



Přírodovědecká
fakulta
Faculty
of Science

The University of South Bohemia in České Budějovice
Faculty of Science

**Vocal Individuality in Yellow-rumped
tinkerbirds (*Pogoniulus bilineatus*)**

Master thesis

Bc. Siddharth Prashant Khopkar

Supervisor: RNDr. Pavel Linhart, Ph.D.

České Budějovice 2021

Siddharth, K., 2021: Vocal Individuality in Yellow-rumped tinkerbirds (*Pogoniulus bilineatus*). Mgr. Thesis, in English. – 24 p., Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic.

Annotation:

Vocal Individuality in Yellow-rumped tinkerbirds (*Pogoniulus bilineatus*), was analysed by using recordings which had already been collected from South Africa and Cameroon and the analysis took place at the University of South Bohemia.

DECLARATION:

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

České Budějovice, 06/12/2021.



Siddharth Prashant Khopkar

AKNOWLEDGEMENTS

First and foremost, I would like to express the deepest thanks to my supervisor, Ph.D. Pavel Linhart, for his unwavering support and belief in me, he convincingly guided and encouraged me even when the journey ahead was tough. Without his persistent help, the goal of this project would not have been accomplished. To Pavel particularly for sending me to the arctic where neither of us had a great idea about and for all his guidance on compiling and presenting my idea to work on Arctic terns. Pavel also provided specific opportunities for me to learn outside of my thesis like the winter school in bioacoustics though I wasn't able to travel because of the pandemic. Though I appreciate him for giving me freedom to explore and learn new things. I would also like to thank the board of Master's in Ecology program, Prof. Jan Lepš, Ph.D Jan Hrček, and Ph.D Petr Blažek for their insightful comments, suggestions and technical support on my study. I would like to thank all my colleagues and students of the Master's in Ecology program for a cherished time spent together. It is their kind help and support that have made my study and life in the Czech Republic easier. I would like to express all my gratitude to my parents, for all their support and love. Finally, I would like to express my gratitude to my family and friends back home in India who believed in me. Without their tremendous understanding and encouragement in the past few years, it would have been impossible for me to complete my study.

TABLE OF CONTENTS

Title page.....	I
AKNOWLEDGEMENTS.....	II
TABLE OF CONTENTS.....	III
Introduction:	1
Vocalisations: -----	1
Importance of individuality to the specific individual: -----	1
Conservation aspects of vocal individuality (human perspective):	2
Stability of individually specific vocal traits: -----	3
Aims of the study:-----	4
Methods:.....	5
Study site: -----	5
Recordings: -----	6
Analysis: -----	6
Results:	11
Population differences in calls: -----	11
Individual variation in calls for each separate variable: -----	12
Individual variation in calls – entire signal -----	15
Individual call stability depending on recording session and use of playback -----	18
Relationship between spatial distribution of individuals and similarity of their calls-----	20
Discussion:.....	21
Differences in call parameters between populations-----	21
Individuality in YRT in comparison with other species -----	22
Stability of individually distinct vocal features in YRT -----	23

Spatial Distribution and call similarity -----	24
Conclusion:	25
Bibliography:	26

Introduction:

Vocalisations:

Many animals produce sounds which serve as a channel to communicate with the members of its own species. Acoustic communication possesses a great significance when it comes to animals, especially when the other member is out of sight i.e. in a dense forest, or at night when it's harder to perceive visual cues (Owings and Morton 1998). The production and transmission of these acoustic signals vary in groups of animals. Animals have been known to produce different kinds of calls depending on the situation, such as, for example, responding to its mate or warding off its competitor or sounding an alarm against a predator (Bradbury and Vehrencamp 1998). One of such signals could be used for attracting a potential mate. This often requires the sound signals to travel over large distances for getting picked up by the receiver.

Importance of individuality to the specific individual:

We can expect that signallers actively broadcast their identity in their vocalizations (Tibbetts and Dale 2007). Individual recognition can be vital for evolution of sociality or maintaining cooperative relationships with others (Holmes 1983, Riolo, Cohen et al. 2001, Box 2003, Bergman and Sheehan 2013). Individual recognition has been documented to help the animal discriminate its mate or offspring (Halpin 1991, Wanker, Apcin et al. 1998, Jouventin, Aubin et al. 1999, Charrier, Jouventin et al. 2001, Charrier, Mathevon et al. 2003, Charrier and Harcourt 2006). Even in the case of solitary animals being different or standing out from others and identifying others can be beneficial allowing it to discriminate among neighbours and intruders. Individual recognition among neighbours can be studied through the "Dear-enemy effect" (Washburn 1955). This concept was documented in territorial birds which were able to discriminate among neighbours and strangers (Weeden and Falls 1959, Wiley and Wiley 1977, Kroodsma 1984, Halpin 1991, Kroodsma and Konishi 1991, Stoddard, Beecher et al. 1991, Westcott 1997, Wanker, Apcin et al. 1998, Jouventin, Aubin et al. 1999, Lovell and Lein 2004, Olendorf, Getty et al. 2004, Oyakawa, Koda et al. 2007, Wei, Lloyd et al. 2011, Draganoiu, Moreau et al. 2014) and even keep them memorised for the upcoming year (Godard 1991, Draganoiu, Moreau et al. 2014).

Conservation aspects of vocal individuality (human perspective):

In many of the studies related to ecology and conservation, individual identification has high priority for researchers as by doing so we are able to apprehend and gain insights on their ecology and behaviour. Individual identification has made it possible for us to estimate or model animal's population demography (number of births, deaths and survival), getting the ability to track individual movements (estimating immigration and emigration). Conservation status of any species is dependent on its population size, which inversely corresponds with the risk of getting extinct (Mace, Collar et al. 2008).

For some individuals it has been possible to visually identify them Based simply on their morphological features (Würsig and Würsig 1977, Karanth and Nichols 1998). However, we also find animals that are similar to each other and it is impossible to differentiate between them. This marks one of the reasons why scientists employ the traditional mark-recapture technique. In this method, some 'marks' are attached to the animal which serve for the as his identity. Marking includes attaching animals with various tags (radio tags, rings, colour bands, pelage marks, PIT tags). Marking individuals opens up the possibility for identifying them over time, when re-sighted or re-captured. Nevertheless, mark-recapture techniques are invasive as the name suggests the animals need to be captured. This involves some risk as capture might harm the animal to various extent depending on the method employed for trapping (Powell and Proulx 2003, Laiolo, Vögeli et al. 2007, Cunningham, Unwin et al. 2015, Soulsbury, Gray et al. 2020). When captures are carried out for endangered species, such risks could be considered extreme. Further, it has been observed that capturing individuals could alter their behaviour which might adversely impact population estimates and results of research (Linhart, Fuchs et al. 2012, Kukalová, Gazárková et al. 2013, Byers, Lee et al. 2019). To outweigh these risks accompanied with mark-recapture techniques acoustic monitoring schemes could be used as they are non-invasive and this could help in identifying individuals solely based on their vocalisations. It is widely known that many species are vocally active and most of these vocalisations can be specific for each individual allowing us to identify individuals in a population (McGregor 2002, Terry, Peake et al. 2005, Thompson, Schwager et al. 2010, Kidney, Rawson et al. 2016, Rhinehart, Chronister et al. 2020, Wood, Klinck et al. 2021). Thus, identifying individuals has always been the priority and tracking their behaviour by means of non-invasive method may help

in conserving and managing protected areas or threatened and endangered species (Terry, Peake et al. 2005, Pimm, Alibhai et al. 2015).

Stability of individually specific vocal traits:

While individual differences in vocalizations have been documented as being present across several taxa, fewer studies looked at how stable this phenomenon was over a period of time (Cavanagh and Ritchison 1987, Jones, Harris et al. 1993, Janik and Slater 2000, Delport, Kemp et al. 2002, Fan, Xiao et al. 2011, Feng, Cui et al. 2014, Fuller 2014) Several studies have shown to exhibit this property. These have often involved species lacking vocal learning . Several other studies have shown that many species lack temporal stability of individually specific vocal features (Eakle, Mannan et al. 1989, Rukstalis, Fite et al. 2003, Puglisi and Adamo 2004, Matrosova, Volodin et al. 2009, Matrosova, Volodin et al. 2010, Cornec, Hingrat et al. 2015, Humphries, Finch et al. 2016).

There are several factors that can affect stability of individually specific vocal features including both, social and environmental factors. For example, vocal traits can change as result of changes in group membership (Nowicki 1989, Hile, Plummer et al. 2000, Rukstalis, Fite et al. 2003) Environment can also affect vocal traits and hinder individual recognition, for example, due to degradation of sound over distance. One of such study looked at the transmission of song features, especially the trill rate, and they showed that the trill sounds are affected by reverberations depending on the surrounding vegetation and distance. Therefore, recording distance maintained in the field between the microphone and the bird can also affect the song structure (Naguib 2003) and therefore, needs to be taken into account when judging potential suitability of the signal for individual recognition. Another study showed that giant panda bleats contain information on the caller's phenotype which could potential be important to receivers in sexual contexts. They found certain acoustic features which provided information on sex, age and body weight/size of the panda. The possible explanation they think is giant pandas could be experiencing various age-related structural changes, maybe leading to lengthening of the vocal tract and more pronounced lowering of formants with aging (Charlton, Zhihe et al. 2009). Such age-related vocal changes might hinder re-identification of individuals. There are also several studies which show that season may affect acoustic structure of vocalizations. For example, in european male starling it was observed that the highest concentrations of testosterone was in

April when the birds increased total song output and sang longer songs whereas in October the levels of testosterone were low for all males and the songs were also shorter (Riters, Eens et al. 2000). Such changes might again make it more difficult to recognize a particular individual by his songs. Ideally, vocalizations dedicated to signalling individual identity should be as stable as possible in different environmental and social conditions.

Aims of the study:

In this study, my aim was to quantify the amount of individual variation present in calls of Yellow-rumped Tinkerbirds (YRT) coming from two different populations (Cameroon and South Africa). Further, I tried to see if individual call features remain robust over different recording sessions and playback stimulation (spontaneous songs vs. playback elicited songs). Last, I was interested to see if similarity of calls is affected by geographical distance among the individuals.

Because we had data from two populations we were first interested whether

- 1) There is acoustic difference in calls between the two populations.

Further, I tested the following hypotheses related to vocal individuality in YRT:

- 2) YRT individuals have individually distinct calls.
- 3) The amount of individuality in calls differs between the two populations.
- 4) Discrimination of individuals does not decrease in following recording sessions.
- 5) There is negative relationship between geographic distance and similarity of calls.

