

STRUCTURAL VARIATION AND COMMUNICATIVE FUNCTIONS OF  
LONG-FINNED PILOT WHALE (*GLOBICEPHALA MELAS*) PULSED CALLS  
AND COMPLEX WHISTLES

by

Leah Nemiroff

Submitted in partial fulfillment of the requirements  
for the degree of Master of Science

at

Dalhousie University  
Halifax, Nova Scotia  
January 2009

© Copyright by Leah Nemiroff, 2009

**DALHOUSIE UNIVERSITY**

DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled “STRUCTURAL VARIATION AND COMMUNICATIVE FUNCTIONS OF LONG-FINNED PILOT WHALE (*GLOBICEPHALA MELAS*) PULSED CALLS AND COMPLEX WHISTLES” by Leah Nemiroff in partial fulfillment of the requirements for the degree of Master of Science.

Dated: 28 January, 2009

Supervisor:

---

Readers:

---

---

---

DALHOUSIE UNIVERSITY

DATE: January 28, 2009

AUTHOR: Leah Nemiroff

TITLE: STRUCTURAL VARIATION AND COMMUNICATIVE  
FUNCTIONS OF LONG-FINNED PILOT WHALE  
(*GLOBICEPHALA MELAS*) PULSED CALLS AND COMPLEX  
WHISTLES

DEPARTMENT: Department of Biology

DEGREE: MSc CONVOCATION: May YEAR: 2009

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions.

---

Signature of Author

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

The author attests that permission has been obtained for the use of any copyrighted material appearing in the thesis (other than the brief excerpts requiring only proper acknowledgement in scholarly writing), and that all such use is clearly acknowledged.

To Sach, for singing to me about lemons.

And to my family, who always believed that I could be a marine biologist, even though  
I'm scared of fish.

# Table of Contents

Table of Contents.....	v
List of Tables.....	viii
List of Figures.....	x
Abstract.....	xv
List of Abbreviations Used.....	xvi
Acknowledgements.....	xviii
<b>CHAPTER 1 – INTRODUCTION.....</b>	<b>1</b>
1.1 General Introduction.....	1
1.2 The Long-Finned Pilot Whale.....	3
1.2.1 Distribution and Abundance.....	3
1.2.2 Movement Patterns.....	4
1.2.3 Individual Identification.....	4
1.2.4 Social Structure.....	4
1.3 Cetacean Vocalization.....	5
1.3.1 Cetacean Sound Production and Hearing.....	5
1.3.2 Odontocete Vocalizations.....	7
1.3.3 Long-Finned Pilot Whale Vocalizations.....	8
1.4 Thesis Overview.....	10
<b>CHAPTER 2 – PILOT WHALE PULSED CALLS.....</b>	<b>11</b>
2.1 Introduction.....	11
2.2 Methods.....	13
2.2.1 Field Sites.....	13
2.2.2 Recording of Vocalizations.....	14
2.2.3 Acoustic Analysis.....	14
2.2.4 Statistical Analysis.....	16
2.3 Results.....	18
2.3.1 Properties of Pilot Whale Pulsed Calls.....	18
2.3.2 Principal Components Analysis.....	23
2.3.3 K-means Cluster Analysis.....	27
2.3.3 Hierarchical Cluster Analysis.....	27
2.4 Discussion.....	31
2.4.1 The Structural Complexity of Pulsed Calls.....	31
2.4.2 The Non-Discrete Nature of Pulsed Calls.....	34
2.4.3 Pilot and Killer Whale Pulsed Calls, an Example of Form Following Function?.....	36
2.5 Summary.....	39
<b>CHAPTER 3 – RATING THE SIMILARITY OF PILOT WHALE CALLS             USING STATISTICAL AND PERCEPTUAL MEASURES.....</b>	<b>40</b>
3.1 Introduction.....	40

3.2 Methods.....	42
3.2.1 Field Sites.....	42
3.2.2 Recording of Vocalizations.....	42
3.2.3 Call Extraction.....	42
3.2.4 Statistical Measures.....	43
3.2.4.1 Acoustic Analysis.....	43
3.2.4.2 Statistical Analysis.....	44
3.2.5 Perceptual Measures.....	44
3.2.5.1 Online Comparison of Calls.....	44
3.2.5.2 Statistical Analysis.....	48
3.2.6 Statistical Measures vs. Perceptual Measures.....	50
3.3 Results.....	51
3.3.1 Similarities from Quantitative Statistical Measures.....	51
3.3.2 Similarities from Qualitative Perceptual Measures.....	51
3.3.3 Statistical Measures vs. Perceptual Measures.....	56
3.4 Discussion.....	57
3.4.1 The Perceptual Method.....	57
3.4.2 Human Perception of Pilot Whale Calls.....	59
3.4.3 The Statistical Method.....	60
3.4.4 Comparing Perceptual Measures with Statistical Measures.....	60
3.5 Summary.....	61

**CHAPTER 4 – SOURCES OF VARIATION AND COMMUNICATIVE FUNCTIONS OF PILOT WHALE PULSED CALLS AND COMPLEX WHISTLES..... 63**

4.1 Introduction.....	63
4.2 Methods.....	65
4.2.1 Field Methods.....	65
4.2.1.1 Field Sites.....	65
4.2.1.2 Encounters.....	65
4.2.1.3 Photographic Effort and Photo-Identification.....	66
4.2.1.3 Recordings.....	66
4.2.2 Acoustic Analysis and Call Similarity Matrices.....	67
4.2.3 Assigning Social Units or Groups to Calls.....	67
4.2.3.1 Key Individuals and Constant Companions Method (KIN).....	68
4.2.3.2 Bayesian Hierarchical Mixture Model (BAY).....	68
4.2.3.3 Network Modularity Technique (NET).....	69
4.2.4 Assigning Contextual Information to Calls.....	70
4.2.5 Statistical Analysis.....	70
4.2.5.1 Relationships between Statistical Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts.....	72
4.2.5.2 Relationships between Perceptual Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts.....	74
4.3 Results.....	75
4.3.1 Statistical Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts.....	75
4.3.1.1 Testing MANOVA Assumptions.....	75

4.3.1.2 Call Similarity and Encounter .....	75
4.3.1.3 Call Similarity and Social Unit Membership .....	75
4.3.1.4 Call Similarity and Behavioural State .....	88
4.3.1.5 Call Similarity and Average Group Size .....	93
4.3.1.6 Call Similarity and Average Number of Calves .....	96
4.3.1.7 Call Similarity and Year .....	99
4.3.2 Perceptual Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts.....	99
4.3.2.1 Call Similarity and Encounter .....	99
4.3.2.2 Call Similarity and Social Unit Membership .....	102
4.3.2.3 Call Similarity and Behavioural State .....	102
4.3.2.4 Call Similarity and Average Group Size .....	106
4.3.2.5 Call Similarity and Average Number of Calves .....	108
4.3.2.6 Call Similarity and Year .....	108
4.4 Discussion .....	110
4.4.1 Investigating the Variability of Call Structure from Different Angles .....	110
4.4.2 What Governs Variability in Pulsed Calls? .....	111
4.4.4 What Governs Variability in Complex Whistles? .....	120
4.5 Summary .....	123
<b>CHAPTER 5 – CONCLUSION .....</b>	<b>124</b>
5.1 General Conclusions and Implications .....	124
5.2 Limitations of the Current Study and Suggestions for Future Work .....	126
5.2.1 Recording Calls, Measuring Spectrograms and Describing Call Similarity....	126
5.2.2 Contextual Information and Pilot Whale Social Structure off Cape Breton....	128
<b>APPENDIX I – php script used for online comparison of calls .....</b>	<b>130</b>
<b>APPENDIX II – Instructions for online call comparisons .....</b>	<b>134</b>
<b>APPENDIX III – Participant deviation from the modal ratings for the first ten     comparisons of pulsed calls and whistles .....</b>	<b>139</b>
<b>APPENDIX IV – Unit membership based on key individuals and constant     companions, Bayesian hierarchical mixture modeling and     aggregative network modularity .....</b>	<b>144</b>
<b>APPENDIX V – Histograms illustrating the statistical similarity of calls from     different encounters between and within social groups (as defined     by the KIN and BAY methods).....</b>	<b>146</b>
<b>APPENDIX VI – Means of each whistle and pulsed call measurement variable     (± 1SE) for mixed groups and single social units (from the KIN     and BAY methods), with associated ANOVA <i>F</i>-statistics and     significance values.....</b>	<b>148</b>
<b>APPENDIX VII – Spectrograms of every pulsed call included in the network     depiction of pulsed call similarity (Figure 4.17).....</b>	<b>156</b>
<b>LITERATURE CITED .....</b>	<b>163</b>

## List of Tables

Table 2.1. Description of the variables measured for each pulsed call.....	15
Table 2.2. Descriptive statistics of pilot whale pulsed calls .....	20
Table 2.3. A comparison of mean pilot whale pulsed call UFC measurements with published pilot whale mean whistle values (1 SD).....	22
Table 2.4. A comparison of pilot whale and killer whale pulsed call characteristics. The overlap reflects the percentage of the ranges that are common to both the pilot whale and the killer whale pulsed call measurements.....	22
Table 2.5. Eigenvalues and percentage of total variance explained (with and without Varimax rotation) of the 5 principal components of pilot whale pulsed calls .....	23
Table 2.6. Loadings (correlations between variables and components) of the Varimax rotated PCA on the spectrographic pulsed call variables. High loadings (greater than 0.5) are bolded. Variables which are highly loaded on the same component are strongly related.....	24
Table 3.1. Description of the variables measured for each whistle. ....	43
Table 3.2. The number of participants and comparisons (available and used) from the online call comparisons and the subsets of data used in subsequent analyses.....	49
Table 3.3. Correlation coefficients and significance values for matrix correlations between both pulsed call and whistle perceptual and statistical similarity matrices. Each value within the perceptual similarity matrices is the mean similarity score of all participant ratings. Only the first ten comparisons for each call class, which were rated by every participant, were considered.....	55
Table 3.4. Mean correlation coefficients for both whistles and pulsed calls for each possible series of matrix correlations. All of the ratings from each participant were compared to all common ratings from other participants, and to the similarity values produced by statistical measures, in a series of pairwise correlations.....	55
Table 4.1. Definitions of the four main categories of pilot whale behaviour, and examples of behavioural comments noted in log books. ....	65
Table 4.2. Common terms describing pilot whale social structure and their definitions, as used in this study. ....	67
Table 4.3. Names and descriptions of the social and contextual similarity matrices produced for both whistles and pulsed calls. ....	71

Table 4.4. Lilliefors tests for normality, Levene’s test statistics for homoscedasticity and Durban Watson D statistics of all measured pulsed call variables before and after standard transformations. Significance values of $P < 0.05$ indicate non-normality and heteroscedasticity. Durban Watson D values between 1 and 2 indicate little to no autocorrelation of the data. ....	76
Table 4.5. Lilliefors tests for normality, Levene’s test statistics for homoscedasticity and Durban Watson D statistics of all measured whistle variables before and after standard transformations. Significance values of $P < 0.05$ indicate non-normality and heteroscedasticity. Durban Watson D values between 1 and 2 indicate little to no autocorrelation of the data. ....	77
Table 4.6. The matrix correlation coefficients and significance values (1000 permutations) of all possible partial Mantel tests for both pulsed calls and whistles, controlling for encounter number. Matrix 1 contains the Mahalanobis multivariate distances between all pairs of calls, transformed into similarity values (see Chapter 3, section 3.2.4.2). Significant values ( $P < 0.05$ ) are indicated by an asterisk (*). ....	78
Table 4.7. Summary of MANOVA results comparing statistical measures of pulsed calls across social units, years, behaviours, group sizes and numbers of calves present during the recording period. The dependent variables included were sqrt(number of elements), sqrt(number of segments), sqrt (number of inflection points), log(SBI start), log (SBI mid), log(SBI end), log(duration), log(highest frequency sideband), lowest frequency sideband, log(start frequency), log(end frequency), and log(fundamental frequency). ....	81
Table 4.8. Summary of MANOVA results comparing statistical measures of whistles across social units, years, behaviours, group sizes and numbers of calves present during the recording period. The dependent variables included were sqrt(number of inflection points), sqrt(number of steps), sqrt (number of parts), log(duration), log(highest frequency), log(lowest frequency), log(start frequency), log(middle frequency), and log(end frequency). ....	85
Table 4.9. The results of the Kruskal-Wallis tests for pulsed call and whistle similarity across social groups and contexts. Similarity was defined by three different combinations of human ratings (either $\geq 3$ , $\geq 4$ or $= 5$ ). Because the grouping variable (similar or dissimilar) only had two levels, the Mann-Whitney U statistic is reported (df = 1). Significance values ( $P < 0.05$ ) are indicated by an asterisk (*), and significant associations that were maintained across all three definitions of similarity are bolded. Only calls from different encounters were compared to each other. ....	103

## List of Figures

Figure 1.1. Schematic of a long-finned pilot whale head. The sound generator is the Monkey Lips/Dorsal Bursae Complex (MLDB). (Image courtesy of Uko Gorter Natural History Illustrations. Modified and adapted from Cranford et al. 1996.).....	6
Figure 1.2. Spectrograms (frequency-time diagrams) showing examples of the three types of pilot whale vocalizations. (a) clicks, (b) a complex whistle, and (c) a pulsed call. ....	8
Figure 1.3. The graded nature of pilot whale whistles. Note the continuum of intermediate contour shapes between the seven labeled basic whistle types (from Taruski 1979).....	9
Figure 2.1. Spectrographic example of a pilot whale pulsed call. Calls may consist of two components, an upper frequency component (UFC) that is a narrow-band tone, and a lower frequency component (LFC) that is a broadband pulse. The pulse repetition rate (PRR) is reflected by the sideband interval (SBI). Elements are distinguished by abrupt shifts in the PRR.....	12
Figure 2.2. Map of the northwest tip of Cape Breton Island, Nova Scotia, Canada where the two field sites are located. The position of each pilot whale encounter from which pulsed calls were extracted is plotted (n = 94). Inset map shows Nova Scotia and surrounding maritime provinces. ....	19
Figure 2.3. Number of elements per pulsed call (n = 419).....	21
Figure 2.4. Number of inflection points per pulsed call (n = 419).....	21
Figure 2.5. Plot of eigenvalues of the principal components. Most of the variance in the pulsed call data is contained in the first five principal components. ....	25
Figure 2.6. Scores plots of component 2 (frequency of the maximum visible sideband) with (a) component 1 (sideband intervals of the first element), (b) component 3 (fundamental frequency parameters), (c) component 4 (structural elements: number of parts and inflection points), and (d) component 5 (presence or absence of a UFC, duration and final SBI of the call) of the PCA. Only scores plots with component 2 showed any grouping pattern. Consequently, other scores plots are not shown. ....	26
Figure 2.7. Examples of (a) a pulsed call with a maximum visible sideband above 18 kHz, and (b) a pulsed call with a maximum visible sideband below 15kHz. ....	27

Figure 2.8. <i>K</i> -means cluster analysis groupings (with number of clusters from $2 \leq k \leq 10$ ) shown as the grouping variable for the PCA scores plots of component 2 (frequency of maximum sideband) and component 4 (structural elements). Aside from the plots shown, there was no clear delineation of call types. ....	28
Figure 2.9. Modularity graph for the hierarchical cluster analysis of pulsed call similarity. Maximum modularity ( $Q$ ) = 0.003 as indicated by the asterisk. ....	29
Figure 2.10. Hierarchical average linkage dendrogram of measured pulsed calls. Clustering was stopped by maximum modularity at the dashed line (Mahalanobis distance = 7.9). ....	30
Figure 2.11. Examples of (a) a simple pilot whale pulsed call with a single element and inflection point, and (b) a more complex pulsed call with multiple elements, inflection points and a UFC. ....	31
Figure 2.12. The Delphinidae branch of a recent phylogenetic tree produced by analysis of cytochrome b sequences in a Bayesian framework. Note that killer whales ( <i>Orcinus orca</i> ) are in the Orcininae subfamily, and long-finned pilot whales ( <i>Globicephala melas</i> ) are in the Globicephalinae subfamily. Reprinted with permission from May-Collado and Agnarsson (2006). ....	38
Figure 3.1. Example screenshot of the website for aural and visual inspection of spectrograms. Observers chose their similarity ratings (from identical to no similarity) from the drop-down menu for each pair of calls. ....	45
Figure 3.2. Schematic illustrating the random pulling of pilot whale call pairs from predetermined categories for human similarity ratings. Broad categories contained calls that were similar to each other, and the dissimilar category contained all calls. Half of calls rated by each participant were from the dissimilar category and half were from the broadly similar categories (1/6 each). ....	46
Figure 3.3. The background information form filled-out by each individual before rating pairs of pilot whale calls through the website. ....	47
Figure 3.4. Examples of pulsed call pairs rated (a) high similarity and (b) low similarity from the statistical measures. ....	52
Figure 3.5. Examples of whistle pairs rated (a) high similarity and (b) low similarity from the statistical measures. ....	52
Figure 3.6. Examples of pulsed call pairs rated (a) identical and (b) different during the online comparisons. ....	53
Figure 3.7. Examples of whistle pairs rated (a) identical and (b) different during the online comparisons. ....	53

Figure 3.8. Box-and-whisker plots of mean participant deviations from the modal ratings of the first ten comparisons for (a) pulsed calls and (b) whistles. The center vertical line in a box-and-whisker plot marks the median of the sample. The length of each box shows the range within which the central 50% of the values fall (interquartile range). The whiskers show the range of observed values that fall within 1.5 times the interquartile range (Sokal and Rohlf 1995). The far outliers in (b) (designated by empty circles) were removed for subsequent analyses. ....	54
Figure 4.1. Histograms illustrating the statistical similarity of calls between (blue and green) and within (red and purple) encounters for (a) pulsed calls and (b) whistles. Calls were significantly more similar within an encounter than between them for both pulsed calls and whistles (Mantel tests, $P < 0.001$ ). ....	79
Figure 4.2. Histograms illustrating the statistical similarity of calls from different encounters between (blue and green) and within (red and purple) NET defined social groups for (a) pulsed calls and (b) whistles. Note that pulsed calls are slightly more similar within social groups than between them, while whistles appear to be less similar within groups than between them. This pattern is not as obvious for either pulsed calls (c) or whistles (d) when only single units are included. ....	80
Figure 4.3. Means of each pulsed call measurement variable ( $\pm 1$ SE) for mixed and single social units (from the NET method), with associated ANOVA $F$ -statistics and significance values. ....	82
Figure 4.4. Means of each pulsed call measurement variable ( $\pm 1$ SE) for single social units only (from the NET method), with associated ANOVA $F$ -statistics and significance values. ....	83
Figure 4.5. Means of each whistle measurement variable ( $\pm 1$ SE) for mixed and single social units (from the NET method), with associated ANOVA $F$ -statistics and significance values. ....	86
Figure 4.6. Means of each whistle measurement variable ( $\pm 1$ SE) for single social units only (from the NET method), with associated ANOVA $F$ -statistics and significance values. ....	87
Figure 4.7. Histograms illustrating the statistical similarity of calls from different encounters between (blue) and within (red): (a) behavioural categories, (b) average numbers of whales present, (c) average numbers of calves observed, and (d) recording years. Pulsed calls similarity was significantly correlated with behaviour and the number of calves observed (partial Mantel tests, $P < 0.001$ ). ....	89
Figure 4.8. Means of each pulsed call measurement variable ( $\pm 1$ SE) across behavioural categories, where F = foraging, R = resting, S = socializing, and T = travelling. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	90

