0.0769			
Cumulative Proportion	0.3219	0.5436	0.7103	0.7873			
Eigenvalue	9.3338	6.4305	4.8353	2.2305			

Appendix 7

Table A7. Linear mixed-effects model results of chuck calls showed no significant difference between sexes in the top four variables influencing the variation.

Acoustic parameters and sex	Linear mixed effects model statistics		
	Coefficient	Confidence interval	<i>P</i>
Mean frequency			
Female chuck call (reference)	-	-	-
Male chuck call	0.081	0.236	0.733
Mean dominant frequency			
Female chuck call (reference)	-	-	-
Male chuck call	0.115	0.273	0.673
Median frequency			
Female chuck call (reference)	-	-	-
Male chuck call	0.066	0.251	0.793
Third quartile frequency			
Female chuck call (reference)	-	-	-
Male chuck call	0.092	0.271	0.733

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Appendix 8

Table A8. Principal component analysis results illustrating the contribution of acoustic features in the first four principal components to the sex variation of pip calls, sorted in decreasing order according to the total squared cosine (\cos^2) score of the first two principal components (values more than 0.8 in bold).

Acoustic features	Loadings				Cos ²		
	PC1	PC2	PC3	PC4	PC1	PC2	Total
maxdom	-0.2942	0.0203	-0.0421	0.0189	0.9641	0.0023	0.9664
top.freq	-0.2912	0.0233	-0.0265	0.0319	0.9447	0.0030	0.9477
freq.Q75	-0.2890	0.0342	-0.0890	0.0667	0.9304	0.0065	0.9369
time.Q75	0.0030	-0.4086	-0.0808	-0.0346	0.0001	0.9317	0.9318
time.median	-0.0155	-0.4041	-0.0735	-0.0258	0.0027	0.9114	0.9141
duration	0.0159	-0.4027	-0.0899	-0.0339	0.0028	0.9054	0.9082
meanpeakf	-0.2753	0.0277	-0.0787	0.1209	0.8441	0.0043	0.8484
meandom	-0.2736	0.0241	-0.1620	0.0640	0.8339	0.0032	0.8372
time.IQR	0.0153	-0.3832	-0.0920	-0.0616	0.0026	0.8197	0.8223
time.Q25	-0.0148	-0.3791	-0.0518	0.0094	0.0025	0.8020	0.8045
freq.median	-0.2600	0.0456	-0.1890	0.1370	0.7528	0.0116	0.7644
meanfreq	-0.2489	0.0588	-0.2332	0.0693	0.6900	0.0193	0.7093
entropy	-0.2340	-0.1207	0.1371	-0.1892	0.6101	0.0814	0.6914
sp.ent	-0.2268	-0.1161	0.1217	-0.2563	0.5729	0.0752	0.6482
sd	-0.2382	-0.0302	0.2590	0.0804	0.6319	0.0051	0.6370
freq.IQR	-0.2358	-0.0404	0.2606	-0.0224	0.6194	0.0091	0.6285
bw	-0.2287	0.0046	0.2539	0.1423	0.5828	0.0001	0.5829
sfm	-0.2029	-0.0946	0.1495	-0.2320	0.4585	0.0500	0.5084
dfrange	-0.2104	-0.0345	0.2698	0.0551	0.4932	0.0066	0.4998
modindx	-0.0381	-0.2669	-0.0472	-0.2175	0.0162	0.3976	0.4138
startdom	-0.1624	0.1427	-0.1293	-0.1549	0.2937	0.1137	0.4074
freq.Q25	-0.1770	0.0802	-0.3430	0.1074	0.3488	0.0359	0.3846
enddom	-0.1617	-0.1007	-0.1805	0.1142	0.2912	0.0566	0.3478
skew	0.0918	-0.1336	-0.0028	0.5185	0.0938	0.0996	0.1934
kurt	0.0533	-0.1360	0.0038	0.4949	0.0317	0.1033	0.1349
dfslope	0.0190	-0.1235	-0.0378	0.2012	0.0040	0.0851	0.0891
time.ent	-0.0786	-0.0502	0.0813	0.2720	0.0689	0.0141	0.0830
mindom	-0.0532	0.0685	-0.4044	-0.0516	0.0315	0.0262	0.0577
bottom.freq	0.0412	0.0173	-0.4085	-0.1805	0.0189	0.0017	0.0206
Standard deviation	3.3373	2.3626	2.1299	1.5754			
Proportion of Variance	0.3841	0.1925	0.1564	0.0856			
Cumulative Proportion	0.3841	0.5765	0.7330	0.8186			
Eigenvalue	11.1379	5.5818	4.5366	2.4818			

Appendix 9

Table A9. Linear mixed-effects model results of pip calls showed no significant difference between sexes in the top nine variables influencing the variation.