Methods:

Tested species:

The species I focused on for the present study was the Yellow-rumped Tinker bird. It belongs to the Lybiidae family which is the family of African barbets. The bird is a commonly found african forest species that occurs in primary or secondary forests, forested highlands or lowlands, often at the forest edges even in thickets, tree plantations and gardens. Their size usually ranges between 10 – 12 cm. While their weight is around 11 – 18.6 g. It is easy to identify the Yellow-rumped Tinker bird by its contrastingly marked face with a song bill and short tail. Both the sexes are similar looking having black above along with golden-rump, golden-yellow in their wings, white supercelia and white line across their forehead and down to the neck side and the prominent white throat. These are solitary birds living in stable pairs which maintain year-long territories. They are mostly frugivorous which makes them dependent on a wide variety of fruits, including figs. In addition to fruits they may consume small insects. The songs of these birds are simple made up of a series of “pop” sounds which makes them perfect subject to study various aspects of animal vocal communication including signalling of individual identity in calls. The bird is largely sedentary as it maintains year round territories but it has been recorded that the dispersal of their offsprings can be unto 20 km.

Study site:

Focal Individuals of the Yellow-rumped Tinkerbird were recorded from two distinct geographical regions: Cameroon (Babanki, GPS coordinates: 6°05'35.7"N 10°17'51.7"E) and South Africa (Umlalazi, GPS coordinates: 28°57'24.9"S 31°46'01.0"E). Birds from the two locations belonged to different subspecies: *P. b. leucolaimus* (Cameroon) and *P. b. bilineatus* (South Africa). Both populations were recorded in primary and secondary forest fragments characterized by dense vegetation. In both populations, the recordings were obtained during the November and December corresponding to possible breeding period in both areas but exact breeding stage was not known in any of the recorded birds. In Cameroon the recordings were collected in the year

2017 from November 11 to December 3. In South Africa the recordings were collected in the year 2018 from November 28 to December 1.

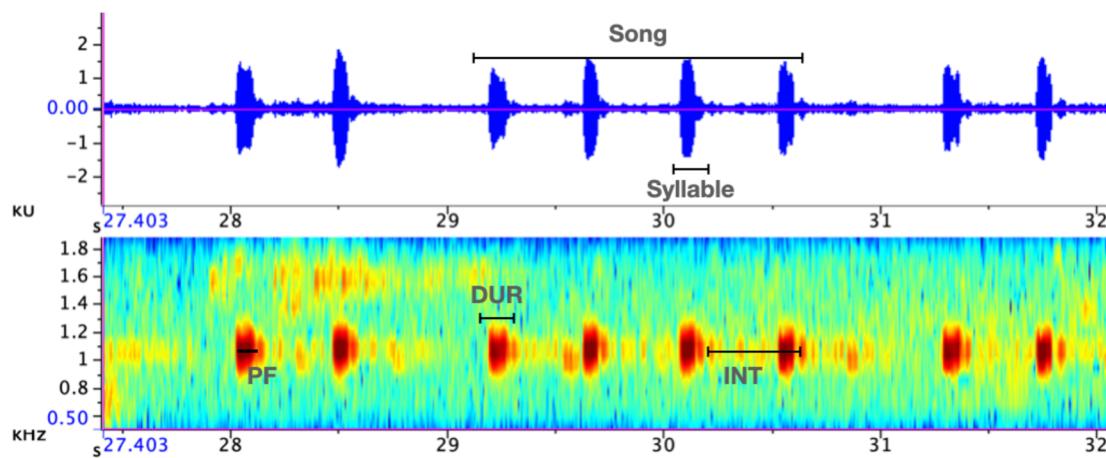
Recordings:

The recordings from the birds were taken early morning from 7:00 to 11:00 or late afternoon 16:30 to 18:30 during these times the birds were found to be vocally active. Sometime playback was used to elicit vocal response from the birds. For the recording equipment we used Zoom H4N recorder paired with a Sennheiser ME67 directional microphone. Distance to birds varied widely between 10 – 60m. Recording person tried to approach singing birds as much as possible but the distance was maintained during the recording sessions so that the bird wasn't disturbed by the presence of observers and stopped singing. Especially in Cameroon, individuals were sometimes recorded in several different sessions over a period of several days or multiple times on the same day. Sampling was only done on days with acceptable weather (no rain, no strong wind). For analysis, we included birds with at least 10 song sequences that were judged as having acceptable quality for the quantitative analysis (clearly visible song structure on the spectrogram).

Analysis:

The data analyses took place in Czech Republic at the University of South Bohemia in the year 2020 – 21. I was using Cornell Raven Pro 1.6.1 for analysing the sound files. I did this by marking each specific song syllable when the bird was singing on the recording (See Table 1 for an overview of available data). Then followed the extraction of sound variables. For this I took just three basic acoustic variables because simple structure of Yellow-rumped Tinkerbirds calls did not allow taking larger number of meaningful call features. Peak frequency (PF) was measured automatically by Raven but required adjustment of spectrogram parameters for precise spectral measurements (spectrogram window focus (FFT size) was kept at 550, frequency bandwidth was kept between 180Hz and 1800Hz everything above and below that was filtered). The second variable was duration of the syllable (DUR) this was calculated by subtracting the syllable end time from the syllable begin time. I also calculated the interval between syllables (INT). This was done by subtracting the begin time of a syllable from the begin time of the previous syllable. Always, for the first syllable of the song sequence, syllable interval was omitted because interval to syllable ending previous song sequence was variable and very large

compared to intervals within a song sequence. All statistical analyses were computed using R



3.4.4 (R 92 Development Core Team 2018).

Figure 1. Shows how the spectrogram view of Cornell's raven pro looks like and the type of variables which were extracted for the analysis.

Population differences in calls. To test the difference present between the two populations I calculated mean value of each variable for each individual and ran a *t*-test on these data.

Individual variation in calls. To test for presence of acoustic individuality in calls, first, I graphically checked box-plots on individual level for each of the variables. Further, I conducted linear discriminant analysis (LDA) using 60% of measured syllables from a particular male as the training data and remaining 40% of syllables as the testing data (split sample cross-validation). To evaluate LDA performance, I extracted the LDA classification matrix and calculated discrimination score as percentage of syllables correctly assigned to individual emitting the call. Initially, three separate LDAs were conducted in which either both populations were combined, or individuals from the Cameroon and the South African populations were used separately in LDA. Further I calculated Beecher's information statistic (HS, Beecher 1989, Linhart et al. 2019) to estimate individuality in each separate variable and within the entire signal. HS is not that dependent on sample size as LDA discrimination score.

Individual call stability depending on recording session and use of playback. To evaluate whether discrimination of individuals does decrease in following recording sessions., I conducted another LDAs. In these LDAs, I used:

- 1) spontaneous songs from two different recording sessions, calls from one session were used for training the LDA model and the other session for testing its performance (BOTH SPONTANEOUS)
- 2) playback elicited calls from two different recording sessions, calls from one session were used for training and the other session for testing (BOTH PLAYBACK)
- 3) spontaneous calls from one session used for training and playback elicited calls from second session used for testing (SPONT-PLAYBACK)

I quantified average amount of decrease in the classification success for each individual so that I subtracted discrimination score for that individual based on testing dataset from the discrimination score based on the training dataset only (leave-one-out cross-validation). I expected to get none or only a mild decrease in classification success if calls of the individual remain stable between two recording sessions and high decrease in classification success if acoustic structure of calls changes during the time or depending on use of playback to elicit the songs.

Relationship between spatial distribution of individuals and similarity of their calls. Finally, I used Mantel test to see if there is any sort of correlation between the geographic distance among individuals and similarity of their calls. Euclidean distances were calculated based on average values of the three measured variables as a measure of similarity for each pair of individuals. This analysis was only conducted on the Cameroonian population because of the larger number of individuals and suitable spatial distribution of individuals.

Table 1. An overview of data used for analyses.

Individual	Population	Number of analysed syllables	Total number of recording session	Number of recording sessions elicited by playback
PB01	Cameroon	1166	4	2
PB02	Cameroon	764	2	1
PB03	Cameroon	785	6	2
PB04	Cameroon	1425	5	5
PB05	Cameroon	251	2	1
PB06	Cameroon	397	2	2
PB07	Cameroon	183	1	1
PB08	Cameroon	204	1	1
PB09	Cameroon	991	1	1
PB10	Cameroon	750	3	2
PB11	Cameroon	520	3	2
PB12	Cameroon	474	2	0
PB13	Cameroon	389	1	1
PB14	Cameroon	182	1	1
PB15	Cameroon	378	2	0
PB16	Cameroon	141	1	0
PB17	Cameroon	489	1	1
PB18	Cameroon	350	1	1
PB20	South Africa	232	1	0
PB22	South Africa	121	1	1
PB23	South Africa	505	1	1
PB24	South Africa	204	2	0
PB25	South Africa	92	2	2
PB26	South Africa	200	2	0
PB27	South Africa	438	1	0
PB28	South Africa	145	3	2

PB29	South Africa	138	1	1
PB30	South Africa	166	1	1

Results:

Population differences in calls:

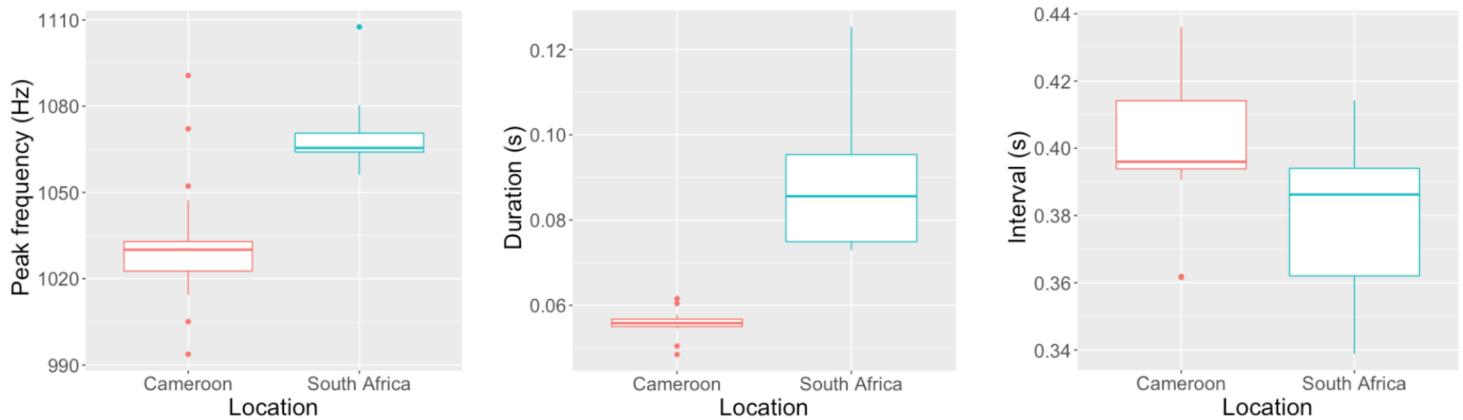


Figure 2. Box-plot showing differences between the two populations. Each individual has one point in the box-plot representing mean value of the parameter for that particular individual. The solid line refers to the median value, box represents 50% quantile, whiskers refer to non -outlier range and dots refer to outliers.