Figure 4.9. Histograms illustrating the statistical similarity of whistles from different encounters between (green) and within (purple): (a) behavioural categories, (b) average numbers of whales present, (c) average numbers of calves observed, and (d) recording years. Complex whistle similarity was found to be significantly correlated with the average group size (partial Mantel test, $P = 0.001$ ). .....	91
Figure 4.10. Means of each whistle measurement variable ( $\pm 1$ SE) across behavioural categories, where F = foraging, R = resting, S = socializing, and T = travelling. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	92
Figure 4.11. Means of each pulsed call measurement variable ( $\pm 1$ SE) across average group size categories. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	94
Figure 4.12. Means of each whistle measurement variable ( $\pm 1$ SE) across average group size categories. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	95
Figure 4.13. Means of each pulsed call measurement variable ( $\pm 1$ SE) across average number of calves categories. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	97
Figure 4.14. Means of each whistle measurement variable ( $\pm 1$ SE) across average number of calves categories. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	98
Figure 4.15. Means of each pulsed call measurement variable ( $\pm 1$ SE) across years. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	100
Figure 4.16. Means of each whistle measurement variable ( $\pm 1$ SE) across years. Also shown are the associated ANOVA $F$ -statistics and significance values. ....	101
Figure 4.17. Network depiction of pulsed call similarity as rated by human observers, using a random subsample of calls ( $n = 21$ ) produced by two social units (defined using the NET method). Social units are colour coded (red: F, blue: T, green: FT), and different encounters are distinguished by node shape. The first 6 digits of each pulsed call name also indicate the encounter number. Line thickness reflects the degree of similarity between two compared calls. Unconnected pairs of calls were not compared. The initial position of calls was determined from multidimensional scaling and then moved interactively to improve clarity. The spectrogram of each call included can be found in Appendix VII. Drawn using NetDraw (ver. 2.083, Borgatti 2002). ....	104

Figure 4.18. The distribution of dissimilar and similar pulsed calls recorded in different encounters from the same social units (red) and different social units (blue), as defined by the NET method, for all three similar/dissimilar category groupings. Pulsed calls were always significantly more similar when produced by the same social unit than when produced by different units (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how rigid the definition of “similar” was (a, b and c)..... 105

Figure 4.19. The distribution of dissimilar and similar pulsed calls recorded in different encounters with the same behavioural state (red) and different behavioural states (blue) for all three similar/dissimilar category groupings. Pulsed calls were always significantly more similar when produced during the same behavioural state than when produced during different behavioural states (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how rigid the definition of “similar” was (a, b and c)..... 107

Figure 4.20. The distribution of dissimilar and similar whistles recorded in different encounters within the same year (purple) and different years (green) for all three similar/dissimilar category groupings. Whistles were always significantly more similar when produced in the same year than when produced in different years (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how strict the definition of “similar” was (a, b and c). ..... 109

Figure 4.21. Spectrographic examples of resident killer whale (*Orcinus orca*) typical and aberrant versions of discrete call types N2 and N7 (from Ford 1989). Note the increased number of inflection points and elements in the aberrant versions. . 117

## Abstract

Long-finned pilot whales (*Globicephala melas*) are an extremely vocal species, producing clicks, whistles and pulsed calls during a variety of contexts. For mobile marine mammals, the acoustic channel is often the primary method of communication between individuals, and pilot whale vocalizations likely play an important role in both social and behavioural interactions. I examined the pulsed calls and complex whistles of a population of pilot whales off the northwest coast of Cape Breton, Nova Scotia using recordings made during 4 field seasons spanning 8 years. Pilot whale pulsed calls were found to be physically complex, with multiple components that are likely rich in information and difficult for eavesdroppers to imitate. The structure of pilot whale pulsed calls was highly similar to those of killer whales (*Orcinus orca*), which raises the question of whether the distantly related species, sharing a common rare social structure, evolved similar call structures to solve similar communication problems.

Both the pilot whale pulsed calls and whistles appear to be non-discrete. Statistical measures of similarity from measurements of call spectrograms and perceptual measures of similarity from human observers were used to produce similarity matrices for pulsed calls and complex whistles. Naïve and experienced human participants were highly consistent with each other when rating both sound classes, although the statistical and perceptual methods were only moderately correlated. Each method of rating call similarity had important advantages, and thus both were used to examine the similarity of complex whistles and pulsed calls across social, behavioural and group composition contexts.

Pulsed calls vary strongly between social units or groups producing the calls, as well as among the behavioural or arousal states of the whales. The similarity of aspects of pulsed call structure within clusters of social units suggests the possibility of broader vocal clans. The structure of complex whistles, which are produced mainly during active behaviours, is instead most strongly influenced by the average number of whales present. Pulsed calls may function in unit membership identification, group cohesion and the transmission of information during social interactions. Complex whistles may serve a more population-wide function, facilitating group coordination during active behaviour and over large distances.

## **List of Abbreviations Used**

% – percent

ANOVA – analysis of variance

BAY – Bayesian hierarchical mixture model

B.C. – British Columbia

CCC – cophenetic correlation coefficient

DNA – deoxyribonucleic acid

eV – electron volt

F – foraging

FFT – fast Fourier transformation

freq. – frequency

hrs – hours

Hz – hertz

ID – identification

IP – internet provider

kg – kilogram

kHz – kilohertz

KIN – key individuals and constant companions

LFC – lower frequency component

m – meter

MANOVA – multivariate analysis of variance

min – minimum

max – maximum

MLDB – monkey lips/dorsal bursae

MP – mark point

NET – network modularity technique

PCA – principal components analysis

PRR – pulse repetition rate

Q – modularity coefficient (clustering) and quality assessment (photo-ID)

R – resting

S – socializing

SBI – sideband interval

SE – standard error (of the mean)

sec – second

T – travelling

UFC – upper frequency component

U.K. – United Kingdom

vs. – versus

## Acknowledgements

I have been lucky enough to be surrounded by a wonderful network of people during the completion of this degree. First and foremost, I am grateful to my supervisor, Hal Whitehead, for his brilliance, understanding and, most of all, patience. His statistical prowess helped turn chaotic piles of data into meaningful results, and his guidance and spirit kept me motivated and excited about my research. Without him, I would not have had these magical few years studying whales. So, *thank you*.

This project would not have been possible without the cooperation of Captain Mark Timmons, as well as his family and the entire crew and staff of Captain Mark's Whale and Seal Cruise. My most heartfelt thanks go out to them all, not only for providing me with a research vessel and helping me collect data, but for their unfailing kindness, enthusiasm and friendship. Many thanks also to Leo Tobin, who stepped in as my field assistant on several occasions, and kept us smiling on every occasion. Jessica Mitchell was a priceless help during the 2007 field season. Her easy-going personality and dedication to our research improved the quality of the data tenfold. I also could not have done it without the guidance and expertise of Marie Auger-Méthé who found time in her overloaded schedule to help us get settled and learn the ropes. Thanks also to the entire crew of Captain Cox's Whale Watch for their support during the 1998-2000 field seasons.

This project used recordings, photo-ID, behaviour and group membership data collected and analyzed since 1998 by a steady stream of Whitehead Lab students, including (but not limited to) Marie Auger-Méthé, Meaghan Jankowski, David Lusseau, Jessica Mitchell, Sara Pullen, Andrea Ottensmeyer, Erika Smith, and Tonya Wimmer. My sincere thanks to everyone who took part in the ongoing pilot whale project.

Harald Yurk provided insightful answers to my many questions about spectrograms and specific pilot whale calls, and I can't thank him enough. Alain Bryden provided key php scripting and technical help with the vocalization website. Bill Harnett went above and beyond the call of duty to help me finally get the website up and overcome endless server permission errors. Because of their expertise, over 200 people were able to participate in the human observation aspect of my work. I sincerely thank all of the volunteers who took the time out of their busy lives to compare calls for the

website part of my thesis. An entire section of this research would literally have been impossible without them. Uko Gorter (of Uko Gorter Natural History Illustrations) generously modified his bottlenose dolphin MLDB complex schematic to illustrate a long-finned pilot whale for this thesis. His artistic ability and attention to anatomical detail are much appreciated. I would also like to thank Jennifer Strang for her assistance creating the GIS map. Thank you as well to my committee members and external examiner: Drs Colleen Barber, Marty Leonard, Diana Reiss and Cindy Staicer, all of whom provided important feedback on this thesis.

The help, support, friendship and unshakable good humour of everyone in the Whitehead Lab kept me plowing through even the most frustrating problems. Many thanks to Shane, David and Susan, Hilary, Tyler, Manolo, Lucie, Tonya and Sarah. I am especially grateful to Marie and Catalina for the endless chats and kindness. I owe my present level of sanity in large part to my Thursday evening yoga group, thanks especially to Louise for teaching us, for being a calming influence, and for getting it.

I was financially supported by a PGS-M NSERC scholarship, Hal Whitehead's NSERC operating grant, and the Dr. Patrick Lett fund. Jessica Mitchell was supported by a summer undergraduate NSERC research scholarship.

And, of course, I could not have done this without my family's support. Mom, Dad, Day, Darlene and Fabien: *thank you*. Special thanks to Sacha Vais for keeping me standing, keeping me smiling and keeping me sane. Mostly, though, for surrounding me with a love that knows no bounds. And to Walden, for being furry and warm.

# CHAPTER 1 – INTRODUCTION

## 1.1 General Introduction

Animals communicate in myriad ways, using smells, sounds, movements, colors and electric signals to send and receive information. Beneath each method of communication lies the same concept: the transfer of a signal (containing information) from a sender to a receiver, and the subsequent use of that information by the receiver in deciding how to respond (Bradbury and Vehrencamp 1998). This classic view of communication involves the transmission of information that *benefits* the sender and is able to be accessed by, and reduce uncertainty of, the receiver (Dusenbury 1992, Bradbury and Vehrencamp 1998).

Communication can also be considered from a much broader perspective. In a more functional view, signals may be used to manipulate other individuals through advertisements or dishonest signaling. There may be multiple intended recipients of a signal, and eavesdroppers may intercept the signal and use the information to their own advantage (Myrberg 1981, Tyack 2000). Within this definition of communication, individuals can broadcast their identity, status and location, provide information about their environment, and manipulate other animals. They can mediate competition, facilitate reproduction and enable group cohesion (Bradbury and Vehrencamp 1998, Tyack 2000).

For cetaceans, the mode of communication of a species is also often closely linked with its social structure (Tyack 1986). For instance, individually specific signals are typically found among animals that maintain individual social bonds within fluid groupings (Tyack 1986, 2000). Bottlenose dolphins (*Tursiops truncatus*) have a fission-fusion system with frequently changing associations. While differing whistle types are predominant in some contexts (McCowan and Reiss 1995, 2001), signature whistles that facilitate individual recognition may often be observed during separations and immediately before individuals reunite (Tyack 1997, Janik and Slater 1998). Conversely, for species in which animals are found in stable social units, it is likely more important for an individual to recognize and stay in contact with its group than with any particular individual within it (Tyack 1986, 2000). Matrilineal “resident” type killer whales (*Orcinus orca*) off British Columbia use group-specific vocal repertoires as group

identifiers, which serve as a bonding call for members of the same unit (Ford 1989, 1991). For species that lack both stable individual and group bonds, communication often takes the form of advertisement displays that vary between populations (Tyack 1986, 2000).

Vocal learning, the modification of vocalizations as a result of experience with those of other individuals, appears to play a fundamental role in the development of such signals in cetaceans (Tyack 2000). A well-known example of this is the concurrent rapid change of humpback whale (*Megaptera novaeangliae*) advertisement calls within an ocean basin. All male humpbacks in the same breeding area progressively modify their songs over time to one converged sequence, which suggests that individuals are adjusting their vocalizations by replicating song elements they hear being used by other males (Payne and McVay 1971, Medrano et al. 1994, Mercado et al. 2005). Vocal learning can also allow for the transmission of vocal traditions, enabling individuals to differentiate groups based on learned vocal repertoires (Rendell and Whitehead 2001). The best-described examples of this form of vocal culture in animals are the structured song repertoires of birds (Price 1998) and the group-specific dialects of some mammals, including bats, humans, odontocetes and some baleen whales and phocid seals (Ford 1991, Boughman 1997, Janik and Slater 1997, Weilgart and Whitehead 1997, Tyack 2000, Rendell and Whitehead 2003a, Richerson and Boyd 2006).

The research presented here is part of a long-term study of long-finned pilot whales (*Globicephala melas*) taking place off Cape Breton, Canada, and is focused on broadening our knowledge of pilot whale bioacoustics. This continuing project has spanned approximately a decade. While there have been studies on the social structure of these animals (see Ottensmeyer and Whitehead 2003, Jankowski 2005) and other populations of long-finned pilot whales (e.g. Amos 1993a), we still know relatively little about their vocalizations. What is the basic structure of their pulsed calls? Do they use a repertoire of discrete call types? Do different social units use group-specific calls? This thesis addresses such questions. This chapter contains a short overview of the study species, the long-finned pilot whale, as well as an introduction to general cetacean and pilot whale vocal communication. There is also a brief overview of the topics that will be covered in this thesis.

## 1.2 The Long-Finned Pilot Whale

The long-finned pilot whale (*Globicephala melas*; previously called *Globicephala melaena*) is a medium-sized toothed whale (suborder Odontoceti) and a member of the dolphin family (Delphinidae). It shares the *Globicephala* genus with the short-finned pilot whale, *Globicephala macrorhynchus* (LeDuc et al. 1999). The two can be distinguished by differences in flipper length and cranial characteristics (Sergeant 1962, Bloch et al. 1993a). In this thesis, “pilot whale” refers exclusively to *G. melas*, and reference to *G. macrorhynchus* is made explicit.

### 1.2.1 Distribution and Abundance

Pilot whales are abundant and widespread. The short-finned pilot whale is commonly found in tropical waters, in the northwest Atlantic from the south of North Carolina, off the Caribbean, in the Gulf of Mexico, to Venezuela (Payne and Heinemann 1993). The long-finned pilot whale can be found in temperate to subpolar marine waters. There are two living subspecies of *G. melas*: one in the North Atlantic and one in the Southern Hemisphere (Reeves et al. 2003). The Southern subspecies has a circumpolar distribution and can be found from approximately 20°S to 68°S (Reeves et al. 2002). The North Atlantic subspecies is boreal and subarctic and can be in deep offshore waters from North Carolina all the way to the Azores at its southern limit and to Newfoundland and the Greenland and Barents Seas at its northern limit (Mercer 1975, Payne et al. 1984, Bloch et al. 1993c, Reeves et al. 2003).

Surveys in 1987 and 1989 estimated that the central and northeast North Atlantic population of pilot whales was approximately 780,000 animals (Buckland et al. 1993). The conservative population estimate for the eastern Newfoundland and southeastern Labrador population is 13,167 ( $\pm 3155$ ) (Hay 1982). A more recent aerial survey carried out in the Gulf of St. Lawrence (including my study area off the northeastern coast of Cape Breton) estimated the population of pilot whales in that area to be only 1,600 animals (Kingsley and Reeves 1998). However, this is based on few sightings and the estimates are not considered reliable (Kingsley and Reeves 1998). There is little information on population divisions in North Atlantic pilot whales. *G. melas* is currently listed as “not at risk” in Canada by the Committee on the Status of Endangered Species in

Canada (COSEWIC 2008), and “lower risk (least concern)” globally by the World Conservation Union (Cetacean Specialist Group 1996).

### **1.2.2 Movement Patterns**

Seasonal movements of pilot whales in the western North Atlantic appear to coincide with the abundance of squid (*Illex illecebrosus*, *Loligo pealei*) and mackerel (*Scomber scombrus*), following the shelf-edge and slope during the winter and moving northward and onto the coastal shelf in the late-summer and fall (Mercer 1975, Desportes and Mouritsen 1993, Payne and Heinemann 1993, Abend and Smith 1997). This movement brings pilot whales into the southeastern Gulf of St. Lawrence and along the Cape Breton coastline for the duration of the summer, where they are the principal cetacean species observed by the local whale-watching industry, established along the northwest coast in 1989 (Wimmer 2000, Smith et al. 2008).

### **1.2.3 Individual Identification**

Pilot whales are individually identified off Cape Breton using photo-identification of natural markings (Ottensmeyer and Whitehead 2003, Auger-Méthé and Whitehead 2007). The most efficient method compares the notches and protruding pieces of different dorsal fins (Auger-Méthé and Whitehead 2007), and currently allows the identification of 33.6% of the Cape Breton population (Ottensmeyer and Whitehead 2003).

### **1.2.4 Social Structure**

Pilot whales are highly social and have been recorded traveling in groups ranging in size from one or two animals to occasional sightings of over 1000 individuals (Bloch et al. 1993c). They are most often seen in groups of 20-150, composed of members of both sexes and all age groups (Sergeant 1962, Bloch et al. 1993c, Desportes et al. 1993, Ottensmeyer and Whitehead 2003). Within these unstable larger groups, individuals often form long-term associations with 8-12 other individuals that can last for years and are referred to as social units (Ottensmeyer and Whitehead 2003, Jankowski 2005). These social units likely represent extended matrilineal groups of adult females and their offspring (Amos et al. 1993b). DNA fingerprinting of pilot whales caught during the Faroese drive fisheries suggest that they may be one of the few species that exhibit natal

group philopatry, where neither male nor female offspring disperse from the natal group (Amos et al. 1991, 1993a, 1993b). This is further supported by a pedigree analysis of 11 hunted schools, which indicated that a portion of males stay within their natal pod, even after reaching sexual maturity (Fullard 2000). Adult males are also rarely the fathers of the calves within their group (Amos et al. 1993a). Mating probably occurs when two or more units join to form temporary larger groups or when a male pays brief visits to other units (Amos et al. 1991, 1993, Andersen and Siegismund 1994). Bisexual natal group philopatry is rare in mammals, only concretely observed in resident killer whales along the west coast of Canada and the northern USA (Bigg et al. 1990a, Connor et al. 1998). Natal philopatry may also be related to the strong level of social cohesion in pilot whales that renders them vulnerable to mass strandings and drive fisheries (Bloch et al. 1993c, Hooker et al. 1997).

### **1.3 Cetacean Vocalization**

#### **1.3.1 Cetacean Sound Production and Hearing**

Sound travels approximately 4.5 times faster through seawater than air (Mackenzie 1981), but light and chemicals travel slower and dissipate more quickly (Bradbury and Vehrencamp 1998). Because of the physical characteristics of the ocean, the acoustic channel is a more efficient way to sense or communicate over a long distance underwater than any visual or chemical cues. Rapid, long-distance communication is especially important for mobile animals like cetaceans, where individuals that share bonds are often separated by kilometers, and potential mates may be large distances apart (Connor et al. 1998, Tyack 2000).