Acoustic parameters and sex	Linear mixed effects model statistics		
	Coefficient	Confidence interval	<i>P</i>
Maximum dominant frequency			
Female pip call (reference)	-	-	-
Male pip call	-0.011	0.220	0.959
Maximum frequency			
Female pip call (reference)	-	-	-
Male pip call	-0.134	0.308	0.665
Third quartile frequency			
Female pip call (reference)	-	-	-
Male pip call	0.077	0.142	0.588
Median time			
Female pip call (reference)	-	-	-
Male pip call	-0.0005	0.001	0.703
Third quartile time			
Female pip call (reference)	-	-	-
Male pip call	-0.001	0.002	0.613
Mean dominant frequency			
Female pip call (reference)	-	-	-
Male pip call	0.114	0.163	0.483
Duration			
Female pip call (reference)	-	-	-
Male pip call	-0.001	0.002	0.620
Time inter-quartile range			
Female pip call (reference)	-	-	-
Male pip call	-0.0002	0.001	0.745
Mean peak frequency			
Female pip call (reference)	-	-	-
Male pip call	0.153	0.176	0.383

P* < 0.05, *P* < 0.01 and ****P* < 0.001.

Appendix 10

Table A10. Principal component analysis results illustrating the contribution of acoustic features in the first four principal components to the sex variation of zip calls, sorted in decreasing order according to the total squared cosine (\cos^2) score of the first two principal components (values more than 0.8 in bold).

Acoustic features	Loadings				Cos ²		
	PC1	PC2	PC3	PC4	PC1	PC2	Total
freq.Q25	0.3208	0.1229	0.0013	-0.0172	0.8793	0.0829	0.9623
meandom	0.2951	0.1716	0.0923	0.0362	0.7440	0.1616	0.9057
freq.median	0.2957	0.1656	0.0918	0.0002	0.7470	0.1504	0.8974
meanfreq	0.2878	0.1643	0.1292	-0.0312	0.7076	0.1482	0.8558
time.Q75	0.1389	-0.3265	0.1640	0.1492	0.1648	0.5851	0.7499
duration	0.1540	-0.3111	0.1544	0.1674	0.2025	0.5311	0.7336
meanpeakf	0.2811	0.0943	0.0006	0.0235	0.6748	0.0488	0.7236
mindom	0.2500	0.1781	-0.1137	0.0928	0.5341	0.1740	0.7080
time.median	0.1355	-0.3104	0.1769	0.1168	0.1569	0.5286	0.6855
bottom.freq	0.2472	0.1527	-0.1060	0.2018	0.5219	0.1280	0.6499
freq.Q75	0.2247	0.1959	0.2301	-0.0077	0.4313	0.2106	0.6419
time.Q25	0.1415	-0.2799	0.1531	0.0609	0.1711	0.4299	0.6010
sp.ent	-0.1949	0.1713	0.2386	0.2736	0.3246	0.1611	0.4857
sfm	-0.1955	0.1672	0.1571	0.2618	0.3265	0.1535	0.4800
skew	0.1536	-0.2159	-0.1173	-0.2060	0.2014	0.2557	0.4571
time.IQR	0.0878	-0.2669	0.1197	0.1988	0.0658	0.3909	0.4567
enddom	0.1533	0.2024	0.1756	-0.0420	0.2007	0.2248	0.4254
entropy	-0.1755	0.1390	0.2642	0.3061	0.2630	0.1060	0.3689
kurt	0.1382	-0.1928	-0.1098	-0.1628	0.1632	0.2039	0.3670
dfslope	-0.0543	0.2349	0.0895	-0.2163	0.0252	0.3028	0.3280
freq.IQR	-0.1689	0.0919	0.3260	0.0152	0.2436	0.0463	0.2899
startdom	0.1793	-0.0259	-0.0024	0.1954	0.2747	0.0037	0.2784
modindx	0.0107	-0.2198	0.1229	0.1917	0.0010	0.2652	0.2661
sd	-0.1620	-0.0164	0.3171	-0.1731	0.2241	0.0015	0.2255
maxdom	0.1391	0.0952	0.2896	-0.0682	0.1653	0.0498	0.2150
bandwidth	-0.0481	-0.1214	0.2590	-0.4322	0.0197	0.0809	0.1007
top.freq	0.1004	-0.0481	0.2432	-0.3897	0.0861	0.0127	0.0988
time.ent	0.0419	-0.0921	0.1236	0.1539	0.0150	0.0466	0.0616
dfrange	-0.0280	-0.0233	0.3257	-0.1167	0.0067	0.0030	0.0097
Standard deviation	2.9226	2.3425	2.1973	1.5847			
Proportion of Variance	0.2945	0.1892	0.1665	0.0866			
Cumulative Proportion	0.2945	0.4838	0.6502	0.7368			
Eigenvalue	8.5418	5.4873	4.8280	2.5112			

Appendix 11

Table A11. Linear mixed-effects model results of zip calls showed significant difference between sexes in the top three variables influencing the variation.

Acoustic parameters and sex	Linear mixed effects model statistics		
	Coefficient	Confidence interval	<i>P</i>
First-quartile frequency			
Female zip call (reference)	-	-	-
Male zip call	0.476	0.228	0.037*
Mean dominant frequency			
Female zip call (reference)	-	-	-
Male zip call	0.552	0.268	0.040*
Median frequency			
Female zip call (reference)	-	-	-
Male zip call	0.610	0.260	0.019*

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.