The visualized overview of peak frequency values (PF, Figure 2 and Figure 3) show that there are differences present between the two populations. The highest PF value is around 1170 Hz, and it is almost similar in both populations, but when we consider the lowest point to see how low it can go. In Cameroon, the lowest PF value is around 940 and most of the syllables range between 970 and 1100. Whereas, In the South African population the lowest PF value is 1010 even the band here looks more refined and most of the values range between 1030 and 1130 (Figure 2). Individuals differ in their average PF values between the two populations with Cameroon PF values being c.a. 30 Hz lower ($t = -5.3523$, $df = 21.754$, $p\text{-value} = 2.338e-05$).

For syllable interval (INT), the highest values of both populations were 0.49 (Figure 2, Figure 5). While there is a slight difference in observed minimum values for INT. In Cameroon, the lowest value was 0.27 and most observed syllables were between 0.34 to 0.46. In the South Africa population, the lowest value was 0.22 and most of the values lied between 0.32 to 0.42. Overall, INT was c.a. 10 ms longer in Cameroonian population ($t = 2.4125$, $df = 13.074$, $p\text{-value} = 0.03125$).

For syllable duration (DUR), values don't go below 0.04 while the highest is 0.19 and most of the syllables lie between 0.05 and 0.12 in South African population. In contrast, in the Cameroon population the lowest value is 0.01 and the highest is 0.17 and the syllables appear to be more clustered between 0.03 and 0.10 (Figure 2, Figure 4). Average individual duration of syllables in the South African population is longer by c.a. 30 ms than the average duration of individuals from the Cameroon population ($t = -5.2688$, $df = 8.2137$, $p\text{-value} = 0.0006942$).

Individual variation in calls for each separate variable:

For Peak frequency, the lowest value is for PB06 while the highest value is for PB08. If we discard the outlier for PB05, PB08 has the largest spread in values which would probably make this individual difficult to identify. On the other hand, PB11 has the lowest spread in Cameroon population. PB15 and PB16 look almost the same having quite similar PF values. In South Africa, PB29 has the largest spread in the PF values and lowest median PF value. PB23 would have the highest PF values. Here, PB24, PB25 and PB26 have quite similar PF values. Beecher's information statistic calculated separately for PF was equal to 1.04 bits indicating potential for up to 2.056 individual signatures (number of unique signatures = $2^{\wedge} HS$).

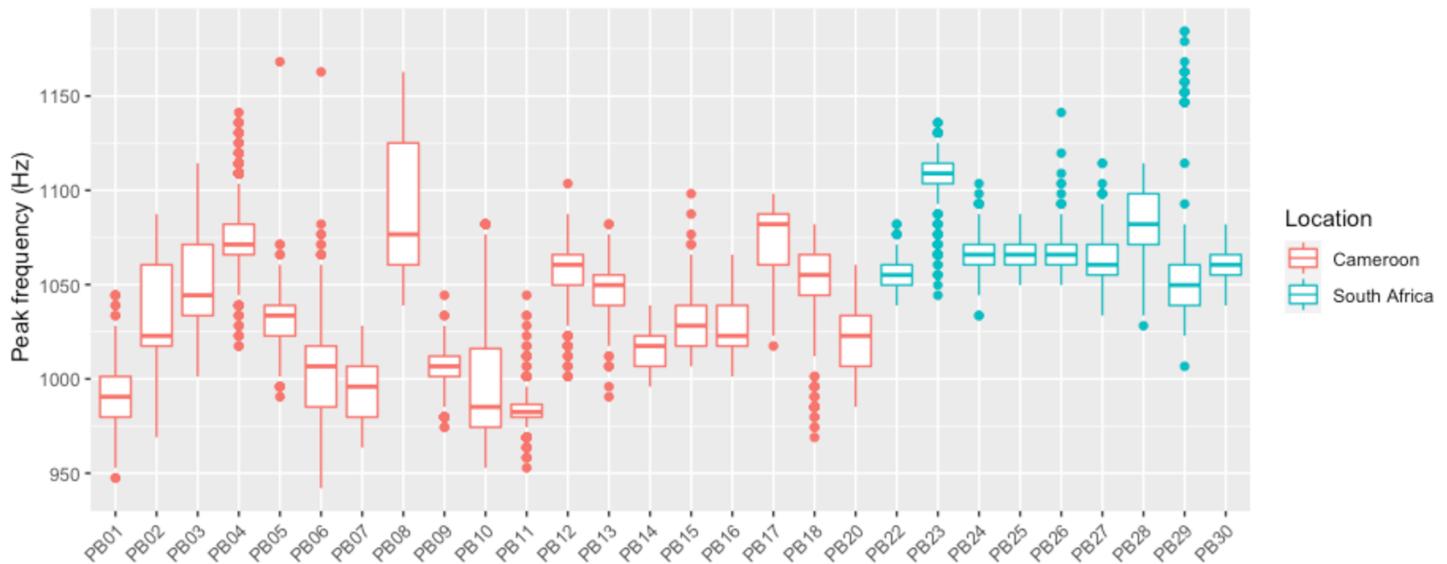


Figure 3. Individual variation present in Peak frequency (Hz) within and among individuals of the two populations. The solid line refers to the median value, box represents 50% quantile, whiskers refer to non-outliers and dots refers to outlier values.

Lowest and the highest INT values belong to PB08 in Cameroon. while PB01 and PB02 have almost the same INT values but INT is otherwise variable for the other individuals. INT seems less individually variable in the South African population. The individual PB29 has the lowest as well as the highest INT values. PB22 and PB23 have almost similar values. Further, when calculating the Beecher's information statistic (HS) separately for INT the HS score I got was equal to 0.76 bits indicating potential for up to 1.69 individual signatures (number of unique signatures = $2^{\wedge} HS$).

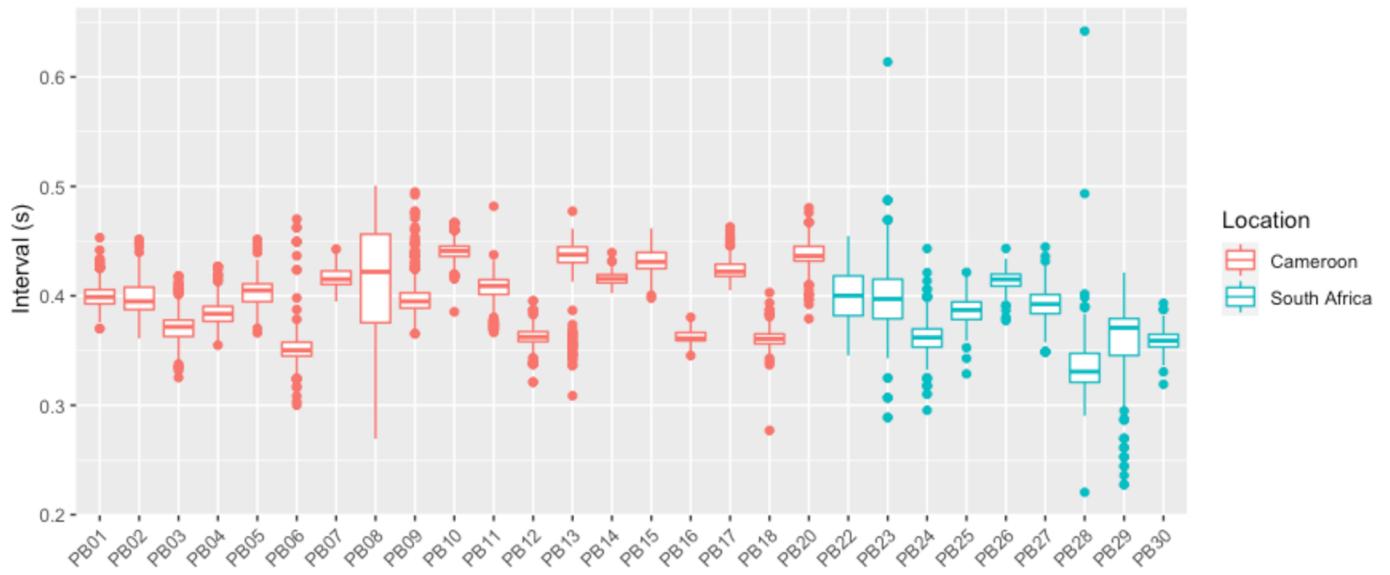


Figure 4. Individual differences present in syllable duration (s) within and among individuals of the two populations. The solid line refers to the median value, box represents 50% quantile, whiskers refer to non-outlier range of values and dots refer to outliers.

For duration (DUR), the highest value in Cameroon is for PB08 while the lowest for PB02. PB08 has the highest spread of DUR values. It seems that every individual has slightly different values but the overlap between individuals seems to be biggest compared to the other two variables. Beecher's information statistic calculated for DUR was equal to 0.85 bits indicating potential for up to 1.80 individual signatures (number of unique signatures = 2^{HS}).

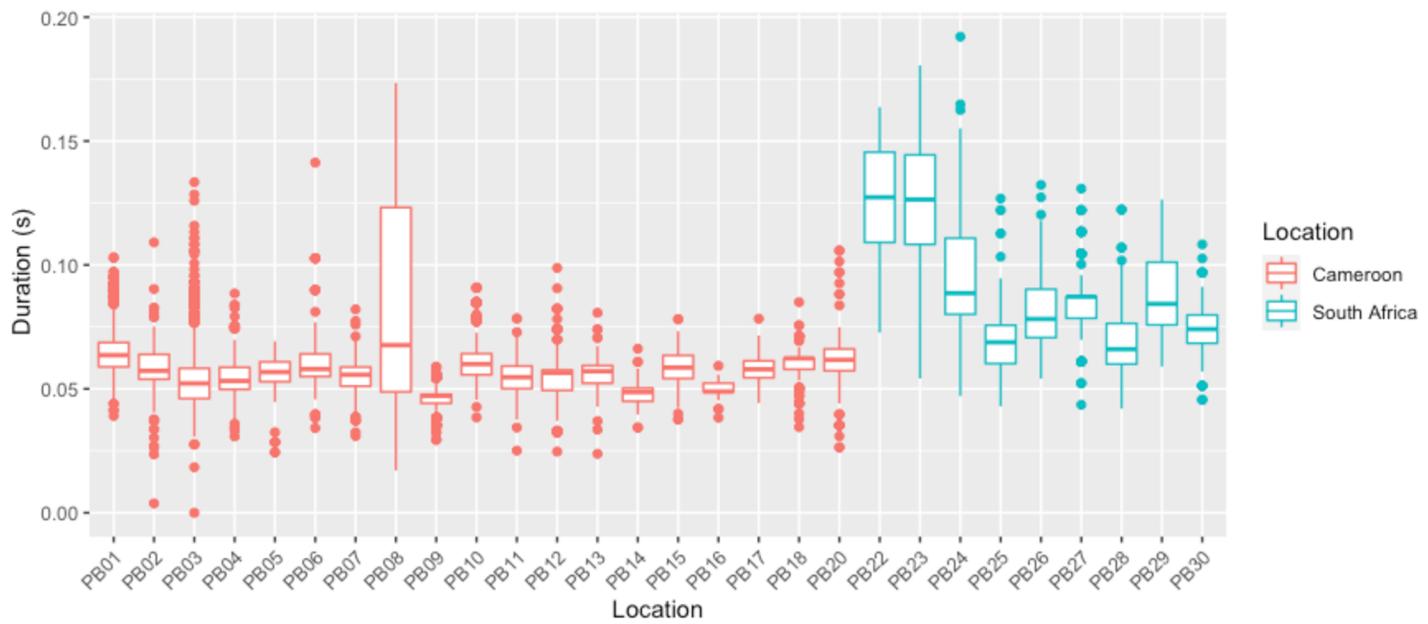


Figure 5. Individual differences present in syllable interval (s) within and among individuals of the two populations. The solid line refers to the median value, box represents 50% quantile, whiskers refer to non-outlier minimum and maximum values and dots represent outliers.