Cetaceans produce sound in a similar way to terrestrial mammals, by passing air under pressure past membranes that vibrate. When cetaceans vocalize underwater, however, sound vibrations in their tissues transfer directly into the surrounding water and they do not need to open their mouths or blowholes (Tyack 2000). For odontocetes, sound generation likely occurs when pressurized air is metered past the internal nares and through the monkey lips/dorsal bursae (MLDB) complex, located in the upper nasal passage (Cranford et al. 1996) (Figure 1.1). Evidence suggests that the fatty dorsal bursae within the phonic lips play a central role in the process of sound generation by acting as

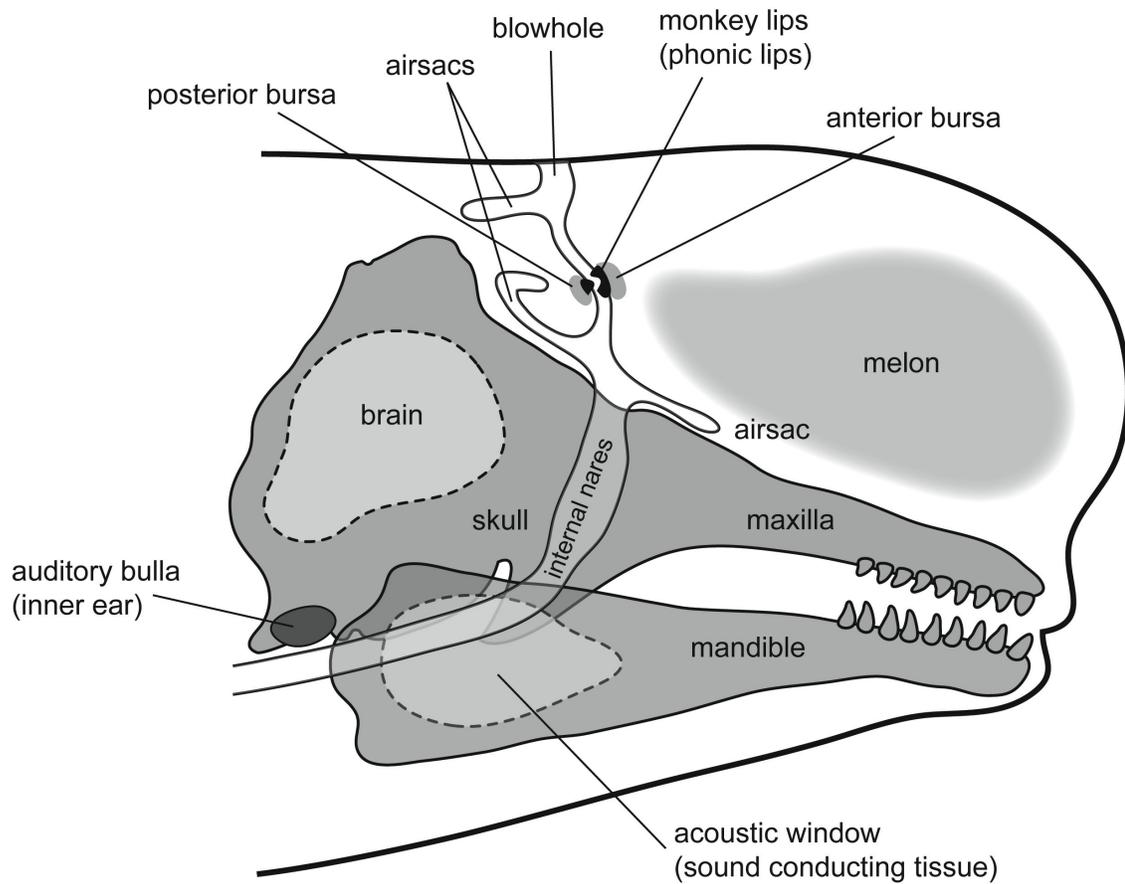


Figure 1.1. Schematic of a long-finned pilot whale head. The sound generator is the Monkey Lips/Dorsal Bursae Complex (MLDB). (Image courtesy of Uko Gorter Natural History Illustrations. Modified and adapted from Cranford et al. 1996.)

sources of vibration (Cranford 2000). The air is stored in the upper respiratory tract and recycled in between vocalizations when the animal is diving (Tyack 2000). The MLDB is homologous in all odontocetes, only varying in size and position (Cranford et al. 1996). However, sperm whales (*Physeter macrocephalus*) have a unilateral configuration, while all other odontocetes have a bilateral configuration with two MLDB complexes (one associated with each of the two nasal passages) (Cranford et al. 1996, Thomas et al. 2004). Dormer (1979) observed that the left nasal plug was associated with whistle production, and speculated that the right nasal plug was associated with pulse and click production. More recently, Cranford et al. (2001) suggested that clicks and pulses appear to be generated from either nasal plug, or with both left and right working in unison. The tissue of the melon infiltrates the muscles of the nasal plug and nasal passage, providing a direct link between vibrations produced in the monkey lips and the rest of the melon. The viscous oil within the melon concentrates outgoing acoustic emissions. The bony structures, air sacs and melon all work together in an odontocete's head to focus acoustic signals into a beam that is directed forward and slightly elevated (Au 2000).

The cetacean auditory system is similar to the basic mammalian design, although it lacks the outer ear and eardrum which, in terrestrial animals, collectively function to transmit sound through air to the fluid-containing inner ear (Tyack 2000). Fatty tissues in the jaw region act as an “acoustic window” and are the primary route for conveying sound to odontocete inner ear (Ketten 2000) (Figure 1.1). The inner ear then converts sound energy into neural signals that are transmitted to the central nervous system (Tyack 2000). Among mammals, dolphins have an ability to detect a change of as little as 0.2% in frequency. This is generally equivalent to human abilities (Thomson and Herman 1975).

### **1.3.2 Odontocete Vocalizations**

Odontocetes use sound for communication, navigation, and the detection of predators and prey (Kellogg et al. 1953, Saayman et al. 1973, Richardson et al. 1995, Evans 1998). Many dolphin species, in particular, appear to use a combination of three broad categories of vocalizations: clicks, pulsed calls and whistles (e.g. Ford 1989). Clicks are rapid and, usually, repetitive bursts of short, broadband sounds, primarily used for

echolocation (Kellogg et al. 1953, Au et al. 2003). Whistles are continuous tonal sounds with few or no harmonics and are thought to be used as contact calls, possibly serving to maintain the cohesion of the group during foraging or travel (Ford 1989, Weilgart and Whitehead 1990). Pulsed calls are rapidly produced broadband sound pulses, with distinct tonal properties caused by high pulse-repetition rates (Schevill and Watkins 1966, Ford 1989). The repetition rate of the pulses is reflected in the intervals between the frequencies of sidebands of the pulsed call (Ford 1989). It is thought that pulsed calls also have an important underwater communication function, and have been shown to act as group identifiers for resident killer whales off British Columbia (Ford 1984).

### 1.3.3 Long-Finned Pilot Whale Vocalizations

Pilot whales use a combination of all three call types (Figure 1.2). The structure of *G. melas* calls was first described by Busnel and Dzedzic (1966), who published a detailed account of a single hour-long encounter with a group of 11 pilot whales. They observed abrupt frequency shifts and amplitude variations in the spectrograms and were able to describe five signal types, some of which were only seen after one of the whales was harpooned. Busnel et al. (1971) then examined pilot whale clicks, which were found to be occasionally composed of double clicks, also observed in killer whales (Ford 1989).

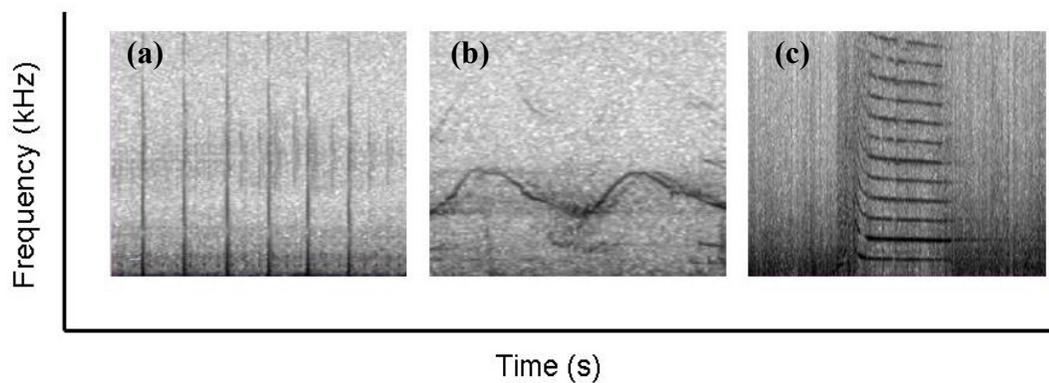


Figure 1.2. Spectrograms (frequency-time diagrams) showing examples of the three types of pilot whale vocalizations. (a) clicks, (b) a complex whistle, and (c) a pulsed call.

Taruski (1979) was the first to attempt to describe the entire pilot whale whistle repertoire from a large and diverse sample. He categorized 822 recorded whistles from over 30 hours of wild pilot whale recordings spanning several years and representing a

large variety of behavioural and environmental contexts. Their whistles were found to be structured in a continuum, where any one whistle could be derived from any other whistle through a series of intermediates and could not be classified into distinct categories (Taruski 1979). From within the continuum, Taruski (1979) was able to create seven somewhat arbitrary broad classes of pilot whale whistles ranging from simple to complex (Figure 1.3). Steiner (1981) and Rendell et al. (1999) each compared *G. melas* whistles to those of four other odontocete species (Steiner 1981: *Tursiops truncatus*, *Lagenorhynchus acutus*, *Stenella frontalis* and *Stenella longirostris*; Rendell et al. 1999: *Pseudorca crassidens*, *Grampus griseus*, *Globicephala macrorhynchus*, and *Lagenorhynchus albirostris*), and both studies found that they are highly species specific.

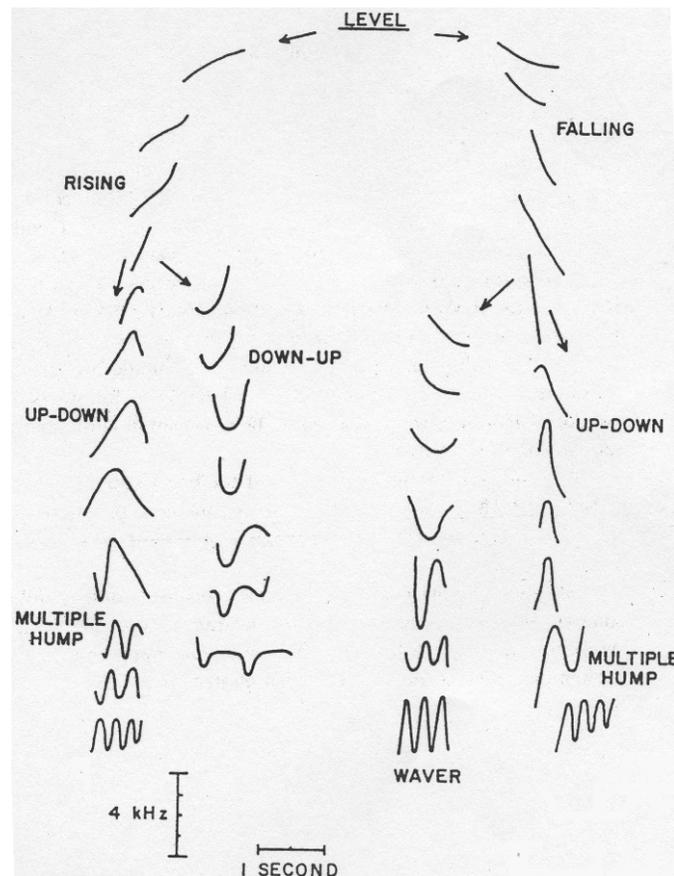


Figure 1.3. The graded nature of pilot whale whistles. Note the continuum of intermediate contour shapes between the seven labeled basic whistle types (from Taruski 1979).

Weilgart and Whitehead (1990) found that whistles are heard ten times as often as pulsed calls in recordings, and that both complex whistles and pulsed calls are heard most frequently during surface active behaviours such as socializing and foraging. Pilot whale pulsed calls themselves have received little study, and their structure and function remain unclear.

#### **1.4 Thesis Overview**

This thesis focuses on three aspects of pilot whale vocal communication. The first (Chapter 2) is a description of long-finned pilot whale pulsed calls. The description is the first for pilot whales and provides fundamental information on this rarely-studied, but almost certainly important, sound class. The remainder of the thesis considers both pulsed calls and whistles. The second part of the study (Chapter 3) examines two currently accepted methods of call similarity rating as applied to pilot whale calls: (1) determining call similarities from measurements taken directly off spectrograms and (2) through aural and visual similarity ratings by human observers. The final part (Chapter 4) explores what governs pulsed call and whistle variability, looking specifically at variation across social units, behavioural states and group composition. The thesis ends with a discussion of this research as a whole, its implications, limitations and suggestions for possible future directions for the long-term pilot whale study in Cape Breton.

## CHAPTER 2 – PILOT WHALE PULSED CALLS

### 2.1 Introduction

Pilot whales (*Globicephala melas*) are extremely vocal, using a combination of clicks, whistles and pulsed calls to communicate and interact with their environment (Taruski 1979, Weilgart and Whitehead 1990). Their clicks, used for echolocation, have been previously described in the literature (Busnel et al. 1971). Their whistles have also been extensively detailed (Schevill 1964, Taruski 1979, Weilgart and Whitehead 1990, Rendell et al. 1999). Their pulsed calls, on the other hand, are rarer (Weilgart and Whitehead 1990), and the difficulty of isolating a large enough sample of them is reflected in the relative dearth of published information detailing their structure. Nevertheless, the dynamic and complex nature of pulsed calls has often roused interest in those who study pilot whales, resulting in many anecdotal descriptions, such as:

“It sounded like the peevish whining of a young child. It had something of the character of the crying of young porcupines or beavers.” (Kritzler 1952)

While this colourful description is accurate, pulsed calls are also interesting because of their complex physical structure. While often referred to as screams, groans, creaks or barks (e.g. Schevill and Watkins 1966), a pulsed call is more precisely defined as a rapidly produced sound pulse, with distinct tonal properties caused by high pulse-repetition rates (PRR) that often shift abruptly (Schevill and Watkins 1966, Ford 1989). It is these sudden shifts in PRR that produce the distinctive aural qualities characteristic of pulsed calls (Ford and Fisher 1983). The PRR is reflected in the intervals between the sidebands (SBI) and is usually modulated over the duration of a call (Watkins 1967, Ford 1989).

Many odontocetes produce pulsed calls, including belugas, *Delphinapterus leucas* (Karlsen et al. 2002), narwhals, *Monodon monoceros* (Ford and Fisher 1978), false killer whales, *Pseudorca crassidens* (Murray et al. 1998) and killer whales, *Orcinus orca* (Ford and Fisher 1983). The most thoroughly described are those of “resident” type killer whales off British Columbia (Ford 1987, 1989), which are aurally very similar to those of

pilot whales. Pulsed calls are often composed of both an upper frequency component (UFC) and a lower frequency component (LFC) (Miller and Bain 2000) (see Figure 2.1). The LFC consists of rapidly produced broadband pulses that overlap to produce the equivalent of sine wave tones (Yurk 2005). It is the SBI between the resulting tones that reflect the PRR of the call. The LFC is equivalent to the “pulse” part of the call. The LFC can often be further divided into elements (parts of the call separated by abrupt shifts in the PRR) and segments (parts of the call separated from each other by empty space) (see Figure 2.1). The UFC, on the other hand, is a narrow band signal that can have true harmonic bands. It is equivalent to a whistle, produced concurrently with an LFC (Yurk 2005). Simultaneous LFC and UFCs are an example of biphonation, the production of two independent fundamental frequencies in a call spectrum (Brown and Cannito 1995). The source of biphonation in odontocetes is likely the result of air being pushed across the two MLDB complexes (tissues located above the superior bony nares) at the same time (Cranford 2000).

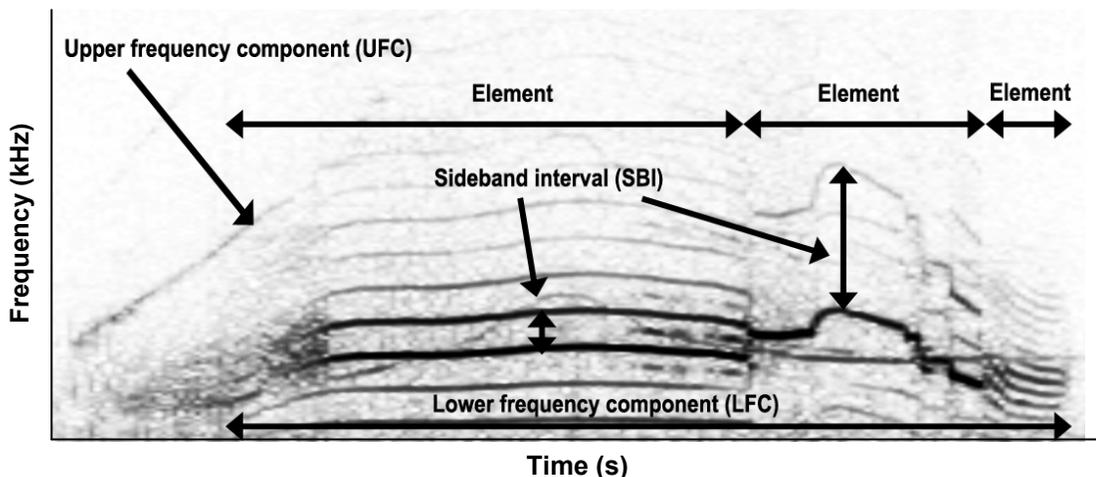


Figure 2.1. Spectrographic example of a pilot whale pulsed call. Calls may consist of two components, an upper frequency component (UFC) that is a narrow-band tone, and a lower frequency component (LFC) that is a broadband pulse. The pulse repetition rate (PRR) is reflected by the sideband interval (SBI). Elements are distinguished by abrupt shifts in the PRR.

Pulsed calls may be categorizable into discrete call types within the pilot whale repertoire. Distinct call types have been recorded for many cetacean species, including killer whale pulsed calls (Ford 1987, Filatova et al. 2007), sperm whale (*Physeter macrocephalus*) codas (Weilgart and Whitehead 1997) and possibly bottlenose dolphin

(*Tursiops truncatus*) signature whistles (Sayigh et al. 2007; but see McCowan and Reiss 2001). Call types may be favoured by species with the need for honest signaling when identifying individuals or groups, as discrete calls are likely more difficult for a non-member to imitate (McGregor 2005). However, this may not always be the case, and calls can instead be graded along a continuum. For example, the calls of adult male beluga whales in Svalbard, Norway are highly graded and cannot be reliably divided into categories (Karlsen et al. 2002). Similarly, the whistles of pilot whales appear to form a graded continuum between seven basic types (Taruski 1979). These graded calls may allow one signal to have multiple functions. For instance, a graded call may communicate arousal level or behavioural state (Taruski 1979, Bain 1986, Murray et al. 1998).

Pilot whale pulsed calls are complex and may have multiple functions. However, there have not been any previous detailed quantitative characterizations of this sound class for this species. There is currently no information available on either general structural characteristics, such as the presence or absence of discrete call types, or fine-scale parameters, such as pulse repetition rates or frequency ranges. In this section, the structural characteristics of pulsed calls from long-finned pilot whales off Cape Breton, Nova Scotia are presented and the presence or absence of discrete call types within their repertoire is investigated. The similarities between pilot whale and killer whale pulsed calls are also discussed.

## **2.2 Methods**

### **2.2.1 Field Sites**

Pilot whale photo-identification, observations and vocalization recordings were carried out by a number of different observers (see Acknowledgements for details) in Bay St. Lawrence (47°02'N, 60°29'W) and Pleasant Bay (46° 50'N, 60° 47'W), along the north-west coast of Cape Breton Island, Nova Scotia, Canada. Opportunistic surveys were conducted through July and August from the whale-watch vessel *Northern Gannet* in Bay St. Lawrence (1998-2000), and from *Double Hookup* in Pleasant Bay (2005). There were three scheduled trips daily out of Bay St. Lawrence, each 2.5-3 hours long. In Pleasant Bay, there were five scheduled trips daily, each 1.5-2 hours long. All scheduled trips were taken, unless weather conditions were unfavorable (determined by the captain), the

Beaufort sea state was greater than 5-6, or too few people signed-up for the trip. The number of scientific observers on the whale-watching vessels was either one or two, depending on the year.

### **2.2.2 Recording of Vocalizations**

Pilot whale vocalizations used in the following analysis were recorded during the 1998-2000 and 2005 field seasons. At the start of an encounter, the boat engine was turned off, and an omnidirectional VEMCO hydrophone (10Hz-20kHz) was lowered over the side of the boat to a depth of 10-15m. The recording systems varied over the years, but mostly consisted of a Sony TCM 5000 eV analog cassette-tape recorder (1998-2000) or a Sony PCM-2800 digital audio track recorder (2005). The frequency responses of these recording systems were between 20 Hz and 20 kHz. Date and time were recorded using a microphone before the hydrophone was lowered into the water, and start and stop times of recordings were also noted. The hydrophone was lifted from the water at the end of an encounter. A total of 274 encounters included recordings, resulting in approximately 65 hours of recorded vocalizations.

### **2.2.3 Acoustic Analysis**

Vocalization recordings from cassette tapes (1998-2000) were played-back and digitized at a sampling rate of 44.1 kHz, with a 16-bit sample size, using the spectrographic software program CoolEdit Pro (ver. 2.0.). This resulted in an analysis range of 0-22kHz. Recordings for all years (1998-2000, 2005) were then displayed graphically on frequency-time plot spectrograms and inspected for the presence of pulsed calls by listening to the recordings while visually monitoring the spectrograms. Only calls with suitable signal to noise levels and well-defined contours were used in the analysis. Pulsed calls were extracted and measured using the acoustics software Raven Pro (ver. 1.3). The spectrograms were produced using 1024 point Fast-Fourier Transformations (FFT) and a Hamming window for each analyzed time series. Resulting spectrograms had a time resolution of two milliseconds and a frequency resolution of 61 Hz. For each call, between 17 and 43 frequency, duration and count (e.g. number of elements) variables were measured (mean = 22.5 variables) depending on the complexity of the call. The measured variables are described in Table 2.1.

Table 2.1. Description of the variables measured for each pulsed call

<b>Variable</b>	<b>Description</b>	<b>Units</b>
NUM_ELEMENTS	Number of parts delineated by abrupt shifts in the pulse repetition rate	
NUM_SEGMENTS	Number of parts separated by empty space	
NUM_INFL_PTS	Number of abrupt frequency modulations along the fundamental frequency	
UFC_Y_N	Presence or absence of an upper frequency component (biphonation)	
UFC_INFL_PTS	Number of abrupt frequency modulations along the UFC	
UFC_ST_FREQ	Start frequency point of the UFC	Hz
UFC_END_FREQ	End frequency point of the UFC	Hz
UFC_DUR	Total duration of the UFC	sec
TC_SBI_ST	Sideband interval at the beginning of a pulsed call (from the FF to the next band)	Hz
TC_SBI_END	Sideband interval at the end of a pulsed call	Hz
SBI_#_ST	Sideband interval at the beginning of each part of a pulsed call	Hz
SBI_#_MID	Sideband interval in the middle of each part of a pulsed call	Hz
SBI_#_END	Sideband interval at the end of each part of a pulsed call	Hz
TC_DURATION	Total duration of the pulsed call, including the UFC	sec
PART_#_DUR	Total duration of each separate part of a pulsed call	sec
SPACE_DUR	Total duration of the empty space between two segments	sec
TC_HIGH_FREQ	Frequency of maximum visible sideband of a pulsed call	Hz
TC_LOW_FREQ	Frequency of minimum visible sideband of a pulsed call	Hz
TC_DELT_FREQ	Change in frequency of a pulsed call from the lowest visible sideband to the highest	Hz
TC_ST_FREQ	Start frequency point of a pulsed call on the fundamental frequency	Hz
TC_END_FREQ	End frequency point of a pulsed call on the fundamental frequency	Hz
FF	Fundamental frequency of the pulsed call (from power spectrum analysis)	Hz

The two primary goals in choosing which time and frequency variables to measure from the spectrograms were: (1) to choose measures that would represent the LFC and UFC contours as effectively as possible, and (2) to remain consistent with measurements made by studies on killer whale pulsed calls (Ford 1987, Miller and Bain 2000). The fundamental frequency was found for each pulsed call using a power spectrum analysis. Power spectra were produced with 32 768 point FFT, with a 3Hz frequency resolution and a time resolution of 429ms.

#### **2.2.4 Statistical Analysis**

##### *Pulsed call description*

Descriptive statistics were performed on the measured parameters to describe the properties of the calls. Only complex whistles (containing at least one inflection point) were extracted and measured for Chapters 3 and 4 of this thesis, so whistle data from the literature (Rendell et al. 1999) were used to compare pilot whale whistles with UFC measurements. A principal components analysis (PCA) using a correlation matrix of the measured variables was then used to further elucidate which parameters appear to contribute most to pulsed call variability. The matrix was rotated using Varimax rotation, which attempts to minimize the variance of squared loadings for each factor and improves interpretability of the factors (Jolliffe 2002). Any variables with many missing data points were excluded from the PCA (for example, any measurements specific to the 2<sup>nd</sup> parts of the more complex calls or the duration of the UFC for biphonic calls). The Kaiser criterion was used to select the number of components (linear combinations of the original variables) to keep in the analysis, which excludes all principal components with an eigenvalue less than one (Jolliffe 2002). Thus, any component that explained less variance than an original variable in the correlation matrix was excluded.

Killer whale pulsed call measurement ranges from various published sources (Schevill and Watkins 1966, Hoelzel and Osborne 1986, Ford 1987) were collected to compare killer whale pulsed calls with those of pilot whales. Pilot whale and killer whale pulsed calls are aurally very similar, the two species have overlapping ranges (Reeves et al. 2002) and both exhibit natal group philopatry (Bigg et al. 1990a, Amos et al. 1993a, 1993b). Other species within the Orcininae and Globicephalinae subfamilies are more

difficult to compare, mainly due to a lack of available information and major differences in call structure and methodology across studies.

### *Call types*

Two automatic classification methods were applied to the measurement data to determine the presence or absence of discrete call types within the pilot whale pulsed call repertoire. The first was a  $k$ -means cluster analysis (20 iterations).  $K$ -means clustering divides a set of values into a selected number of groups ( $k$ ) by maximizing between-group variation relative to within-group variation. It iterates through the data until cases are successfully clustered (Everitt et al. 2001). However, the main disadvantage of  $k$ -means clustering is the partially arbitrary selection of  $k$ . To increase the probability of finding clustering that was meaningful, the test was run several times (from  $2 \leq k \leq 10$ ) and the results were compared.  $K$ -means clustering was done using SYSTAT (ver. 12).

The second method was hierarchical average linkage clustering using Mahalanobis distances and was performed on SOCPROG. Hierarchical average linkage is a clustering technique that groups calls with high indices of similarity into common branches (Johnson 1967). It has been shown to be a successful clustering method for classifying bottlenose dolphin whistles (Janik 1999). Clustering was stopped using maximum modularity ( $Q$ ), which indicates at which number of clusters similarity is maximized within clusters and minimized between them (Newman 2006). The cophenetic correlation coefficient (CCC) was calculated to determine whether the clusters give an accurate representation of the relationships between the calls. A CCC greater than 0.8 is generally considered acceptable (Bridge 1993). The CCC for a hierarchical cluster tree is the linear correlation coefficient between the cophenetic distances obtained from the tree and the original distances (or dissimilarities) used to construct the tree (Atchley and Bryant 1975). Thus, it is a measure of how faithfully the tree represents the dissimilarities among observations.

## 2.3 Results

### 2.3.1 Properties of Pilot Whale Pulsed Calls

From the 65hrs of pilot whale recordings, a total of 419 pulsed calls were isolated and measured, spanning 94 encounters over 4 years (Figure 2.2). The number of elements, parts of the call separated by abrupt shifts in the PRR, in a pulsed call ranged from 1 to 6, with an average of approximately 2 per call (see Figure 2.3, Table 2.2). The majority of calls had relatively few parts, with 47% composed of only 1 element and 93% being completely unsegmented. Segmented calls are composed of two or more sections, separated from each other by empty space. Of the 7% of calls that were segmented, 93% had 2 segments, and only 7% had 3 segments. Segments of calls were separated by an average of 0.089sec of silence. Approximately 20% of all calls contained a UFC. The UFC measurements coincided with the uppermost values of published pilot whale whistle data from recordings off Newfoundland (Table 2.3) (Rendell et al. 1999). However, the UFCs were generally higher frequency and had more inflection points than the published whistle values (Table 2.3).

Approximately half of the calls measured contained between 1-2 inflection points, and 41% had 3 inflection points or more (max = 18) (see Figure 2.4, Table 2.2). The duration of a pulsed call ranged from short chirps (0.172sec) to drawn out squeals (2.173sec). However, duration had the lowest coefficient of variation of all variables measured, indicating that pilot whale pulsed calls are more stereotyped in length than any other characteristic measured. The first element of LFCs ranged in fundamental frequency from 0.81 to 9.4 kHz. Sidebands were visible from as low as 140 Hz to above the 20 kHz limit of the spectrograms, and had an average interval of 1.4 kHz at the beginning of a call and 1.5 kHz at the end of a call. The maximum PRR observed was 5500 pulses/sec. Pulse repetition rate, duration of each element in a call, and the duration of silence between each segment varied the most between calls (see Table 2.2).

The general measurement ranges of pilot whale pulsed calls were similar to those published for killer whales, although killer whales seem to have slightly shorter LFCs, slightly longer UFCs, a narrower range of pulse repetition rates and marginally lower UFC and LFC frequencies (Table 2.4).

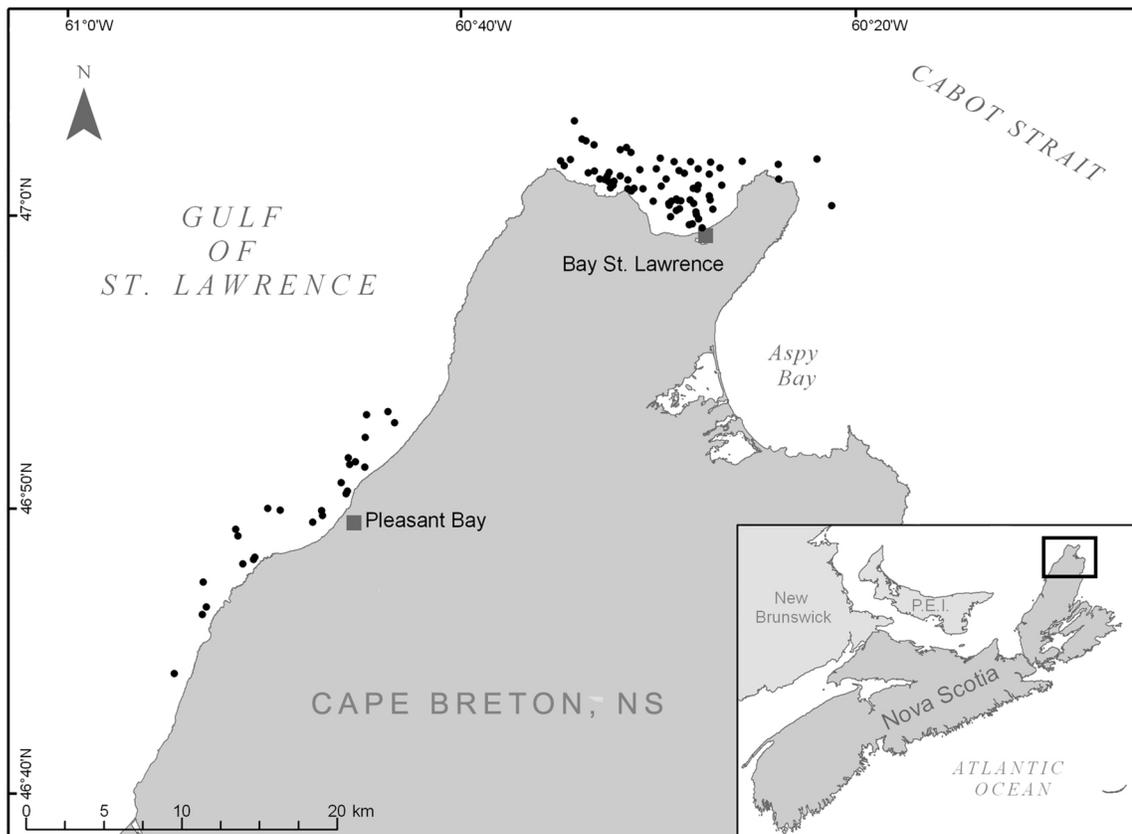


Figure 2.2. Map of the northwest tip of Cape Breton Island, Nova Scotia, Canada where the two field sites are located. The position of each pilot whale encounter from which pulsed calls were extracted is plotted (n = 94). Inset map shows Nova Scotia and surrounding maritime provinces.

Table 2.2. Descriptive statistics of pilot whale pulsed calls

<b>Variable</b>	<b>N</b>	<b>Min</b>	<b>Max</b>	<b>Median</b>	<b>Mean</b>	<b>SE</b>	<b>SD</b>	<b>CV</b>
<i>Total call</i>								
Duration (sec)	419	0.172	2.173	0.761	0.791	0.014	0.277	0.35
Number of elements	419	1	6	2	1.8	0.0	1.0	0.55
Number of segments	419	0	3	0	0.1	0.0	0.5	3.70
Number of inflection points	419	0	18	2	2.8	0.1	2.4	0.85
Minimum frequency (Hz)	419	140	3459	1289	1279	26	525	0.41
Maximum frequency (Hz)	419	3970	20000	12110	13176	236	4834	0.37
Delta frequency (Hz)	419	1774	19797	10706	11897	238	4866	0.41
Start frequency (Hz)	419	490	9238	2510	2739	69	1411	0.52
End frequency (Hz)	419	814	10720	2703	2985	70	1427	0.48
Fundamental frequency (Hz)	419	814	9368	2782	2937	55	1122	0.38
Sideband interval, start (Hz)	419	67	5506	1260	1396	45	915	0.66
Sideband interval, end (Hz)	419	84	4749	1349	1496	35	711	0.48
<i>Part 1</i>								
Duration (sec)	419	0.023	1.441	0.344	0.416	0.015	0.316	0.76
SBI start (Hz)	419	67	5506	1260	1396	45	915	0.66
SBI middle (Hz)	419	67	5188	1221	1407	44	904	0.64
SBI end (Hz)	419	67	5188	1281	1399	40	826	0.59
<i>Part 2</i>								
Duration (sec)	221	0.040	1.626	0.470	0.483	0.022	0.322	0.67
SBI start (Hz)	221	68	5295	1750	1927	61	908	0.47
SBI middle (Hz)	221	68	4959	1835	2016	66	986	0.49
SBI end (Hz)	221	68	4791	1946	2020	66	983	0.49
Duration of silence (sec)	29	0.01	0.43	0.05	0.09	0.02	0.09	0.98
<i>Part 3</i>								
Duration (sec)	94	0.030	1.080	0.220	0.284	0.023	0.226	0.79
SBI start (Hz)	94	71	4203	1540	1804	93	902	0.50
SBI middle (Hz)	94	71	4959	1481	1826	105	1016	0.56
SBI end (Hz)	94	71	4248	1412	1776	96	933	0.53
Duration of silence (sec)	2	0.03	0.09	0.06	0.06	0.03	0.04	0.72
<i>Part 4</i>								
Duration (sec)	28	0.034	0.585	0.123	0.225	0.038	0.199	0.88
SBI start (Hz)	28	68	4925	1718	1971	221	1170	0.59
SBI middle (Hz)	28	136	4791	1839	1964	206	1089	0.55
SBI end (Hz)	28	136	4203	1596	1856	187	988	0.53
<i>Part 5</i>								
Duration (sec)	10	0.090	0.821	0.101	0.225	0.080	0.254	1.13
SBI start (Hz)	10	84	3687	1481	1454	306	969	0.67
SBI middle (Hz)	10	84	4112	1482	1478	351	1110	0.75
SBI end (Hz)	10	84	4041	1297	1449	352	1114	0.77
<i>Part 6</i>								
Duration (sec)	1	0.316	0.316	0.316	0.316	.	.	1
SBI start (Hz)	1	1205	1205	1205	1205	.	.	1
SBI middle (Hz)	1	1064	1064	1064	1064	.	.	1
SBI end (Hz)	1	1418	1418	1418	1418	.	.	1

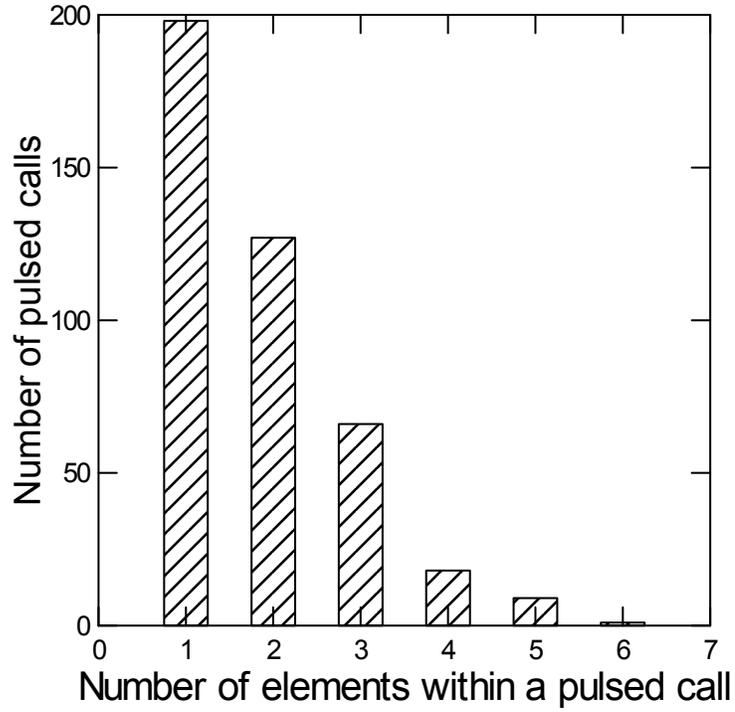


Figure 2.3. Number of elements per pulsed call (n = 419)

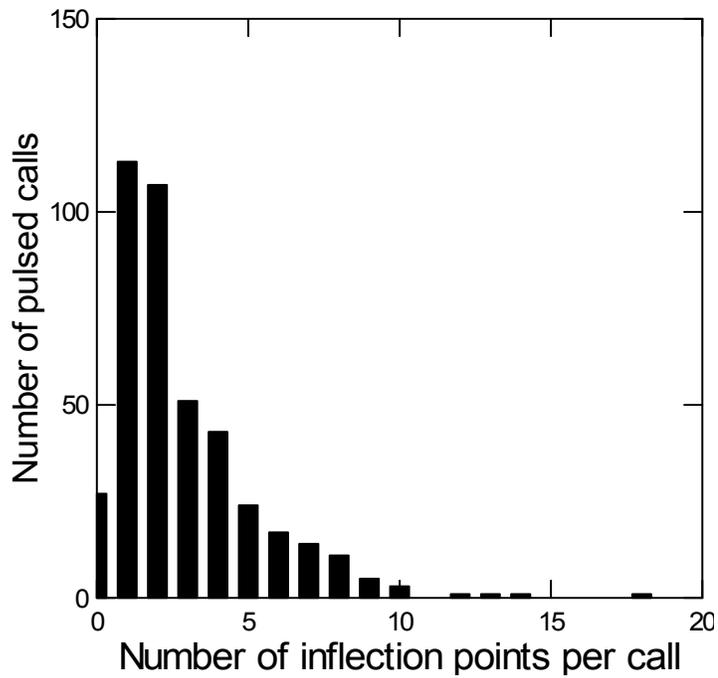


Figure 2.4. Number of inflection points per pulsed call (n = 419)

Table 2.3. A comparison of mean pilot whale pulsed call UFC measurements with published pilot whale mean whistle values (1 SD).