Individual variation in calls – entire signal

Three Linear Discriminant Analyses (LDA) tests were done to see whether calls can be accurately assigned to correct individuals. 1) Combined data, 2) Cameroonian data, 3) South African data. I used 60% of the data as the training set to find discrimination models and the rest 40% of syllables were used to validate discrimination model and to see classification of individuals. For purpose of these LDAs, I mixed syllables from all different sessions, if available, to capture variability within and across sessions in the discrimination models. Finally, I calculated Beecher's information considering all three variables together.

1) Combined data

The overall accuracy of the LDA model was 56%. Diagonal of the confusion matrix is clearly visible indicating that most of the calls were correctly classified to proper individuals (Figure 6). Beecher's information statistics HS was equal to 2.61 bits indicating potential for up to c.a. 6 individual signatures (number of unique signatures = 2^{HS}).

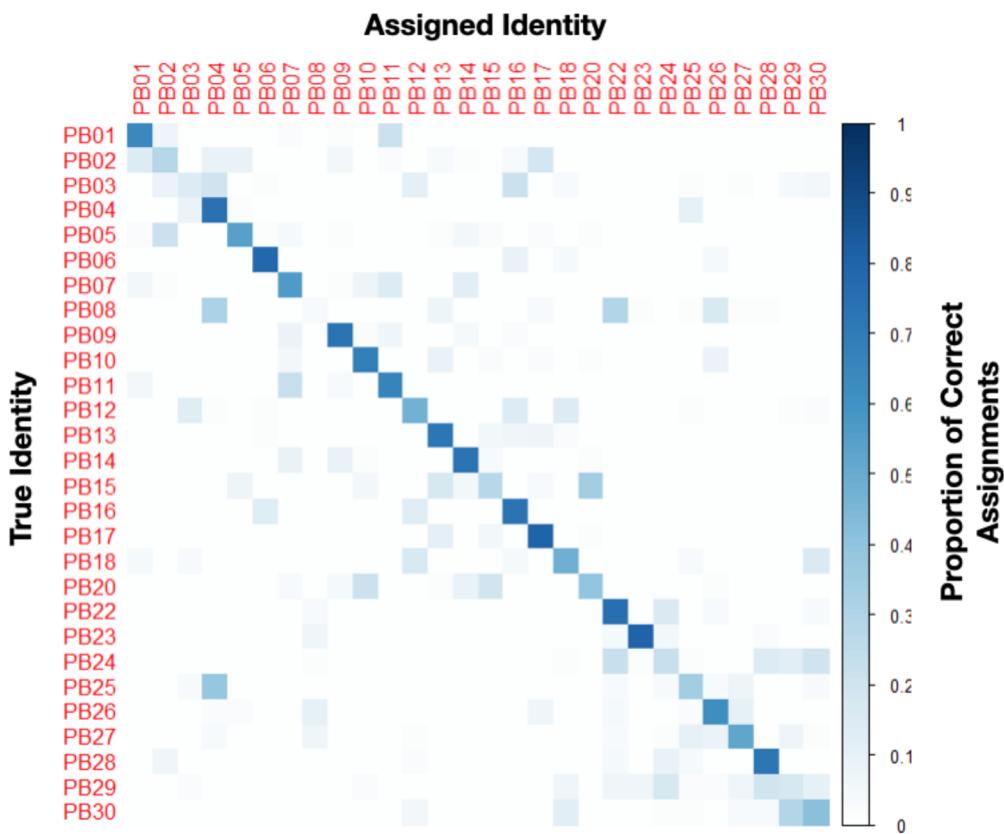


Figure 6. Confusion matrix for summarizing LDA classification accuracy for combined population. Rows represent real identities and columns assigned identities. Colour of the matrix cells indicates proportion of calls assigned to a particular individual. Cells on matrix diagonal represent correctly assigned calls.

2) Cameroonian data only

Here, the overall accuracy of the model was 59%. Again, the diagonal line of the confusion matrix is clearly visible (Figure 7). In a single case, majority of PB03 were classified as belonging to other individual. In the case, where only the Cameroonian data were used to calculate the Beecher's information statistics, HS score was 1.98 bits indicating potential for up to c.a 4 individual signatures (number of unique signatures = $2^{\wedge} HS$).

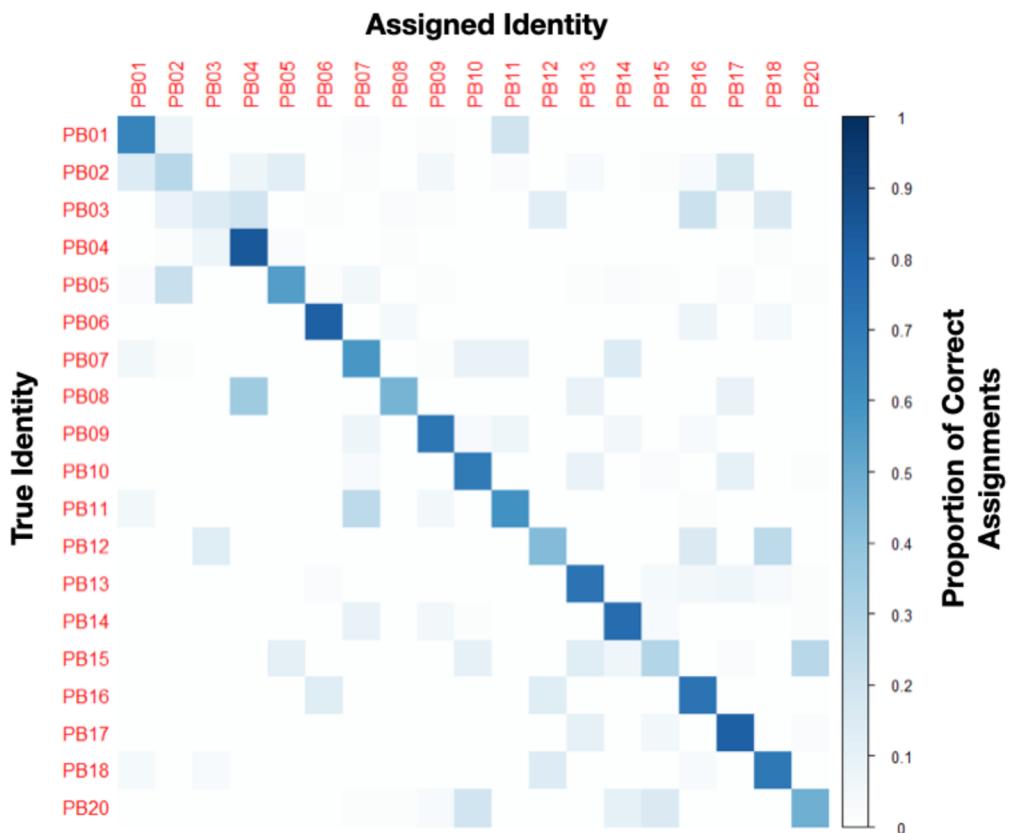


Figure 7. Confusion matrix for summarizing LDA classification accuracy for Cameroonian population. Rows represent real identities and columns assigned identities. Colour of the matrix cells indicates proportion of calls assigned to a particular individual. Cells on matrix diagonal represent correctly assigned calls.

3) South African data

Here, LDA assigned 59% of calls to correct individuals. Diagonal line of the matrix is visible but calls of two males PB24 and PB29 were misclassified to other males (Figure 8). Beecher's statistics was equal to 1.37 bits, indicating potential for up to c.a. 2.5 individual signatures (number of unique signatures = 2^{HS}).

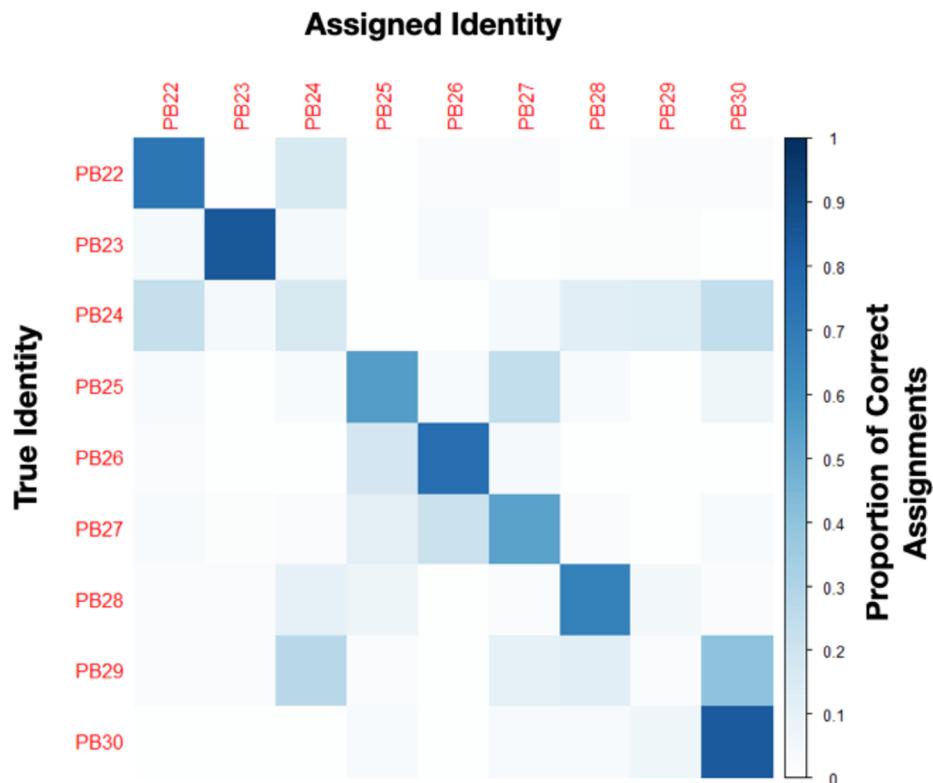


Figure 8. Confusion matrix for summarizing LDA classification accuracy for South African population. Rows represent real identities and columns assigned identities. Colour of the matrix cells indicates proportion of calls assigned to a particular individual. Cells on matrix diagonal represent correctly assigned calls.