<b>Variable</b>	<b><i>G. melas</i> UFC</b>	<b>N</b>	<b><i>G. melas</i> whistle (Rendell et al. 1999)</b>	<b>N</b>
Duration (s)	0.60 (0.40)	85	0.62 (0.38)	384
Start frequency (Hz)	7598 (2029)	85	4180 (2110)	384
End frequency (Hz)	7019 (3369)	85	4280 (2270)	384
No. of inflection points	2.15 (2.02)	85	0.39 (0.80)	384

22

Table 2.4. A comparison of pilot whale and killer whale pulsed call characteristics. The overlap reflects the percentage of the ranges that are common to both the pilot whale and the killer whale pulsed call measurements.

<b>Variable</b>	<b>Pilot whales</b>	<b>N</b>	<b>Killer whales</b>	<b>N</b>	<b>% overlap</b>
LFC frequency range	0.8 – 9 kHz	419	1 – 6 kHz (Ford 1987)	3600	61%
Duration LFC	0.2 – 2.2 sec	419	0.5 – 1.5 sec (Ford 1987)	3600	50%
Pulse repetition rate	67 – 5506 pulses/sec	419	250 – 2000 pulses/sec (Ford 1987)	3600	32%
UFC frequency range	2.6 – 16 kHz	419	2 – 12 kHz (Hoelzel and Osborne 1986)	19	67%
Duration UFC	0.1 - 1.5 sec	419	0.5 –2.5 sec (Schevill and Watkins 1966)		42%

There does not appear to be a substantial enough difference between these values to reliably distinguish pilot whale pulsed calls from those of killer whales when, for instance, categorizing calls from sources such as autonomous recordings.

### 2.3.2 Principal Components Analysis

The PCA produced five principal components with eigenvalues less than 1 that together explained approximately 70% of the total variance observed (Figure 2.5, Table 2.5). This is within the desired range of 70-90% (Jolliffe 2002).

This analysis indicates that the pulsed call data can be summarized by five components. The first component represents the first and middle SBIs of the first element of a call. The second component represents the frequency of the highest visible sideband of a call. The third component encompasses the measurements of the fundamental frequency of a pulsed call. The fourth component relates to the more general structural characteristics of a call, namely the number of elements, segments and inflection points.

Table 2.5. Eigenvalues and percentage of total variance explained (with and without Varimax rotation) of the 5 principal components of pilot whale pulsed calls

Principal Components	Eigenvalue	% of total variance explained	
		without rotation	with Varimax rotation
1	2.82	20.12	15.77
2	2.54	18.14	15.00
3	1.80	12.86	15.64
4	1.50	10.72	14.09
5	1.11	7.89	9.23
Cumulative		69.73	69.73

Finally, the fifth component represents the duration, presence or absence of a UFC, and the final SBI (see Table 2.6). From the scores plots (see Figure 2.6), the clearest delineation appears to be between calls with very high frequency maximum visible sidebands and those with lower frequency maximum visible sidebands. Approximately 70% of all calls measured had a highest visible sideband at or above 18 kHz, while most of the remaining 30% had maximum visible sidebands at or below 15 kHz (Figure 2.7). There do not appear to be any other substantial groupings based on the PCA scores plots.

Table 2.6. Loadings (correlations between variables and components) of the Varimax rotated PCA on the spectrographic pulsed call variables. High loadings (greater than 0.5) are bolded. Variables which are highly loaded on the same component are strongly related.

Variables	<i>Principal Components</i>				
	1	2	3	4	5
NUM_ELEMENTS	-0.033	0.176	-0.143	<b>0.809</b>	0.027
NUM_SEGMENTS	-0.118	-0.034	-0.079	<b>0.558</b>	0.055
NUM_INFL_PTS	0.205	0.031	0.021	<b>0.762</b>	0.047
UFC_Y_N	-0.193	0.144	-0.044	-0.036	<b>-0.769</b>
TC_SBI_ST	<b>0.947</b>	0.043	0.083	0.001	0.147
TC_SBI_END	0.102	0.274	0.217	0.272	<b>0.579</b>
TC_DURATION	0.01	0.156	0.124	<b>0.501</b>	<b>-0.524</b>
TC_HIGH_FREQ	0.048	<b>0.980</b>	0.012	0.076	-0.037
TC_LOW_FREQ	0.362	-0.081	<b>0.548</b>	-0.082	-0.008
TC_DELT_FREQ	0.008	<b>0.983</b>	-0.047	0.085	-0.036
TC_ST_FREQ	0.378	-0.054	<b>0.638</b>	-0.274	0.005
TC_END_FREQ	-0.243	0.072	<b>0.810</b>	-0.008	0.2
SBI_1_MID	<b>0.933</b>	0.048	0.048	0.055	0.14
FF	0.032	0.006	<b>0.850</b>	0.029	-0.017

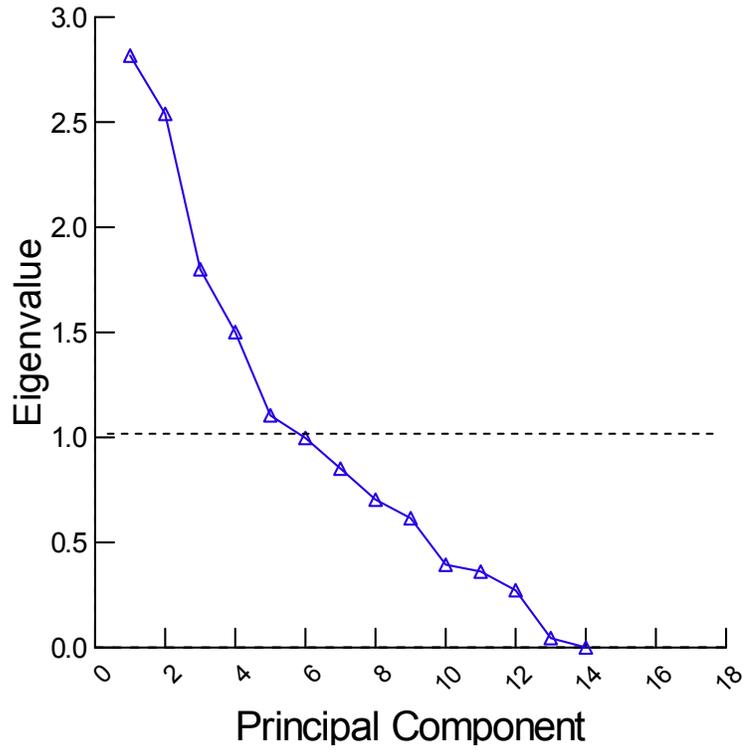


Figure 2.5. Plot of eigenvalues of the principal components. Most of the variance in the pulsed call data is contained in the first five principal components.

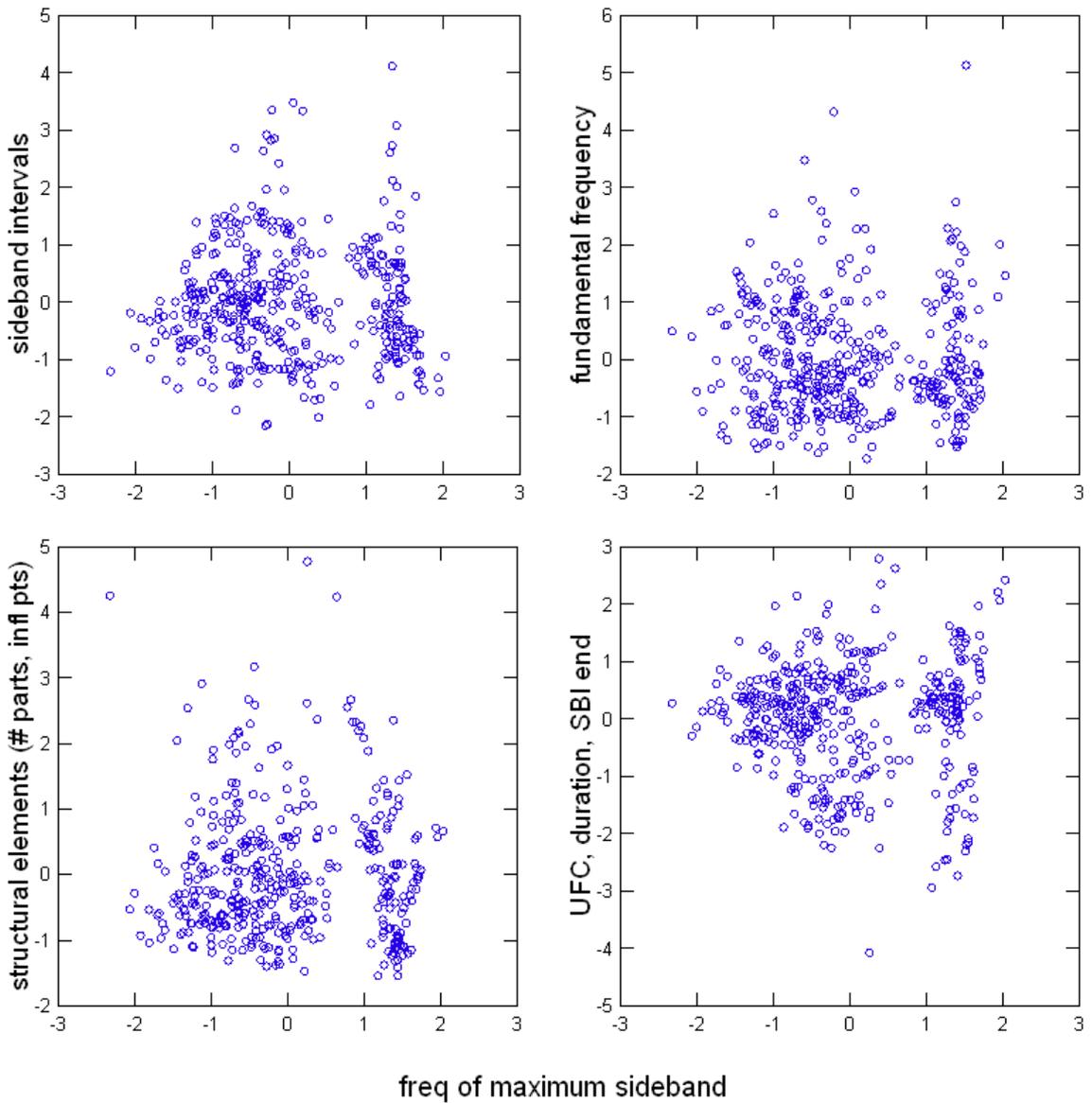


Figure 2.6. Scores plots of component 2 (frequency of the maximum visible sideband) with (a) component 1 (sideband intervals of the first element), (b) component 3 (fundamental frequency parameters), (c) component 4 (structural elements: number of parts and inflection points), and (d) component 5 (presence or absence of a UFC, duration and final SBI of the call) of the PCA. Only scores plots with component 2 showed any clear clustering pattern. Consequently, other scores plots are not shown.

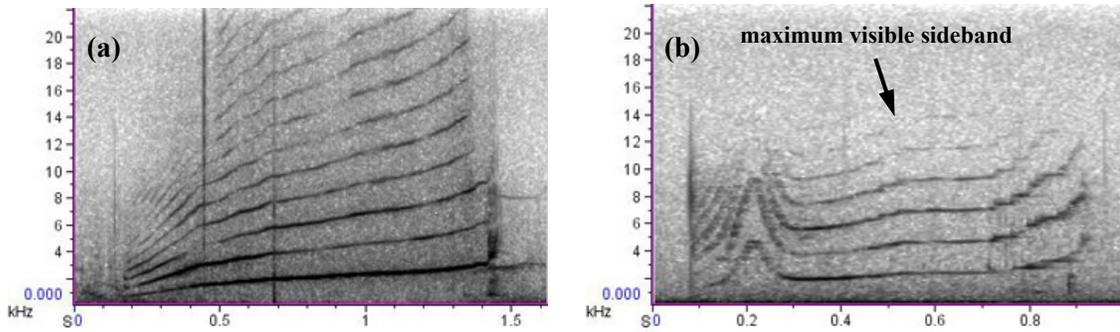


Figure 2.7. Examples of (a) a pulsed call with a maximum visible sideband above 18 kHz, and (b) a pulsed call with a maximum visible sideband below 15kHz.

### 2.3.3 *K*-means Cluster Analysis

The *k*-means cluster analysis was repeated 9 times (using numbers of clusters from  $2 \leq k \leq 10$ ). Clusters were plotted as grouping factors on the PCA scores plots in order to visualize any potential call groupings. The patterns observed were not substantially different across the *k* values, and indicated the presence of two broad call types (those with maximum visible sidebands above 18 kHz and those below 15 kHz) (see Figures 2.7 and 2.8). However, there were no clear delineations of call types in any scores plots that did not include the maximum visible sideband, and there was never any indication of tight, clusters, indicating distinct call types.

### 2.3.3 Hierarchical Cluster Analysis

The average linkage cluster analysis was stopped at a Mahalanobis distance of 7.9, with  $Q = 0.003$  (Figure 2.9). As can be seen in Figure 2.10, this produces a dendrogram with a single main branch. In other words, there is just one universal cluster. The CCC was 0.84, indicating that the clustering was successful at representing the differences between the calls (Bridge 1993). The clustering was repeated with single and complete linkages, however both techniques resulted in CCCs that were less robust than with average linkage (0.79 and 0.59 respectively). The hierarchical cluster analysis, therefore, appears to indicate that there are no discrete pulsed call types for pilot whales in this study. This hypothesis is further supported by the results observed from both the PCA scores plots and the *k*-means cluster analysis.

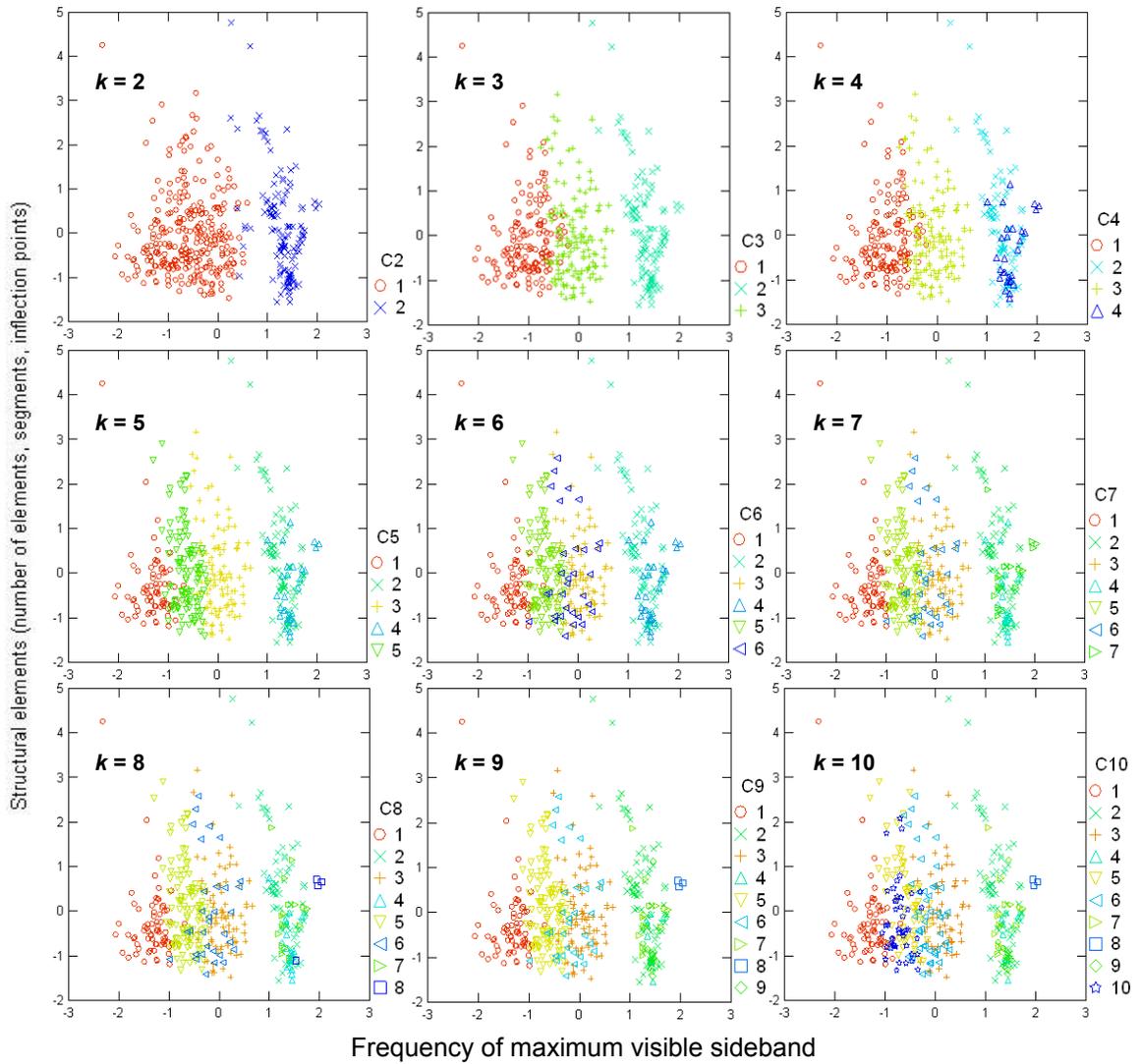


Figure 2.8.  $K$ -means cluster analysis groupings (with number of clusters from  $2 \geq k \leq 10$ ) shown as the grouping variable for the PCA scores plots of component 2 (frequency of maximum sideband) and component 4 (structural elements). Aside from the plots shown, there was no clear delineation of call types.

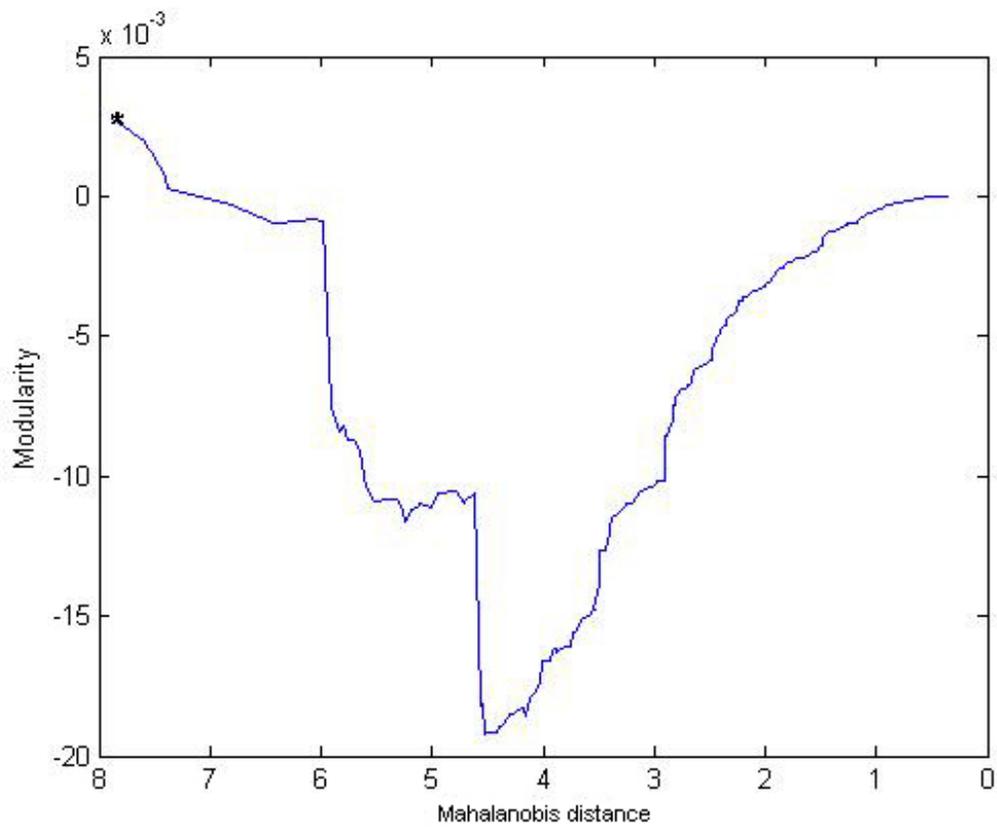


Figure 2.9. Modularity graph for the hierarchical cluster analysis of pulsed call similarity. Maximum modularity ( $Q$ ) = 0.003 as indicated by the asterisk.

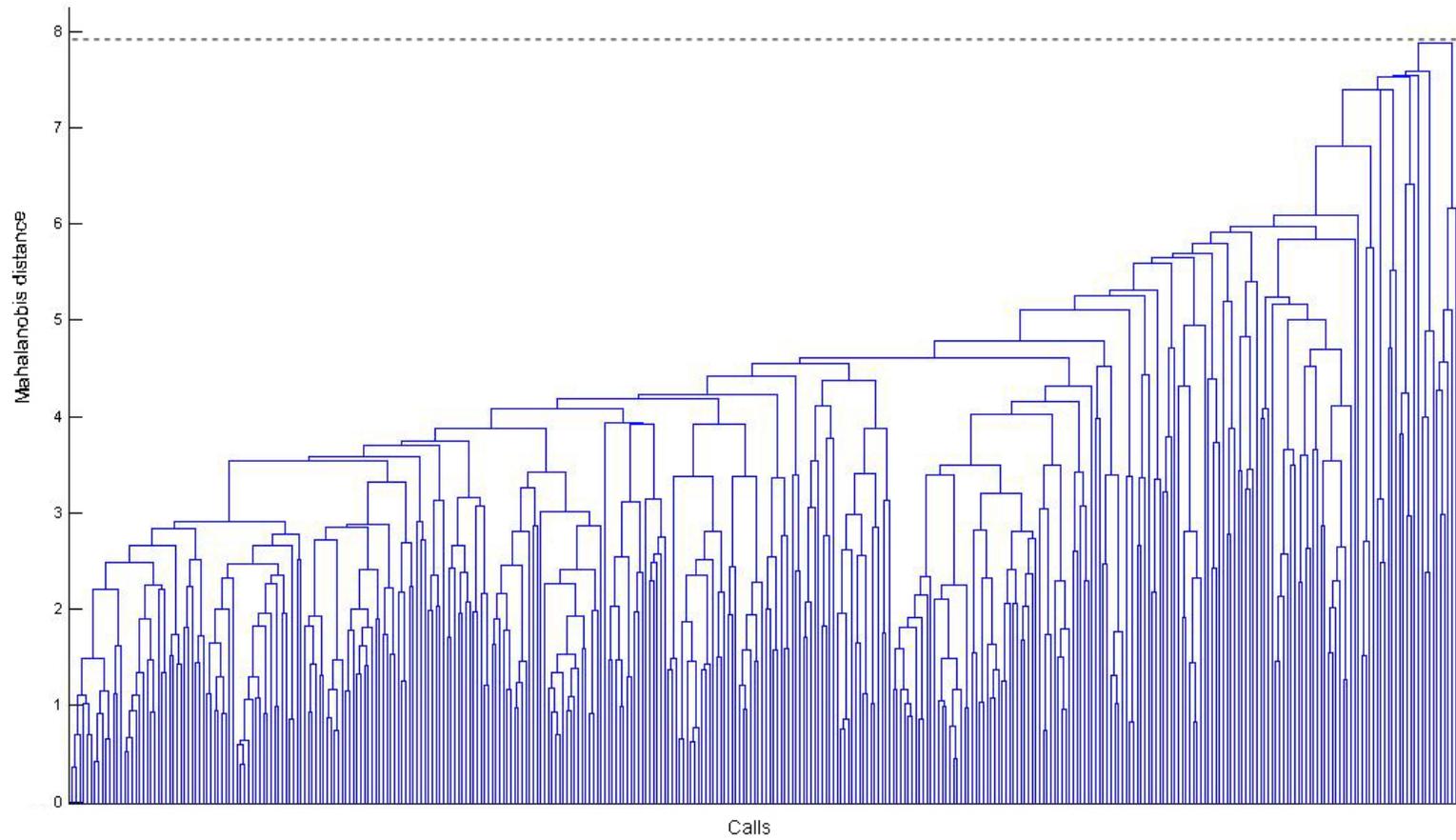


Figure 2.10. Hierarchical average linkage dendrogram of measured pulsed calls. Clustering was stopped by maximum modularity at the dashed line (Mahalanobis distance = 7.9).

## 2.4 Discussion

### 2.4.1 The Structural Complexity of Pulsed Calls

The results of this study show that the pulsed calls of long-finned pilot whales are structurally complex. Although few calls were segmented, more than half contained two or more elements caused by modulated pulse repetition rates over the course of the call. There was a wide variety of call structures, varying from relatively simple (e.g. one element, zero inflection points) to very complex (e.g. 6 elements, 3 segments, or 18 inflection points) (Figure 2.11). Roughly 20% had simultaneous, independently modulated UFCs, equivalent to complex high frequency tonal calls.

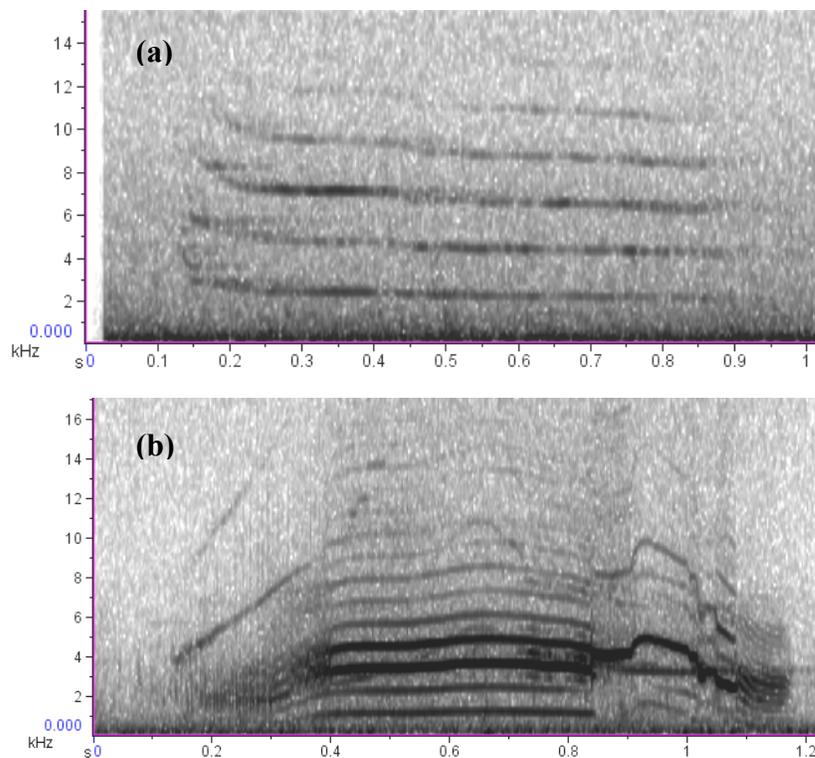


Figure 2.11. Examples of (a) a simple pilot whale pulsed call with a single element and inflection point, and (b) a more complex pulsed call with multiple elements, inflection points and a UFC.

After data reduction through PCA, pulsed calls still required a minimum of five main structural components to be described reasonably. The pulse repetition rate at the beginning and middle of the first element were strongly related to each other, but not to any other variables. As abrupt shifts in the PRR delineate different elements, it is not surprising that multiple measurements of the sideband interval within one element are strongly associated. The final SBI of the call, on the other hand, is not at all associated with the SBIs from the first element, reflecting modulation of the PRR from the start to the end of a call. The frequency of the highest visible sideband and the range of frequencies within a call were highly associated, but showed little relationship with any other variable. All of the frequency variables measured to describe the LFC contour (namely start and end frequency, lowest frequency and fundamental frequency) were moderately related to each other, but not much to any of the other variables. The general structural elements of a call (the number of elements, segments and inflection points) were related to each other and somewhat related to the duration of a call. It appears that calls with a higher number of elements are likely to be more segmented, have more inflection points and be longer than those with fewer elements. Finally, the presence or absence of a UFC was most related to the duration of a call and the final SBI of a call, such that calls with a UFC appear to be longer, with smaller final SBIs than those without a UFC.

Pilot whales produce a range of sounds, from structurally simple whistles (Taruski 1979) to the very complex calls described here, with several structural components that can be independently modulated. The simpler whistles are likely easier for the animals to learn and produce. The complex pulsed calls, on the other hand, could be at the upper limit of their ability to produce complicated signals and may be challenging for eavesdropping whales to imitate. Such calls are often considered honest signals, since their production and emission can offer accurate information to listeners about the quality or properties of the signaler itself (Fitch and Hauser 2003). Signal honesty is traditionally considered to be maintainable when two conditions are met. First, the signal must be costly to produce for the signaler. Second, the cost has to be dependent on the condition of the signaler, such that animals in good condition will produce higher quality signals (discussed in Johnstone 1995).

However, it is unlikely that producing such complex calls is energetically costly for odontocetes. While signal production in ectotherms like frogs requires a substantial increase in oxygen consumption, and is thus energetically costly (see Ryan 1988 for a review), several studies on endotherms have shown that the energetic costs of communication calls are minimal (Vehrencamp et al. 1989, Speakman and Racey 1991, Eberhardt 1994, Horn et al. 1995). Roosters (*Gallus gallus domesticus*), for instance, have a lower oxygen consumption rate when crowing than when performing other low-level activities, such as feeding or drinking, (Horn et al. 1995). Pipistrelle bats (*Pipistrellus pipistrellus*) can echolocate during flight, but appear to incur no additional energetic costs when doing so than when flying silently (Speakman and Racey 1991). Unfortunately, there are apparently no data on the metabolic costs of generating vocalizations in odontocetes. However, it is unlikely that the energetic cost of producing calls would be significant for these large mammals (see Fitch and Hauser 2003, Fitch 2004). Neural costs associated with encoding information into calls or processing signals are also likely to be negligible, as odontocetes have large brains that easily support complex cognitive abilities (reviewed in Marino et al. 2007).

The negligible energetic costs of producing pulsed calls do not, however, mean that they cannot be maintained as honest signals. Maynard Smith (1991) found that an honest signaling system can evolve despite low costs to the signaler if both the sender and receiver's interests do not conflict, as is often the case for closely-related individuals. Multiple studies have shown that, given the partially shared genetic interests among kin, cheap honest signaling systems can evolve and will be evolutionarily stable (see Fitch 2004). This is likely the case for pilot whales as they are matrilineal and exhibit natal group philopatry (Amos et al. 1993a), and thus primarily communicate with close relatives. Despite the minimal energetic costs needed to physically produce them, accurately generating such complicated and information-rich calls is still likely to be difficult. The ability of a whale to properly produce pulsed calls may be dependent on both vertical (from parents) and horizontal (from peers) learning (Sayigh et al. 1990, Deecke et al. 2000, Yurk et al. 2002), such that animals that have been a part of a social unit their entire lives will generate more "authentic" calls than a whale trying to imitate calls from a different unit.

It has also been suggested that complex vocalizations evolved to serve multiple functions (Bradbury and Vehrencamp 1998) and may transmit several pieces of information at the same time (Hebets and Papaj 2005). For pilot whales, the presence of biphonic and monophonic pulsed calls within the same population suggests a possible communicative function of the UFC. Miller (2006) demonstrated that source levels differ across types of Northeast Pacific resident killer whale vocal signals. He found that their vocal repertoire could be partitioned into “long-range” pulsed calls with overlapping high frequency components (equivalent to UFCs), and “short-range” sounds including whistles and pulsed calls without a UFC (Miller 2006). If pilot whale calls containing UFCs do function in longer-range transmission, they may have inter-group functions such as mate attraction (Ford 1991, Yurk et al. 2002) or spatial competition (Miller and Bain 2000), or intra-group functions such as maintaining the cohesion of the group while foraging (Ford 1989, Weilgart and Whitehead 1990). The presence of two independently modulated components within a call could allow senders to convey multiple pieces of information, including identity, status and condition to potential mates (Hebets and Papaj 2005, Yurk 2005).

To my knowledge, source levels and active space (the distance at which another whale can perceive the signal of a conspecific) have not yet been estimated for pilot whale calls. However, the use of biphonation in a fifth of their pulsed calls indicates that this may be an important aspect of their communication and should be investigated further. Chapter 4 offers a more detailed discussion of the possible functions of pulsed calls.

#### **2.4.2 The Non-Discrete Nature of Pulsed Calls**

All methods of automatic classification indicated that the pulsed calls could not be grouped into discrete call types. Graded vocalizations may serve as high information signals, providing fine-grained information on the status, motivation or behavioural context of the sender (Bradbury and Vehrencamp 1998, Compton et al. 2001). For example, specific bottlenose dolphin whistles show subtle contour variations that generally correspond to individual distinctiveness (McCowan and Reiss 2001) and social familiarity (McCowan et al. 1998). False killer whales produce a graded repertoire of

calls that lie along a continuum and may shift as a function of behavioural state (Murray et al. 1998). It is possible that the variation in pilot whale pulsed calls observed here may be a consequence of individuals communicating different states or statuses, such as behaviour, arousal or group membership, through modification of subtle characteristics of the calls. This idea is supported by general observations of increased pulsed call production during surface active behaviours (Weilgart and Whitehead 1990) and is discussed further in Chapter 4.

The diversity of calls may also reflect a communicative plasticity that facilitates adaptation to a variable environment. The pilot whales off Cape Breton are exposed to a highly variable and noisy environment. The field sites of this research (Bay St. Lawrence and Pleasant Bay) are the focal areas of several whale watching companies and groups of pilot whales are often surrounded by multiple vessels at one time (Smith et al. 2008). While this is purely speculative, pilot whales may also be modifying their pulsed calls based on environmental variables, such as fluctuating anthropogenic noise, that were not measured in this study. A large part of the variation between calls could be attributed to differing fundamental frequency measurements and durations. This coincides with strategies that have been observed by other cetacean species to overcome interference from background noise, including modulating the frequency and duration of their signals (Au et al. 1985, Lesage et al. 1999, May-Collado and Wartzok 2008).

Consequently, pilot whales may produce call types with multiple variant forms for each type that were not successfully discriminated by the clustering techniques used in this study. Cluster analysis generally has difficulties differentiating call types when there is a natural gradation between categories (Karlsen et al. 2002). Resident killer whales produce “aberrant” versions of discrete call types that show significant fluctuations in both duration and structural details (Ford 1989). Furthermore, they produce variable “miscellaneous” pulsed signals that cannot be placed in any clearly defined categories (Ford and Fisher 1983). When engaged in foraging behaviour, resident killer whales typically produce discrete calls, with only 6% of the repertoire being variable. However, this trend alters drastically during intense social activity, when 32% of their calls are variable (Ford and Fisher 1983) and there is an increased number of “aberrant” calls

(Ford 1989, 1991). The variable calls are traditionally excluded from further analyses or analyzed separately (Ford and Fisher 1983, Yurk 2005).