Individual call stability depending on recording session and use of playback

To investigate individual call stability I conducted additional 3 LDAs which used calls from different recording session for training the LDA model and testing its performance. I sessions used for training and testing further differed depending on whether playback was used in any of the recording session leading to three combinations I expected decrease in discrimination score if calls change across recording sessions and playback conditions.

SPONT-PLAYBACK condition (number of individuals n = 6). I produced classification matrices for the training and testing data set. In this case the overall accuracy for the training dataset was 90% and this dataset was associated without playback. For the testing data, the overall accuracy dropped to 40%. This shows a decrease of 50%.

BOTH PLAYBACK condition (n = 10). In this case the overall accuracy for the training dataset was 79%. In the case of testing data the overall accuracy dropped to 65% showing a mild decrease of 14%.

BOTH SPONTANEOUS condition (n = 6). In this case the overall accuracy for the training dataset was 91%. For testing data, the overall accuracy dropped to 79% showing the smallest decrease of 12%.

Changes in classification accuracies between training and testing dataset separated for each of the individual are plotted in Figure 9. Both, changes in overall accuracies as well as changes in accuracies separated for each individual, indicate that call structure is not completely stable across recording sessions and that playback elicited calls may be very different from spontaneous calls.

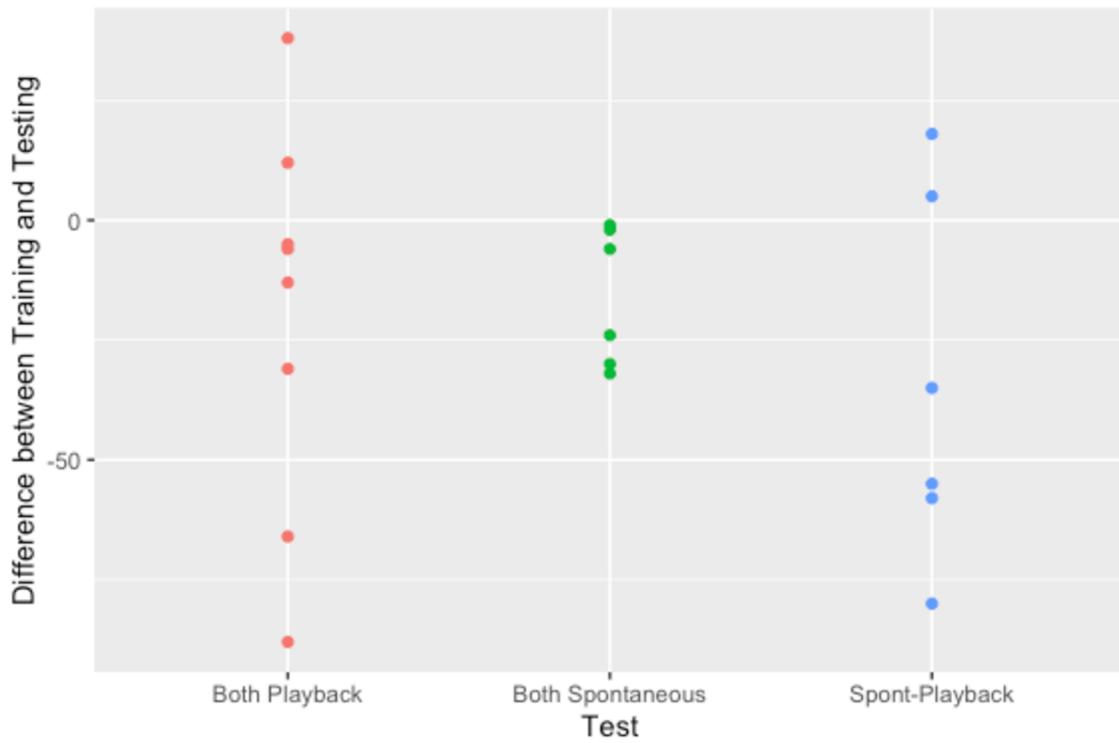


Figure 9. Scatterplot showing reduction in discrimination accuracies calculated by subtracting accuracy based on the testing dataset from the accuracy based on the training dataset.

Relationship between spatial distribution of individuals and similarity of their calls

Based on the higher number of individuals and because individuals in the Cameroonian population were evenly spread on larger space, I focused on Cameroonian population only with this analysis. I ran a Mantel test to see the correlation between two variables - the geographic distances and acoustic similarity. I calculated the pairwise geographic distances for each pair of individuals. Then, I calculated the Euclidian distances based on the three acoustic variables for each pair of individuals giving a metric of similarity between their averaged calls. There was no relationship between acoustic similarity and geographical distance (Mantel test, $r = -0.09$, simulated p-value on 9999 replicates = 0.7804).

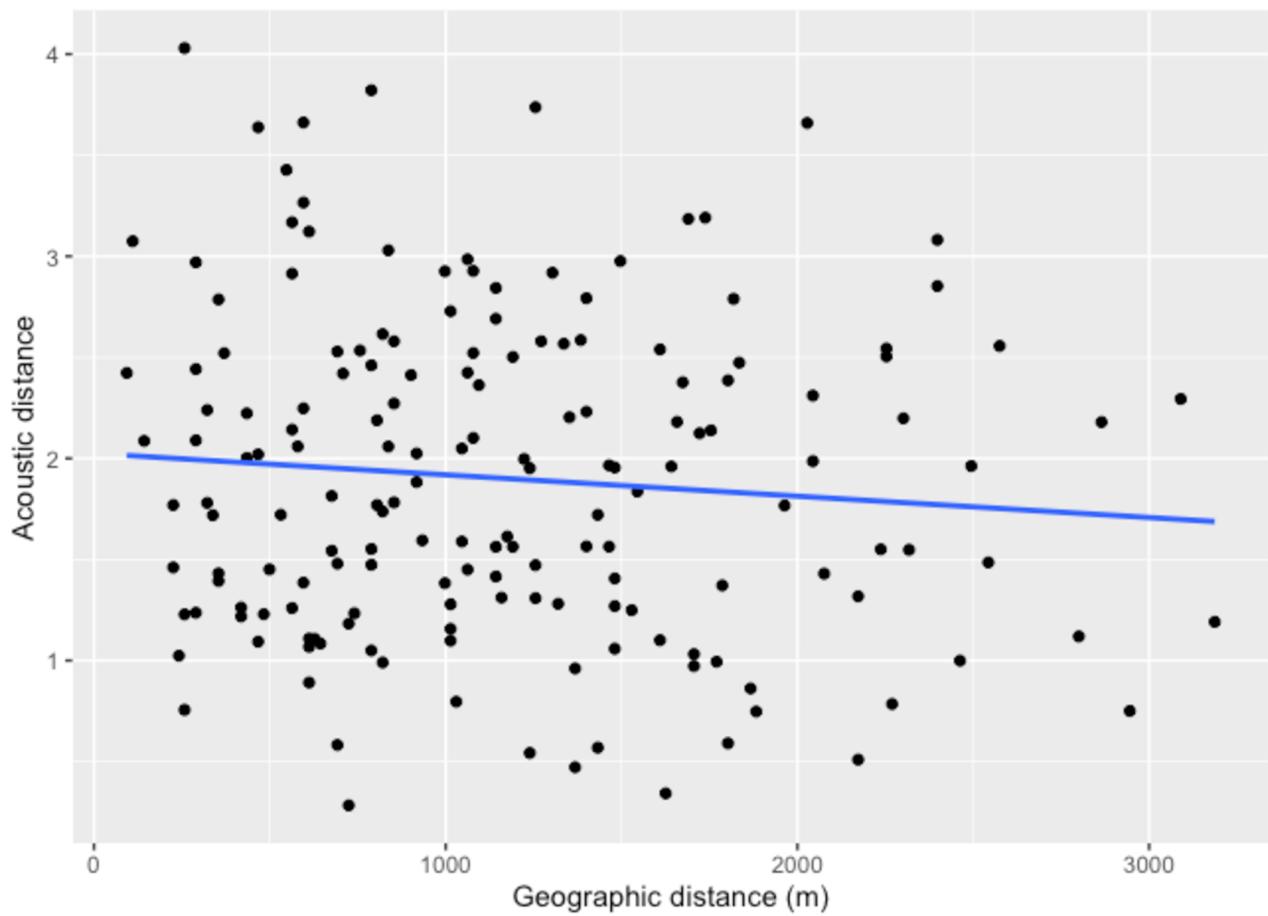


Figure 10. Relationship between acoustic and geographic distance in Cameroonian YRT population. Each point represents pairwise acoustic and geographic distance for a given pair of YRT individuals. Linear regression line was included to illustrate correlation trend.

Discussion:

Studies on bird songs have always been the centre of attention when it came to studying animal communication or identity signalling. The species of yellow-rumped Tinkerbird described in this study is a non-song bird and, therefore, their calls are believed to be innate and they are believed to have only limited capacity to modify its songs during its life time.

Differences in call parameters between populations

All of the three studied call variables differed between Cameroonian and South African population. This might not be surprising as the two populations are located very far away from each other and the birds from the two populations actually represent two different subspecies of the yellow-rumped tinkerbird (*Pogoniulus bilineatus leucolaimus* in Cameroon and *P. b. bilineatus* in South Africa). Song and calls characteristics often differ between distant population or subspecies. There are different reasons why call characteristics differ.

The two subspecies differ in size and *P.b. leucolaimus* found in Cameroon is larger in size when compared to their South African counter part *P. b. bilineatus*. Peak frequency is often negatively related to body size. I found that peak frequency was slightly lower in Cameroon where YRT are larger than in South Africa. Relationship between calls and body size can be also documented in other studies concerning tinkerbirds and even YRT. For example, (Kirschel, Blumstein et al. 2009) suggest that song divergence mirrors body size in the larger *P. bilineatus* in sympatry singing lower frequency songs and the smaller *P. subsulphureus* singing higher frequency songs which fits perfectly with results presented in this thesis. Also, frequency of songs is linked to body size in Asian barbets (Gonzalez-Voyer, den Tex et al. 2013)

Other morphological traits could also affect call characteristics of the two subspecies. For example, in tanagers which is the largest family of Neo-tropical song birds they found that the bill size acts as the modulator for various song elements. The birds which had larger bills sang lower pitched songs with longer notes, longer pauses, and fewer rapid shifts in frequencies. Similarly, morphological bill adaptations were accompanied by similar song changes in sympatric Darwin finch species (Demery, Burns et al. 2021). Thus, bill morphology might affect all the song parameters that I measured. However, I do not know whether and how bill morphology differs between the two YRT populations.

Second, environmental conditions could affect the song parameters. Acoustic adaptation hypothesis states that to overcome certain environmental constraints, like for example, dense vegetation or environmental noise, the species has to adapt to local environment ensuring that message is properly conveyed to the receiver. Vegetation density was not assessed on neither of the sites, so it is difficult to judge whether different vegetation structure might contribute to observed call differences. Both populations live in very dense forests so there is no obvious difference in vegetation structure on both sites. On the other hand, environmental noise might be different on both sites. Cameroonian population was located in a pristine forest which had minimal or none noise disturbance, while South African population is located near to the coast. It can be that because of the rushing air and colliding low frequency noise of waves the birds in the South African population have to communicate at a higher peak frequency. Indeed, ocean noise seems to influence peak frequency across different tinkerbird species(Sebastianelli, Blumstein et al. 2021).

Individuality in YRT in comparison with other species

The individual variation I found in Yellow-rumped tinkerbird is very small. I did not find dramatic differences in individuality between the two populations indicating that there are no fundamental differences in conditions favouring individual recognition. Overall Beecher's information statistic (HS) for the combined population was 2.61 bits. I compared it with HS values from other bird species provided by my supervisor (Linhart et al, unpublished data). YRT HS value is only a bit higher than that found in green dumped parrot which is at the low end of the HS ranges (HS = 1.62 bits). On the other hand, the highest individuality was found in Tawny owls having an HS score of 11.69 bits. The individuality averaged across the bird species is equal to HS = 6.93 bits.

Low individuality in YRT songs is puzzling. It could be that individual recognition is not that important in YRT and, therefore, YRT does not need highly individually distinct songs. But, when I look at YRT life history it rather suggests the exact opposite. They are sedentary and maintain year round territories and in dense vegetation that makes it difficult to recognize individuals visually. These are all conditions that should support ability and need to discriminate neighbours from strangers based on songs.

Low individuality could be partly a result of the simple structure of YRT songs which they sing. This was the reason that I wasn't able to extract more variables. The studies done on owls and

nightjars typically find high individuality. In these species, researchers were able to extract many more variables because the calls were longer and they had more complex acoustic structure. YRT only had a series of popping sounds which probably does not allow for sophisticated signalling of individual identity. Other reason for the fact that I got low discrimination of individuals in LDA might be that I am using the 60-40 cross-validation which is stricter than methods used in other studies. Most studies which have been done so far don't use cross validation or they use leave-one-out cross-validation which provide more optimistic results. One drawback of the study is that individuals were not colour-ringed and individual identity was assumed based on which territory songs were recorded. Although, YRT is described as a resident and sedentary species with year round territories, it could be possible that, in some cases, different birds were recorded on a single territory. Such misidentifications would decrease the estimate of individuality.

Further, YRT might switch to a different call type in situations requiring individual recognition which would have higher individual distinctiveness. The level of individuality may depend on call type. A research which was done on southern white rhinoceros compared individual distinctiveness across their different call types. They had identified three types of calls and denoted them as Grunt, Snort, and Hiss. They found that each call possessed an acoustic structure which made it individually distinctive but the level of individuality varied markedly. After calculating the HS scores for each call type, for Grunt they got an HS score of 2.63 bits. while for Hiss it was a bit lower 1.25 bits, and for Snort it was only 0.50 bits(Linn, Schmidt et al. 2021). This thesis focused on territorial calls of YRT which is the most common vocalization. In some recordings it was apparent that YRT has more call types or singing styles in its repertoire but those were rather rare. Still, there is a some possibility that those not so common vocalizations are used for individual recognition and possess higher individuality. We still lack knowledge about the bird and its behaviour and it would require more field data to be collected.

Stability of individually distinct vocal features in YRT

One reason for the low individuality in YRT songs could also be that vocal parameters are not very stable in time. When analysing the recording I noticed that while the call parameters were sometimes very stable, all the three measured parameters could also sometimes vary remarkably even within a single recording session. For example, there were some individuals which showed tremendous upwards as well as downward shifts in their call frequency. I often observed some

minor shifts especially when a playback was associated with recording session. I even observed that when a bird from the neighbouring territory started duetting the focal individual would increase its peak frequency and sing until the other birds stops and then the focal individual would again lower its peak frequency and start singing normally.

When it came to test the stability of voice across different recording sessions I investigated three conditions depending whether playback was used to elicit songs of YRT. Among three of these conditions I found the highest drop in the classification accuracy was found when the LDA classification model was build from the recordings of spontaneous songs and tested on recordings elicited by playback which further supports that birds change their calls in response to other birds.

Studies often use playbacks to elicit songs in studies investigating individuality, but it likely decreases estimates of individuality – spontaneous songs might be better for proper estimates of individuality.

Spatial Distribution and call similarity

Previous studies documented geographical variation in vocalizations of non-songbirds. Studies have shown differences between populations or clinal variation in vocalizations on larger geographical scales (Goldstein 1978, Galeotti et al. 1996, Bretagnolle and Genevois 1997, Isler et al. 2005, Mager et al. 2007). Geographic variation in vocalizations of non-songbirds linked to genetic differences between populations (Isler et al. 2005) corresponding to the fact that vocalizations of non-songbirds are believed to be genetically determined. I found no effect of spatial distribution on similarity of calls among Yellow-rumped Tinkerbird at the Cameroonian site. No effect of geographic distance on similarity of calls between individuals was also found in Bornean gibbons (Clinken et al. 2017), which are primates, but their songs are also innate as in case of YRT and the study was carried out on a similar small geographic scale which is rare. Usually, studies investigating relationship between similarity of vocalizations and geographic distance are done on larger geographical scales or compare differences between individuals and populations without taking geographic distance into account. The authors expected negative relationship between distance and similarity of gibbon songs due to related females settle close to each other. Clink et al.

(2017) concluded that the geographical scale was too limited or that differences between individuals were too large and overrode geographic variation which could be the case in YRT too.

Conclusion:

I may conclude that there is some level of individuality present in YRT songs. There were differences in call parameters between the two populations and among individuals present in those populations, but individuality in calls of YRT is not that high. One reason for the relatively low individuality in YRT calls could be that, structure of calls seem to change within and across recording sessions especially, during interactions with real or playback simulated rivals. The future studies estimating individuality in animal vocalisations should focus on spontaneous calls if possible. Last but not the least I didn't find any relationship between similarity of calls and geographic distance.

Bibliography:

- Bergman, T. J., & Sheehan, M. J. (2013). Social knowledge and signals in primates. *American Journal of Primatology*, 75(7), 683-694.
- Box, H. O. (2003). Characteristics and propensities of marmosets and tamarins: Implications for studies of innovation.
- Bradbury, J. W., & Vehrenberg, S. L. (1998). Principles of animal communication.
- Byers, K. A., Lee, M. J., Bidulka, J. J., Patrick, D. M., & Himsworth, C. G. (2019). Rat in a cage: Trappability of urban Norway rats (*Rattus norvegicus*). *Frontiers in Ecology and Evolution*, 7, 68.
- Cavanagh, P., & Ritchison, G. (1987). Variation in the bounce and whinny songs of the Eastern Screech-Owl. *The Wilson Bulletin*, 99, 620-627.
- Charlton, B. D., Zhihe, Z., & Snyder, R. J. (2009). Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*). *The Journal of the Acoustical Society of America*, 126(5), 2721-2732. doi:10.1121/1.3224720
- Charrier, I., & Harcourt, R. G. (2006). Individual vocal identity in mother and pup Australian sea lions (*Neophoca cinerea*). *Journal of Mammalogy*, 87(5), 929-938.
- Charrier, I., Jouventin, P., Mathevon, N., & Aubin, T. (2001). Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biology*, 24(5), 378-382.
- Charrier, I., Mathevon, N., & Jouventin, P. (2003). Individuality in the voice of fur seal females: an analysis study of the pup attraction call in *Arctocephalus tropicalis*. *Marine Mammal Science*, 19(1), 161-172.
- Clink, D. J., Bernard, H., Crofoot, M. C., & Marshall, A. J. (2017). Investigating individual vocal signatures and small-scale patterns of geographic variation in female Bornean gibbon (*Hylobates muelleri*) great calls. *International Journal of Primatology*, 38(4), 656-671.
- Corne, C., Hingrat, Y., Robert, A., & Rybak, F. (2015). The meaning of boom calls in a lekking bird: identity or quality information? *Animal Behaviour*, 109, 249-264. doi:<https://doi.org/10.1016/j.anbehav.2015.07.017>
- Cunningham, E. P., Unwin, S., & Setchell, J. M. (2015). Darting primates in the field: a review of reporting trends and a survey of practices and their effect on the primates involved. *International Journal of Primatology*, 36(5), 911-932.
- Delgado Jr, R. A. (2007). Geographic variation in the long calls of male orangutans (*Pongo* spp.). *Ethology*, 113(5), 487-498.