It is possible that the lack of discrete calls observed in this study is the result of a high number of variable calls in the pilot whale repertoire. No attempt was made to separate the wide spectrum of pulsed sounds extracted for the pilot whale measurements into typical or variable (squeaks, squawks) categories before analysis. The inclusion of variable call measurements in the cluster analyses may have obscured possible call type categories of the more stereotyped pulsed calls. Additionally, variants of the more typical calls (or “aberrant” calls) may have further masked any discrete call types. Whether pilot whale pulsed calls could be categorized into call types when analyzed at a coarser resolution (i.e. by disregarding small variations in frequencies and excluding variable calls) remains to be investigated. However, it is possible that pilot whales can discriminate between versions of a call type themselves, despite differences in frequencies of the variant forms. Bottlenose dolphins are known to be able to recognize and classify sounds independent of their specific spectral content by transposing the complex sounds immediately from one frequency range to another (Richards et al. 1984, Ralston and Herman 1995).

Pilot whale pulsed calls were found to be non-discrete in this study. This may be because they are diverse and easily modified to communicate the status of the sender and compensate for different environmental conditions. It may also be that call types exist but were not observed due to the presence of multiple variable and “aberrant” calls in the same sample. Regardless, pilot whale pulsed calls should, at least initially, be treated as non-categorical in future research.

### **2.4.3 Pilot and Killer Whale Pulsed Calls, an Example of Form Following Function?**

When comparing calls between species, it is expected that, generally, vocalization characteristics will follow taxonomic lines (Steiner 1981, Ding et al. 1995, Matthews et al. 1999). Additionally, body size has been found to be an important morphological factor influencing signal frequency as body size and the size of sound production organs correlate (Fletcher 1992), which consequently places physiological constraints on signal

production. Small body sizes, for instance, limit animals to the production of relatively high-frequency calls (Gerhardt 1994). In cetaceans, body size may be an important factor influencing maximum and minimum frequency of tonal signals (e.g. Matthews et al. 1999). Varying selection pressures relating to signal function are also likely to contribute to differences between species (Rendell et al. 1999).

Pilot whale pulsed calls appear to be structurally similar to those of killer whales. There is a predictable difference in frequency, as expected based on the body size-frequency relationship discussed above. Pilot whales reach a maximum size of 6m and 2320kg (Bloch et al. 1993b) and killer whales are obviously larger, reaching a maximum size of 9.8m and 2587kg (Klinowska 1991, Trites and Pauly 1998). Consequently, the slightly higher frequency ranges of pilot whale pulsed call variables are not surprising. What is surprising, however, is the general overlap between the compared structural components of the calls from the two species. The overlap is such that calls captured on autonomous recording devices in areas where the two species are sympatric could not be divided accurately based on their pulse repetition rates, LFC frequencies, UFC frequencies or durations.

Taxonomically, both species are members of the Delphinidae family, although the phylogeny of the Delphinidae itself is not well resolved (LeDuc et al. 1999). However, recent phylogenetic trees based on cytochrome b sequences place killer whales in the subfamily Orcininae and pilot whales in the subfamily Globicephalinae (Figure 2.12) (LeDuc et al. 1999, May-Collado and Agnarsson 2006). Unfortunately, other species within the Orcininae and Globicephalinae families (namely, the pygmy killer whale (*Feresa attenuata*), the short-finned pilot whale, Risso's dolphin (*Grampus griseus*), the melon-headed whale (*Peponocephala electra*), the false killer whale (*Pseudorca crassidens*), and the Irrawaddy dolphin (*Orcaella brevirostris*)) are difficult to include in the comparison, mainly due to a lack of available information and major differences in call structure and methodology across studies. For instance, false killer whale vocalizations appear to be gradually modulated from pulse trains to whistles and have a highly graded structure (Murray et al. 1998) that does not allow direct comparison with pilot whale pulsed calls. Risso's dolphins produce a wide variety of sounds, including "barks" and "grunts" that are pulsed tones (Corkeron and Van Parijs 2001) but

impossible to compare with pilot whale pulsed calls. Melon-headed whales appear to produce only whistles and click-bursts (Watkins et al. 1997). Interestingly, Irrawaddy dolphins, the only other species to share the Orcininae subfamily with killer whales, produce clicks, whistles and a variety of pulsed calls that do not resemble those of killer whales (Van Parijs et al. 2000). To my knowledge, there have not yet been any quantitative characterizations of pygmy killer whale or short-finned pilot whale pulsed calls.

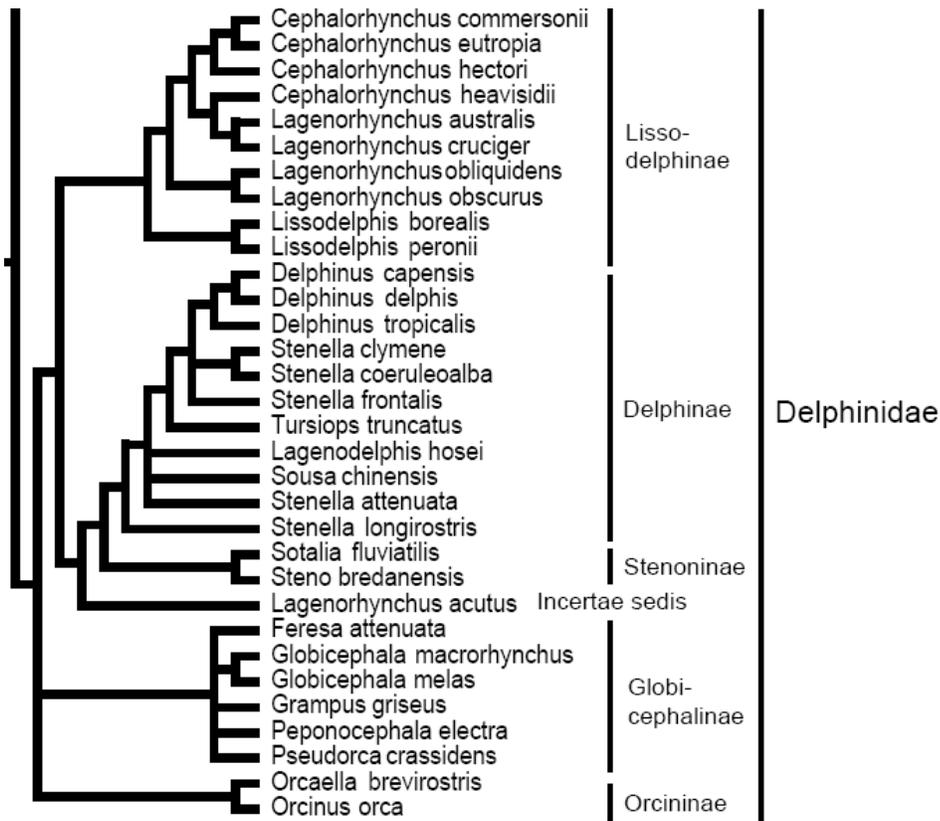


Figure 2.12. The Delphinidae branch of a recent phylogenetic tree produced by analysis of cytochrome b sequences in a Bayesian framework. Note that killer whales (*Orcinus orca*) are in the Orcininae subfamily, and long-finned pilot whales (*Globicephala melas*) are in the Globicephalinae subfamily. Reprinted with permission from May-Collado and Agnarsson (2006).

The structural similarity of pilot whale pulsed calls to those of killer whales may reflect the relative importance of signal function on the evolution of delphinid vocalizations. Both pilot whales and killer whales are matrilineal and exhibit natal group philopatry, an

extremely rare social structure where neither male nor female offspring disperse from the natal group (Bigg et al. 1990a, Amos et al. 1991, 1993a, 1993b). Consequently, the structure of their pulsed calls may be ideal for the transmission of short-range group membership information and long-range mate attraction necessary to reduce potential inbreeding costs (Amos et al. 1993a, Price 1999, Yurk et al. 2002), and promote within-group bonding to maintain and reinforce long-term bonds within a social unit (e.g. Schulz et al. 2008). Despite their relative distance on the phylogenetic tree, both species produce pulsed calls that are structurally indistinguishable. Such convergence in design suggests that call function may have played an important role in the evolution of the complex pulsed call produced by both species.

## **2.5 Summary**

Pilot whale pulsed calls are physically complex. They contain multiple components that are likely rich in information and difficult for eavesdroppers to imitate. The production of such structurally complicated signals suggests that they play an important role in pilot whale communication. The lack of obviously distinct call types within the pilot whale pulsed call repertoire may indicate communicative plasticity, allowing the whales to communicate status, such as arousal or behavioural state (Taruski 1979, Bain 1986, Murray et al. 1998) and to compensate for variable background noise levels (e.g. May-Collado and Wartzok 2008). Pilot whales may produce a mix of stereotyped calls, their variants and variable calls that were not successfully differentiated by the clustering methods used, as no attempt was made to separate them before analysis. Nonetheless, pilot whale pulsed calls do not appear to be categorizable into call types and should be considered non-discrete in future analyses. The structural and aural similarity of pilot whale and killer whale pulsed calls raises the question of whether the distantly related whale species, with a common rare social structure, have evolved similar call structures to solve similar communication challenges.

## CHAPTER 3 – RATING THE SIMILARITY OF PILOT WHALE CALLS USING STATISTICAL AND PERCEPTUAL MEASURES

### 3.1 Introduction

One of the largest problems in the study of animal communication lies in describing and quantifying the *similarity* between calls as opposed to simply determining the characteristics of a call or class of calls (as was done in Chapter 2). However, a quantitative measure of acoustic similarity is needed when comparing vocalizations, whether between individuals, social groups, or behavioural and environmental circumstances. There are currently two main methods for doing this: *perceptual measures* that quantify acoustic similarity based on ratings by human observers (e.g. Tyack 1986, Podos et al. 1992, Price 1998, Yurk 2005) and *statistical measures* using multivariate statistics on measures extracted from spectrograms (see Williams and Slater 1991).

The perceptual method is the most common process and uses the distinctive audible characteristics of a number of calls to group them or rate their similarities. It appears to be an effective way to classify bottlenose dolphin, *Tursiops truncatus*, signature whistles (Janik 1999, Sayigh et al. 2007)<sup>1</sup> and killer whale, *Orcinus orca*, pulsed calls (e.g. Yurk et al. 2002). The perceptual method is based on the idea that calls can be described by their gestalt (Katz 1950), meaning that acoustic similarities and dissimilarities of calls can be differentiated by humans without previous experience based on the overall pattern of the sound (Katz 1950, Yurk 2005). The inter-observer consistency of call-type rating has been found to be usually very high regardless of experience (Bain 1986, Deecke et al. 2000). Perceptual measures are advantageous in that they analyze calls as a unit rather than breaking them into disjunct measurements (Deecke et al. 1999). However, a major caveat is that such measures are based on the assumption that what appears to be different and biologically meaningful to us is also different and meaningful to the animals (discussed in Rendell 2003). This assumption has never been tested for pilot whales.

---

<sup>1</sup> There is an ongoing debate regarding bottlenose whale signature whistles (see McCowan and Reiss 2001 and Sayigh et al. 2007 for reviews).

Perceptual measures also have the problem of observer bias, such that ratings made by observers may be influenced by knowledge of the context of the call or the identification of the caller (Janik 1999). A researcher's subjective decision to group calls into one type over another can thus drastically alter the entire picture (Filatova et al. 2007). This can be avoided by limiting the amount of information available to observers when comparing calls (see Milinski 1997). Reproducibility of the ratings is another concern, such that ratings made by different observers may not correspond (Janik 1999). Perceptual measures also often present a logistical challenge in studies with large sample sizes (Deecke et al. 1999).

The statistical method involves direct measurements of spectrographic variables, followed by multivariate statistics to determine the distance (dissimilarity) between pairs of calls in multivariate space. Unlike the perceptual method, it has the advantage of being objective and repeatable, allowing comparisons between the results of different studies (Clark et al. 1987). It is also logistically simpler to undertake. Unfortunately, statistical measures from spectrograms are not always biologically meaningful, as they are based solely on the physical characteristics of the signals with no indication of how those signals are perceived (Horn and Falls 1996, Deecke et al. 1999). Examples of cetacean sounds successfully classified based on statistical measures include killer whale pulsed calls (e.g. Brown et al. 2006) and sperm whale (*Physeter macrocephalus*) codas (e.g. Rendell and Whitehead 2003b).

All classification methods require decisions by the researcher as to what parameters should be considered and how they should be weighed (Janik 1999). Small parameter differences that might be important to the animal may be missed by the researcher when measuring the spectrogram or by observers when rating calls based on gestalt. Consequently, conclusions supported by results from both methods are concomitantly stronger (Rendell 2003).

There have not yet been any studies comparing perceptual methods and statistical methods when rating the similarity of long-finned pilot whale (*Globicephala melas*) vocalizations. Both whistles and pulsed calls of pilot whales are not obviously discrete (Taruski 1979, Chapter 2), and therefore a similarity measure between calls is very helpful if they are to be analyzed in the context of social structure or behaviour. Both

statistical and perceptual measures of similarity between calls can be organized into similarity (or dissimilarity) matrices that can then be used to explore differential use of calls across various contexts. In this chapter, the similarities within the same set of pilot whale whistles and pulsed calls are measured using both statistical measures and visual and aural ratings by human observers, and the resulting similarity matrices are compared.

## **3.2 Methods**

### **3.2.1 Field Sites**

See field sites methods section 2.2.1 in Chapter 2

### **3.2.2 Recording of Vocalizations**

See recording of vocalizations methods section 2.2.2 in Chapter 2

### **3.2.3 Call Extraction**

#### *Pulsed calls*

See acoustic analysis methods section 2.2.3 in Chapter 2. Only pulsed calls from encounters in which at least one individual present had been linked to a social unit (see Chapter 4, section 4.2.3) were used in these analyses. This allowed the similarity matrices produced here to be later correlated with social association in Chapter 4.

#### *Whistles*

Recordings for all study years (1998-2000, 2005) were displayed graphically on frequency-time plot spectrograms and inspected for the presence of complex whistles (containing a minimum of one inflection point) by listening to the recordings while visually monitoring the spectrograms. Only encounters in which at least one individual present had been linked to a social unit (see Chapter 4, section 4.2.3) were examined for whistles, as discussed above. Only complex whistles were extracted for this analysis due to logistical restrictions and the assumption that complex whistles contain more fine-grain information than simple whistles (Weilgart and Whitehead 1990, Lindström and Kotiaho 2002). Only calls with suitable signal to noise levels and well-defined contours were used in the analysis. Whistles were extracted using Raven Pro (ver. 1.3.).

### 3.2.4 Statistical Measures

#### 3.2.4.1 Acoustic Analysis

##### *Pulsed calls*

The number of elements, segments and inflection points, presence/absence of a UFC, start, mid and end SBIs, total call duration, frequencies of the maximum/minimum sidebands, delta frequency, start/end frequencies of the primary energy, and fundamental frequency measured in Chapter 2 were used in this analysis for pulsed calls.

##### *Whistles*

Whistles were measured using Raven Pro (ver. 1.3.). The spectrograms were produced using 1024 point Fast-Fourier Transformations (FFT) and a Hamming window for each analyzed time series. Resulting spectrograms had a time resolution of two milliseconds and a frequency resolution of 61 Hz. Eleven variables were measured for each whistle: number of inflections points, steps and parts, presence/absence of a harmonic, total call duration, start, middle, end, maximum and minimum frequencies, and bandwidth (described in Table 3.1). These variables were chosen to best represent the contour and complexity of each whistle, for consistency with previous studies (e.g. Steiner 1981), and because they could be easily measured from a spectrogram.

Table 3.1. Description of the variables measured for each whistle.

<b>Variable</b>	<b>Description</b>	<b>Units</b>
Inflection points	Number of abrupt frequency modulations along the primary energy	
Steps	Number of sections of a whistle with a horizontal slope of zero	
Parts	Number of sections separated temporally by empty space	
Harmonic	The presence or absence of a harmonic	
Total duration	Total duration of the whistle	sec
Start freq.	Frequency at the starting point of a whistle	Hz
Middle freq.	Frequency at the middle of a whistle	Hz
End freq.	Frequency at the end of a whistle	Hz
Max freq.	Highest frequency point of a whistle's primary energy	Hz
Min freq.	Lowest frequency point of a whistle's primary energy	Hz
Bandwidth	The frequency difference between the maximum and minimum frequencies	Hz

### **3.2.4.2 Statistical Analysis**

Mahalanobis multivariate distances were calculated between each pair of calls using the variables of both pulsed calls and whistles using MATLAB (ver. R2006b). Mahalanobis distances indicate the separation of the calls as represented by points in multivariate space defined by the standardized measured variables, accounting for correlations between the measured variables (Manly 1994). The dissimilarity matrices were then transformed to similarity matrices by multiplying all values by -1 for subsequent analyses.

### **3.2.5 Perceptual Measures**

#### **3.2.5.1 Online Comparison of Calls**

Acoustic similarities and differences between calls can be distinguished by humans with or without any prior experience (Katz 1950, Deecke et al. 2000, Yurk 2005). To obtain similarity ratings from a number of observers, I developed an interactive website that allowed a wide variety of people to rate pairs of calls online. To recruit a large number of participants, it was advertised through notices sent to several email lists, including MARMAM, Cornell Bioacoustics, and the Dalhousie graduate student, marine biology undergraduate student and faculty lists.

Once on the website, participants were given the choice of rating pulsed calls or whistles and then presented with a series of spectrograms and associated sound files to compare, as well as an interactive form in which to enter their similarity ratings (Figure 3.1). Ratings were based on the distinctive audible characteristics of the calls complemented by structural differences in the spectrographic contours. Participants were asked to focus on the general contour, the number and location of inflection points, the general frequency ranges, the duration and the number of parts when examining the spectrograms (as in Ford and Fisher 1983, Yurk 2005).

Calls were presented in 80 pair-wise comparisons, and no information on recording context or caller identification was provided. The first ten were predetermined and identical for all individuals to allow for the identification of highly deviant participants and to ensure that I could later test for inter-observer consistency.

**LONG-FINNED PILOT WHALE VOCALIZATIONS**  
Conservation through the pursuit of knowledge

**HOME**  
**INSTRUCTIONS**  
**DO THE RESEARCH!**  
**MORE ABOUT PILOT WHALES**  
**FAQ and HELP**  
**CONTACT ME**

**Page 3 -- Do the Research! -- Compare each set of images and sounds**

Need instructions? [Click here](#) to open them in a new window! Note: calls may sometimes be quiet, so use your computer and/or speaker volume controls to increase the volume

**Look at the spectrograms and listen to the audio files for each pair. Chose a similarity rating from the drop-down menu and submit your answer.**

Frequency (kHz)  
Time (s)

Frequency (kHz)  
Time (s)

Evaluate Similarity

Submit I quit!

Figure 3.1. Example screenshot of the website for aural and visual inspection of spectrograms. Observers chose their similarity ratings (from identical to no similarity) from the drop-down menu for each pair of calls.

Each pair of calls was pulled from the total sample pool using a php script (Appendix I) that specified the first ten comparisons and randomly pulled the remaining 70 pairs of calls from four different folders: half the time from the dissimilar folder containing all calls, and the rest of the time divided equally between three broadly similar folders which contained calls that I had categorized as similar before testing began (Figure 3.2). Whistles were loosely grouped by number of inflection points (1 inflection point = folder similar1, 2 inflection points = folder similar2,  $\geq 3$  inflection points = folder similar3). Pulsed calls were grouped by number of elements (1 element = folder similar1, 2 elements = folder similar2,  $\geq 3$  elements = folder similar3). This was done to increase the number of comparisons between similar calls made by different observers.