- Delport, W., Kemp, A. C., & Ferguson, J. W. H. (2002). Vocal identification of individual African Wood Owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency. *Ibis*, 144(1), 30-39. doi:<https://doi.org/10.1046/j.0019-1019.2001.00019.x>
- Demery, A.-J. C., Burns, K. J., & Mason, N. A. (2021). Bill size, bill shape, and body size constrain bird song evolution on a macroevolutionary scale. *Ornithology*, 138(2). doi:10.1093/ornithology/ukab011
- Draganoiu, T. I., Moreau, A., Ravaux, L., Bonckaert, W., & Mathevon, N. (2014). Song stability and neighbour recognition in a migratory songbird, the black redstart. *Behaviour*, 151(4), 435-453.
- Eakle, W. L., Mannan, R. W., & Grubb, T. G. (1989). Identification of individual breeding bald eagles by voice analysis. *Journal of Wildlife Management*, 53(2), 450-455. doi:10.2307/3801149
- Fan, P.-F., Xiao, W., Feng, J.-J., & Scott, M. (2011). Population Differences and Acoustic Stability in Male Songs of Wild Western Black Crested Gibbons (*Nomascus concolor*) in Mt. Wuliang, Yunnan. *Folia primatologica; international journal of primatology*, 82, 83-93. doi:10.1159/000329128
- Feng, J.-J., Cui, L.-W., Ma, C.-Y., Fei, H.-L., & Fan, P.-F. (2014). Individuality and Stability in Male Songs of Cao Vit Gibbons (*Nomascus nasutus*) with Potential to Monitor Population Dynamics. *Plos One*, 9(5), e96317. doi:10.1371/journal.pone.0096317
- Fuller, J. (2014). The Vocal Repertoire of Adult Male Blue Monkeys (*Cercopithecus mitis stuhlmanni*): A Quantitative Analysis of Acoustic Structure. *American Journal of Primatology*, 76. doi:10.1002/ajp.22223
- Godard, R. (1991). Long-term memory of individual neighbours in a migratory songbird. *Nature*, 350(6315), 228-229.
- Gonzalez-Voyer, A., den Tex, R. J., Castelló, A., & Leonard, J. A. (2013). Evolution of acoustic and visual signals in Asian barbets. *J Evol Biol*, 26(3), 647-659. doi:10.1111/jeb.12084
- Halpin, Z. T. (1991). Kin recognition cues of vertebrates. *Kin recognition*, 220-258.
- Hile, A. G., Plummer, T. K., & Striedter, G. F. (2000). Male vocal imitation produces call convergence during pair bonding in budgerigars, *Melopsittacus undulatus*. *Animal Behaviour*, 59(6), 1209-1218. doi:<https://doi.org/10.1006/anbe.1999.1438>
- Holmes, W. G. (1983). Recognition Behavior: Comparative Social Recognition. Patrick Colgan. Wiley-Interscience, New York, 1983. xvi, 282 pp., illus. \$37.50. *Science*, 221(4614), 945-945.

- Humphries, D. J., Finch, F. M., Bell, M. B. V., & Ridley, A. R. (2016). Vocal Cues to Identity: Pied Babblers Produce Individually Distinct But Not Stable Loud Calls. *Ethology*, 122(7), 609-619. doi:<https://doi.org/10.1111/eth.12508>
- Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, 60(1), 1-11. doi:<https://doi.org/10.1006/anbe.2000.1410>
- Jones, B. S., Harris, D. H. R., & Catchpole, C. K. (1993). The stability of the vocal signature in phee calls of the common marmoset, *Callithrix jacchus*. *Am J Primatol*, 31(1), 67-75. doi:10.1002/ajp.1350310107
- Jouventin, P., Aubin, T., & Lengagne, T. (1999). Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour*, 57(6), 1175-1183.
- Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79(8), 2852-2862.
- Kidney, D., Rawson, B. M., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An Efficient Acoustic Density Estimation Method with Human Detectors Applied to Gibbons in Cambodia. *Plos One*, 11(5), e0155066. doi:10.1371/journal.pone.0155066
- Kirschel, A. N., Blumstein, D. T., & Smith, T. B. (2009). Character displacement of song and morphology in African tinkerbirds. *Proc Natl Acad Sci U S A*, 106(20), 8256-8261. doi:10.1073/pnas.0810124106
- Kroodsma, D. E. (1984). Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *The Auk*, 101(1), 13-24.
- Kroodsma, D. E., & Konishi, M. (1991). A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behaviour*, 42(3), 477-487.
- Kukalová, M., Gazárková, A., & Adamík, P. (2013). Should I stay or should I go? The influence of handling by researchers on den use in an arboreal nocturnal rodent. *Ethology*, 119(10), 848-859.
- Laiolo, P., Vögeli, M., Serrano, D., & Tella, J. L. (2007). Testing acoustic versus physical marking: two complementary methods for individual-based monitoring of elusive species. *Journal of Avian Biology*, 38(6), 672-681.
- Linhart, P., Fuchs, R., Poláková, S., & Slabbekoorn, H. (2012). Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers *Phylloscopus trochilus*. *Journal of Avian Biology*, 43(2), 186-192.

- Linn, S. N., Schmidt, S., & Scheumann, M. (2021). Individual distinctiveness across call types of the southern white rhinoceros (*Ceratotherium simum simum*). *Journal of Mammalogy*, 102(2), 440-456.
- Lovell, S. F., & Lein, M. R. (2004). Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behavioral Ecology*, 15(5), 799-804.
- Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., . . . Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation biology*, 22(6), 1424-1442.
- Matrosova, V. A., Volodin, I. A., & Volodina, E. V. (2009). Short-Term and Long-Term Individuality in Speckled Ground Squirrel Alarm Calls. *Journal of Mammalogy*, 90(1), 158-166. doi:10.1644/08-mamm-a-032.1
- Matrosova, V. A., Volodin, I. A., Volodina, E. V., Vasilieva, N. A., & Kochetkova, A. A. (2010). Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*. *Journal of Mammalogy*, 91(3), 620-627. doi:10.1644/09-mamm-a-143.1
- McGregor, P. (2002). Census and monitoring based on individually identifiable vocalizations: the role of neural networks. *Animal Conservation*, 5, 103-111. doi:10.1017/S1367943002002147
- Naguib, M. (2003). Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication. *J Acoust Soc Am*, 113(3), 1749-1756. doi:10.1121/1.1539050
- Nowicki, S. (1989). Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence. *Animal Behaviour*, 37, 64-73. doi:[https://doi.org/10.1016/0003-3472\(89\)90007-9](https://doi.org/10.1016/0003-3472(89)90007-9)
- Olendorf, R., Getty, T., Scribner, K., & Robinson, S. K. (2004). Male red-winged blackbirds distrust unreliable and sexually attractive neighbours. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1543), 1033-1038.
- Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: a new approach*: Cambridge University Press.
- Oyakawa, C., Koda, H., & Sugiura, H. (2007). Acoustic features contributing to the individuality of wild agile gibbon (*Hylobates agilis agilis*) songs. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 69(7), 777-790.
- Pimm, S. L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., . . . Loarie, S. (2015). Emerging Technologies to Conserve Biodiversity. *Trends Ecol Evol*, 30(11), 685-696. doi:10.1016/j.tree.2015.08.008

- Powell, R. A., & Proulx, G. (2003). Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense. *ILAR journal*, 44(4), 259-276.
- Puglisi, L., & Adamo, C. (2004). Discrimination of Individual Voices in Male Great Bitterns (*Botaurus stellaris*) in Italy. *Auk*, 121, 541-547. doi:10.2307/4090417
- Rhinehart, T. A., Chronister, L. M., Devlin, T., & Kitzes, J. (2020). Acoustic localization of terrestrial wildlife: Current practices and future opportunities. *Ecology and Evolution*, 10(13), 6794-6818. doi:<https://doi.org/10.1002/ece3.6216>
- Riolo, R. L., Cohen, M. D., & Axelrod, R. (2001). Evolution of cooperation without reciprocity. *Nature*, 414(6862), 441-443.
- Riters, L. V., Eens, M., Pinxten, R., Duffy, D. L., Balthazart, J., & Ball, G. F. (2000). Seasonal changes in courtship song and the medial preoptic area in male European starlings (*Sturnus vulgaris*). *Horm Behav*, 38(4), 250-261. doi:10.1006/hbeh.2000.1623
- Rukstalis, M., Fite, J. E., & French, J. A. (2003). Social Change Affects Vocal Structure in a Callitrichid Primate (*Callithrix kuhlii*). *Ethology*, 109(4), 327-340. doi:<https://doi.org/10.1046/j.1439-0310.2003.00875.x>
- Sebastianelli, M., Blumstein, D., & Kirschel, A. (2021). Higher-pitched bird song towards the coast supports a role for selection in ocean noise avoidance. *Bioacoustics*. doi:10.1080/09524622.2021.1879680
- Soulsbury, C. D., Gray, H. E., Smith, L. M., Braithwaite, V., Cotter, S. C., Elwood, R. W., . . . Collins, L. M. (2020). The welfare and ethics of research involving wild animals: A primer. *Methods in Ecology and Evolution*, 11(10), 1164-1181.
- Stoddard, P. K., Beecher, M. D., Horning, C. L., & Campbell, S. E. (1991). Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behavioral Ecology and Sociobiology*, 29(3), 211-215.
- Terry, A., Peake, T., & McGregor, P. (2005). The role of vocal individuality in conservation. *Frontiers in Zoology*, 2, 10. doi:10.1186/1742-9994-2-10
- Thompson, M. E., Schwager, S. J., Payne, K. B., & Turkalo, A. K. (2010). Acoustic estimation of wildlife abundance: methodology for vocal mammals in forested habitats. *African Journal of Ecology*, 48(3), 654-661. doi:<https://doi.org/10.1111/j.1365-2028.2009.01161.x>
- Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. *Trends in Ecology & Evolution*, 22(10), 529-537.

- Wanker, R., Apcin, J., Jennerjahn, B., & Waibel, B. (1998). Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behavioral Ecology and Sociobiology*, 43(3), 197-202.
- Washburn, S. (1955). Evolution as a process. Edited by Julian Huxley, AC Hardy, and EB Ford. 367 pp. George Allen and Unwin, London. 1954.(Distributed by Macmillan, \$4.25.). *American Journal of Physical Anthropology*, 13(1), 162-164.
- Weeden, J. S., & Falls, J. B. (1959). Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. *The Auk*, 343-351.
- Wei, M., Lloyd, H., & Zhang, Y. (2011). Neighbour–stranger discrimination by Yellow-bellied Tit *Parus venustulus*: evidence for the “dear-enemy” effect. *Journal of Ornithology*, 152(2), 431-438.
- Westcott, D. A. (1997). Neighbours, strangers and male-male aggression as a determinant of lek size. *Behavioral Ecology and Sociobiology*, 40(4), 235-242.
- Wiley, R. H., & Wiley, M. S. (1977). Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis*. *Behaviour*, 10-34.
- Wood, C. M., Klinck, H., Gustafson, M., Keane, J. J., Sawyer, S. C., Gutiérrez, R. J., & Peery, M. Z. (2021). Using the ecological significance of animal vocalizations to improve inference in acoustic monitoring programs. *Conserv Biol*, 35(1), 336-345. doi:10.1111/cobi.13516
- Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, 198(4318), 755-756.
- Goldstein, R. B. 1978. Geographic variation in the “Hoy” call of the Bobwhite. *Auk* 95: 85-94
- Galeotti, P. R., Appleby, B. M. and Redpath, S. M. 1996. Macro and microgeographical variations in the ‘hoot’ of Italian and English Tawny Owls (*Strix aluco*). *Italian Journal of Zoology* 63: 57-64.
- Bretagnolle, V. and Genevois, F. 1997. Geographic variation in the call of the Blue Petrel: effects of sex and geographic scale. *The Condor* 99: 985-989.
- Isler, M. L., Isler, P. R. and Brumfield, R. T. 2005. Clinal variation in vocalization of an antbird (Thamnophilidae) and implications for defining species limits. *The Auk* 122: 433-444.
- Mager III, J. N., Walcott, C. and Evers, D. 2007. Macrogeographic variation in the body size and territorial vocalizations of male Common Loons (*Gravia immer*). *Waterbirds* 30: 64-72.

Bibliography

Bergman, T. J. and M. J. Sheehan (2013). "Social knowledge and signals in primates." American Journal of Primatology **75**(7): 683-694.

Box, H. O. (2003). "Characteristics and propensities of marmosets and tamarins: Implications for studies of innovation."

Bradbury, J. W. and S. L. Vehrenamp (1998). "Principles of animal communication."

Byers, K. A., et al. (2019). "Rat in a cage: Trappability of urban Norway rats (*Rattus norvegicus*)."
Frontiers in Ecology and Evolution **7**: 68.

Cavanagh, P. and G. Ritchison (1987). "Variation in the bounce and whinny songs of the Eastern Screech-Owl." The Wilson Bulletin **99**: 620-627.

Charlton, B. D., et al. (2009). "Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*)."
The Journal of the Acoustical Society of America **126**(5): 2721-2732.

Charrier, I. and R. G. Harcourt (2006). "Individual vocal identity in mother and pup Australian sea lions (*Neophoca cinerea*)."
Journal of Mammalogy **87**(5): 929-938.

Charrier, I., et al. (2001). "Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*."
Polar Biology **24**(5): 378-382.

Charrier, I., et al. (2003). "Individuality in the voice of fur seal females: an analysis study of the pup attraction call in *Arctocephalus tropicalis*."
Marine Mammal Science **19**(1): 161-172.

Corne, C., et al. (2015). "The meaning of boom calls in a lekking bird: identity or quality information?"
Animal Behaviour **109**: 249-264.

Cunningham, E. P., et al. (2015). "Darting primates in the field: a review of reporting trends and a survey of practices and their effect on the primates involved."
International Journal of Primatology **36**(5): 911-932.

Delport, W., et al. (2002). "Vocal identification of individual African Wood Owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency."
Ibis **144**(1): 30-39.

Demery, A.-J. C., et al. (2021). "Bill size, bill shape, and body size constrain bird song evolution on a macroevolutionary scale."
Ornithology **138**(2).

Draganoiu, T. I., et al. (2014). "Song stability and neighbour recognition in a migratory songbird, the black redstart."
Behaviour **151**(4): 435-453.

Eakle, W. L., et al. (1989). "Identification of individual breeding bald eagles by voice analysis."
Journal of Wildlife Management **53**(2): 450-455.

- Fan, P.-F., et al. (2011). "Population Differences and Acoustic Stability in Male Songs of Wild Western Black Crested Gibbons (*Nomascus concolor*) in Mt. Wuliang, Yunnan." *Folia primatologica: international journal of primatology* **82**: 83-93.
- Feng, J.-J., et al. (2014). "Individuality and Stability in Male Songs of Cao Vit Gibbons (*Nomascus nasutus*) with Potential to Monitor Population Dynamics." *Plos One* **9**(5): e96317.
- Fuller, J. (2014). "The Vocal Repertoire of Adult Male Blue Monkeys (*Cercopithecus mitis stulmanni*): A Quantitative Analysis of Acoustic Structure." *American Journal of Primatology* **76**.
- Godard, R. (1991). "Long-term memory of individual neighbours in a migratory songbird." *Nature* **350**(6315): 228-229.
- Gonzalez-Voyer, A., et al. (2013). "Evolution of acoustic and visual signals in Asian barbets." *J Evol Biol* **26**(3): 647-659.
- Halpin, Z. T. (1991). "Kin recognition cues of vertebrates." *Kin recognition*: 220-258.
- Hile, A. G., et al. (2000). "Male vocal imitation produces call convergence during pair bonding in budgerigars, *Melopsittacus undulatus*." *Animal Behaviour* **59**(6): 1209-1218.
- Holmes, W. G. (1983). "Recognition Behavior: Comparative Social Recognition. Patrick Colgan. Wiley-Interscience, New York, 1983. xvi, 282 pp., illus. \$37.50." *Science* **221**(4614): 945-945.
- Humphries, D. J., et al. (2016). "Vocal Cues to Identity: Pied Babblers Produce Individually Distinct But Not Stable Loud Calls." *Ethology* **122**(7): 609-619.
- Janik, V. M. and P. J. B. Slater (2000). "The different roles of social learning in vocal communication." *Animal Behaviour* **60**(1): 1-11.
- Jones, B. S., et al. (1993). "The stability of the vocal signature in phee calls of the common marmoset, *Callithrix jacchus*." *Am J Primatol* **31**(1): 67-75.
- Jouventin, P., et al. (1999). "Finding a parent in a king penguin colony: the acoustic system of individual recognition." *Animal Behaviour* **57**(6): 1175-1183.
- Karanth, K. U. and J. D. Nichols (1998). "Estimation of tiger densities in India using photographic captures and recaptures." *Ecology* **79**(8): 2852-2862.
- Kidney, D., et al. (2016). "An Efficient Acoustic Density Estimation Method with Human Detectors Applied to Gibbons in Cambodia." *Plos One* **11**(5): e0155066.
- Kirschel, A. N., et al. (2009). "Character displacement of song and morphology in African tinkerbirds." *Proc Natl Acad Sci U S A* **106**(20): 8256-8261.
- Kroodsma, D. E. (1984). "Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate." *The Auk* **101**(1): 13-24.

Kroodsma, D. E. and M. Konishi (1991). "A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback." *Animal Behaviour* **42**(3): 477-487.

Kukalová, M., et al. (2013). "Should I stay or should I go? The influence of handling by researchers on den use in an arboreal nocturnal rodent." *Ethology* **119**(10): 848-859.

Laiolo, P., et al. (2007). "Testing acoustic versus physical marking: two complementary methods for individual-based monitoring of elusive species." *Journal of Avian Biology* **38**(6): 672-681.

Linhart, P., et al. (2012). "Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers *Phylloscopus trochilus*." *Journal of Avian Biology* **43**(2): 186-192.

Linn, S. N., et al. (2021). "Individual distinctiveness across call types of the southern white rhinoceros (*Ceratotherium simum simum*)."*Journal of Mammalogy* **102**(2): 440-456.

Lovell, S. F. and M. R. Lein (2004). "Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*."*Behavioral Ecology* **15**(5): 799-804.

Mace, G. M., et al. (2008). "Quantification of extinction risk: IUCN's system for classifying threatened species."*Conservation biology* **22**(6): 1424-1442.

Matrosova, V. A., et al. (2009). "Short-Term and Long-Term Individuality in Speckled Ground Squirrel Alarm Calls."*Journal of Mammalogy* **90**(1): 158-166.

Matrosova, V. A., et al. (2010). "Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*."*Journal of Mammalogy* **91**(3): 620-627.

McGregor, P. (2002). "Census and monitoring based on individually identifiable vocalizations: the role of neural networks."*Animal Conservation* **5**: 103-111.

Naguib, M. (2003). "Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication."*J Acoust Soc Am* **113**(3): 1749-1756.

Nowicki, S. (1989). "Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence."*Animal Behaviour* **37**: 64-73.

Olendorf, R., et al. (2004). "Male red-winged blackbirds distrust unreliable and sexually attractive neighbours."*Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**(1543): 1033-1038.

Owings, D. H. and E. S. Morton (1998). *Animal vocal communication: a new approach*, Cambridge University Press.

Oyakawa, C., et al. (2007). "Acoustic features contributing to the individuality of wild agile gibbon (*Hylobates agilis agilis*) songs."*American Journal of Primatology: Official Journal of the American Society of Primatologists* **69**(7): 777-790.

Pimm, S. L., et al. (2015). "Emerging Technologies to Conserve Biodiversity." Trends Ecol Evol **30**(11): 685-696.

Powell, R. A. and G. Proulx (2003). "Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense." ILAR journal **44**(4): 259-276.

Puglisi, L. and C. Adamo (2004). "Discrimination of Individual Voices in Male Great Bitterns (*Botaurus stellaris*) in Italy." Auk **121**: 541-547.

Rhinehart, T. A., et al. (2020). "Acoustic localization of terrestrial wildlife: Current practices and future opportunities." Ecology and Evolution **10**(13): 6794-6818.

Riolo, R. L., et al. (2001). "Evolution of cooperation without reciprocity." Nature **414**(6862): 441-443.

Riters, L. V., et al. (2000). "Seasonal changes in courtship song and the medial preoptic area in male European starlings (*Sturnus vulgaris*)."Horm Behav **38**(4): 250-261.

Rukstalis, M., et al. (2003). "Social Change Affects Vocal Structure in a Callitrichid Primate (*Callithrix kuhlii*)."Ethology **109**(4): 327-340.

Sebastianelli, M., et al. (2021). "Higher-pitched bird song towards the coast supports a role for selection in ocean noise avoidance."Bioacoustics.

Soulsbury, C. D., et al. (2020). "The welfare and ethics of research involving wild animals: A primer."Methods in Ecology and Evolution **11**(10): 1164-1181.

Stoddard, P. K., et al. (1991). "Recognition of individual neighbors by song in the song sparrow, a species with song repertoires."Behavioral Ecology and Sociobiology **29**(3): 211-215.

Terry, A., et al. (2005). "The role of vocal individuality in conservation."Frontiers in Zoology **2**: 10.

Thompson, M. E., et al. (2010). "Acoustic estimation of wildlife abundance: methodology for vocal mammals in forested habitats."African Journal of Ecology **48**(3): 654-661.

Tibbetts, E. A. and J. Dale (2007). "Individual recognition: it is good to be different."Trends in Ecology & Evolution **22**(10): 529-537.

Wanker, R., et al. (1998). "Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition."Behavioral Ecology and Sociobiology **43**(3): 197-202.

Washburn, S. (1955). "Evolution as a process. Edited by Julian Huxley, AC Hardy, and EB Ford. 367 pp. George Allen and Unwin, London. 1954.(Distributed by Macmillan, \$4.25.)."American Journal of Physical Anthropology **13**(1): 162-164.

Weeden, J. S. and J. B. Falls (1959). "Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals." The Auk: 343-351.

Wei, M., et al. (2011). "Neighbour-stranger discrimination by Yellow-bellied Tit *Parus venustulus*: evidence for the “dear-enemy” effect." Journal of Ornithology **152**(2): 431-438.

Westcott, D. A. (1997). "Neighbours, strangers and male-male aggression as a determinant of lek size." Behavioral Ecology and Sociobiology **40**(4): 235-242.

Wiley, R. H. and M. S. Wiley (1977). "Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis*." Behaviour: 10-34.

Wood, C. M., et al. (2021). "Using the ecological significance of animal vocalizations to improve inference in acoustic monitoring programs." Conserv Biol **35**(1): 336-345.

Würsig, B. and M. Würsig (1977). "The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*)."Science **198**(4318): 755-756.