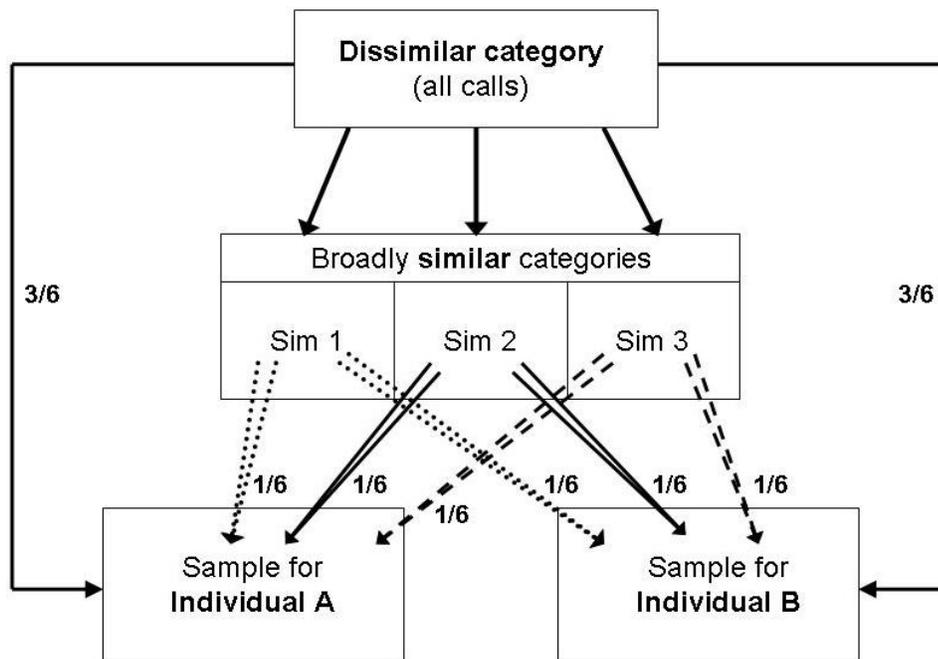


Figure 3.2. Schematic illustrating the random pulling of pilot whale call pairs from predetermined categories for human similarity ratings. Broad categories contained calls that were similar to each other, and the dissimilar category contained all calls. Half of calls rated by each participant were from the dissimilar category and half were from the broadly similar categories (1/6 each).

For each comparison, participants chose one of five similarity ratings based on what percentage of the calls they thought were the same: (1) totally different, less than 10% of the two calls are the same; (2) low similarity, between 10-40% of the two calls are the same; (3) medium similarity, between 40-60% of the two calls are the same; (4) high similarity, between 60-90% of the two calls are the same; (5) identical, more than 90% of the two calls are the same (see Appendix II for examples).

Individuals self-identified their level of experience at audio analysis on the background information form (Figure 3.3). I verified each claim of familiarity with acoustics and labeled them as experienced based on the participant's description of their relevant background in bioacoustics. All other participants were classified as naïve for the purposes of this study. Each participant's background information, IP address and similarity ratings were automatically inputted into an Excel file after they ended the session and stored on a secure server. In addition to the comparisons, the website contained general pilot whale information, a detailed "frequently asked questions" section, thorough instructions (Appendix II) and contact information.

**Background Information**

1) Age:

2) Profession (incl. student):

3) Prior experience with bioacoustic research?\*:

4) If yes, please explain the nature of your research/experience:

Briefly describe your experience with bioacoustics and/or spectrographic analysis here...

\* Please note that prior experience is NOT required

All information provided in this form will be kept strictly confidential. No names or email addresses are needed for this study. Background information is for data analysis purposes only.

Figure 3.3. The background information form filled-out by each individual before rating pairs of pilot whale calls through the website.

### 3.2.5.2 Statistical Analysis

Individual consistency was examined by determining each participant's deviation from the modal similarity rating for the first ten pairs. A value of 0 was given for a participant whose scores were the same as the modal response for all 10 calls, a value of +1 (+2, etc.) indicated the participant had specified one (two, etc.) rating higher than the mode, and a value of -1 (-2, etc.) indicated the participant had specified one (two, etc.) rating lower than the mode. The sum of the absolute values of each individual's deviations from the modal rating was calculated, and the mean deviations for all individuals were then box-and-whisker plotted. Any individuals with overall deviations beyond 3 times the interquartile range for the population were considered highly inconsistent and their ratings were removed for subsequent analyses.

MATLAB (ver. R2006b) was used to process the similarity values assigned to all pairs of whistles and pulsed calls rated by participants. Final values in the similarity matrices were the average ratings of all observers who compared the same pairs of calls. Pairs of calls that were not rated by any participant were given a value of NaN ("not a number" in MATLAB).

#### *First ten comparisons*

Separate similarity matrices were produced for the first ten pairwise comparisons of calls, which were rated by all participants. Final similarity values were the average ratings of all participants for each pair of calls. To allow comparisons between experience levels, the data set was then divided into mean experienced and mean naïve ratings of the first ten call pairs. A random subset of the naïve data was used in order to make the two participant groups equivalent in size, as there were more naïve individuals than experienced ones (see Table 3.2). The data were then further subdivided into two groups of experienced (exp1 and exp2) and naïve (naïve1, naïve2) participants to allow within group comparisons (Table 3.2). Similarity matrices were created for the groups containing all experienced and naïve individuals, as well as for the subgroups from each experience category.

Table 3.2. The number of participants and comparisons (available and used) from the online call comparisons and the subsets of data used in subsequent analyses. (W = whistles, PC = pulsed calls.)

<b>Data set</b>		<b>No. participants</b>	<b>No. comparisons</b>	<b>No. participants used</b>	<b>No. comparisons used</b>
First ten comparisons only	PC naïve	97	964	54	540
	PC exp	54	540	54	540
	W naïve	90	897	50	498
	W exp	50	498	50	498
Subgroups (from first 10 comparisons only)	PC naïve 1	54	540	27	270
	PC naïve 2	54	540	27	270
	PC exp 1	54	540	27	270
	PC exp 2	54	540	27	270
	W naïve 1	50	498	25	249
	W naïve 2	50	498	25	249
	W exp 1	50	498	25	249
	W exp 2	50	498	25	249
All data	PC naïve	97	6638	97	6638
	PC exp	54	3631	54	3631
	W naïve	90	5536	90	5536
	W exp	50	3270	50	3270

The complete, experienced, exp1, exp2, naïve, naïve1 and naïve2 similarity matrices were compared by generating the matrix correlation coefficients (pairwise) and significance values for all possible comparisons. This determined how consistent mean ratings were between groups (e.g. experienced vs. naïve vs. all) and within groups (e.g. exp1 vs. exp2).

#### *Entire set of comparisons*

Call similarity matrices were also produced for each participant that contained all call pair ratings made by that individual. Each participant's matrix was then compared to every other participant's matrix by generating the correlation coefficients for all possible comparisons made by both participants. Consequently, the ratings made by each observer were compared to any common ratings made by all other observers in a series of pairwise correlations. The matrix correlation coefficients were then averaged for comparisons between all participants, between only experienced participants, between only naïve participants, and between experienced and naïve participants. These mean correlations indicated the level of consistency between pairs of participants.

### **3.2.6 Statistical Measures vs. Perceptual Measures**

#### *First ten comparisons*

The perceptual similarity matrices containing mean similarity ratings and the statistical similarity matrices of the first ten pairs of calls were then compared by calculating the matrix correlation coefficient and significance values for all possible comparisons. This indicated, for both whistles and pulsed calls, the consistency between mean human ratings and those produced by statistical measures.

#### *Entire set of comparisons*

Each participant's similarity matrices for whistles and pulsed calls were compared to the statistical similarity matrices by generating the correlation coefficients (pairwise) for all possible comparisons. The matrix correlation coefficients were then averaged for comparisons between all participants and the statistical measures, between only experienced observers and the statistical measures, and between only naïve observers and

the statistical measures. This was done to examine how similar human ratings were with those produced by statistical measures for both whistles and pulsed calls when all comparisons made by each participant were considered. All analyses were carried out on MATLAB.

### **3.3 Results**

A total of 637 whistles and 370 pulsed calls were extracted and used in both the distance analyses and call comparison website.

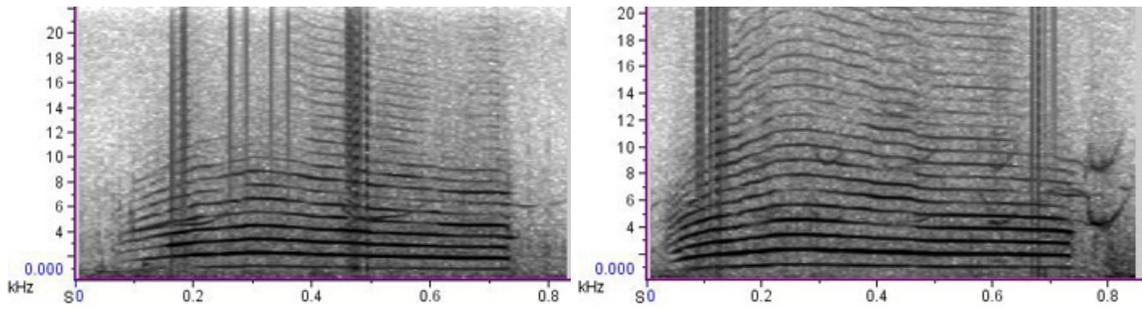
#### **3.3.1 Similarities from Quantitative Statistical Measures**

Similarity matrices were obtained by transforming the dissimilarity matrices produced by the Mahalanobis multivariate distance measurements. See Figures 3.4 and 3.5 for examples of calls rated as highly similar and very different based on the statistical measures of similarity.

#### **3.3.2 Similarities from Qualitative Perceptual Measures**

During the two months the website was available, 230 people categorized calls by ear and visual inspection of spectrograms. Pulsed calls were rated by 151 participants making a collective 10,269 comparisons. Of the 151, 54 were experienced and 97 were naïve. Whistles were rated by 142 participants making a total of 8,926 comparisons. Of the 142, 50 were experienced and 92 were naïve. 27% of participants rated both pulsed calls and whistles. The age of participants ranged from 18 to 76, and their occupations were varied, including students, lawyers, marine biologists, professors, paramedics and veterinarians. See Figures 3.6 and 3.7 for examples of calls rated as very similar and very different based on the human measure of similarity. Despite the high number of participants, the resulting matrices were still very sparse. The production of complete matrices would have required 405,769 unique whistle comparisons (over 5,000 participants) and 136,900 unique pulsed call comparisons (over 1,700 participants), which is logistically unfeasible. The observer consistency of call similarity ratings was fairly high for both pulsed calls and whistles (Figure 3.8). However, participants had a wider range of deviations from the modal rating when scoring pulsed calls (Figure 3.8a) than when comparing whistles (Figure 3.8b).

(a) BS1153\_pc\_18 vs. BS1153\_pc\_19



(b) BS1155\_pc\_24 vs. PB3134\_pc\_100

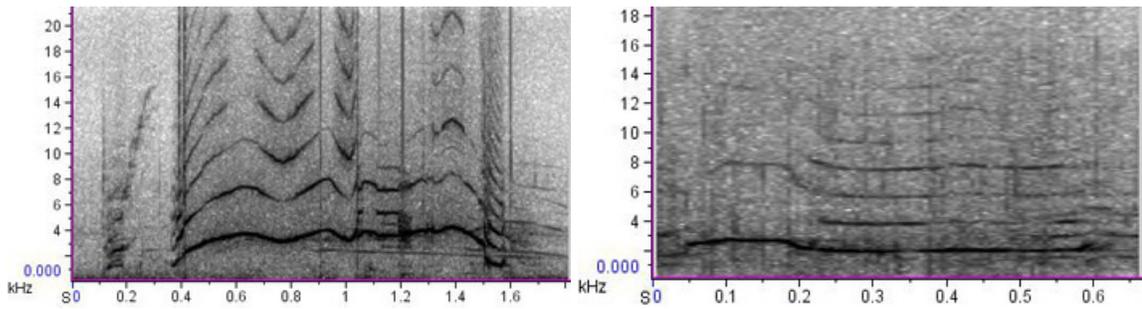
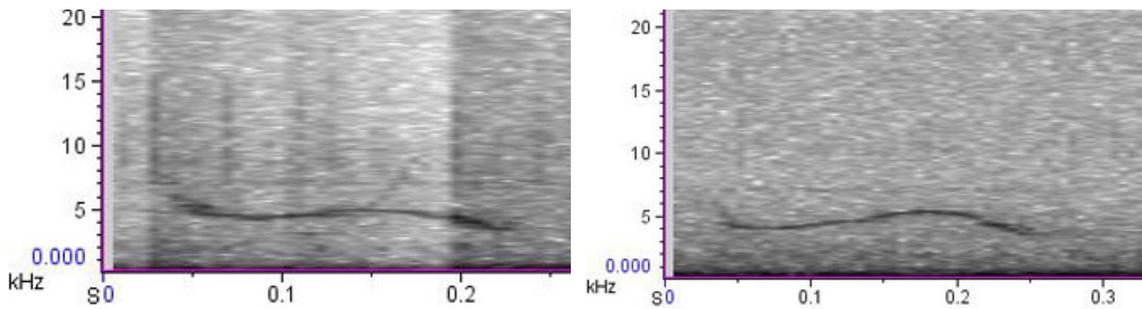


Figure 3.4. Examples of pulsed call pairs rated (a) high similarity and (b) low similarity from the statistical measures.

(a) BS1031\_w\_14 vs. BS1033\_w\_24



(b) BS0166\_w\_7 vs. BS2129\_w\_8

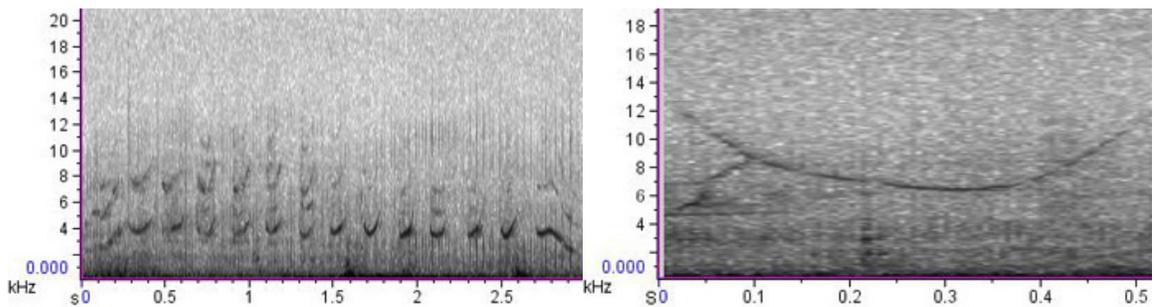
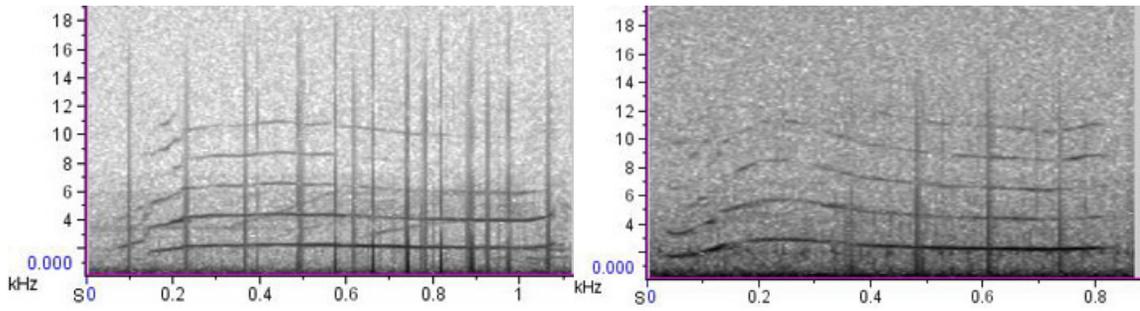


Figure 3.5. Examples of whistle pairs rated (a) high similarity and (b) low similarity from the statistical measures.

(a) BS1033\_pc\_1 vs. BS1033\_pc\_9



(b) BS0095\_pc\_10 vs. BS1033\_pc\_24

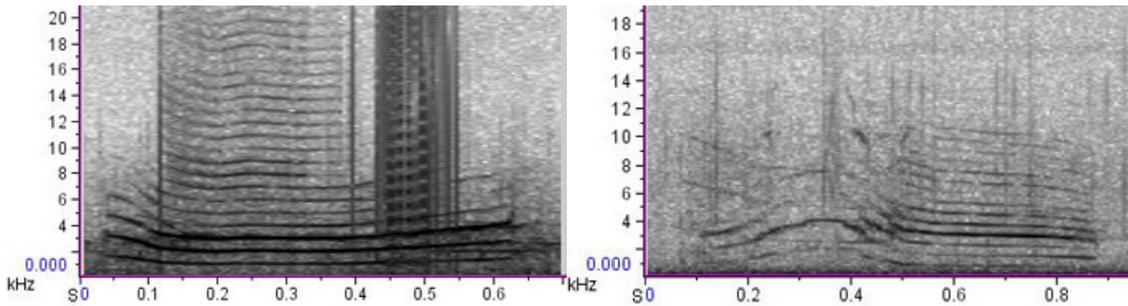
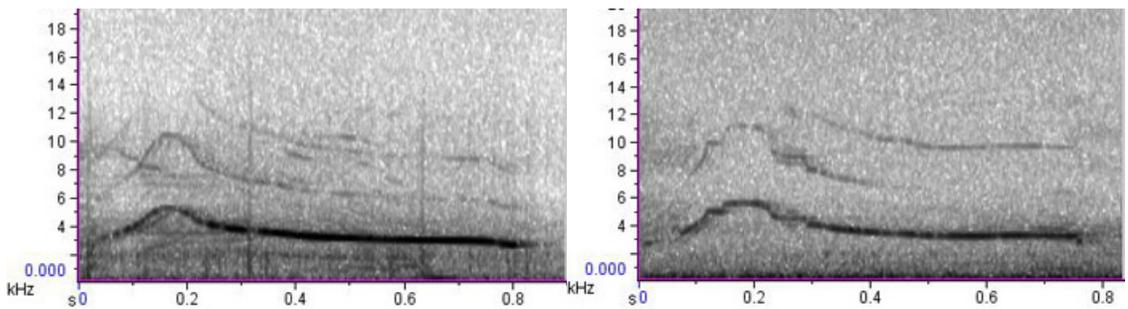


Figure 3.6. Examples of pulsed call pairs rated (a) identical and (b) different during the online comparisons.

(a) BS0204\_w\_10 vs. BS0204\_w\_16



(b) BS2157\_w\_6 vs. B0095\_w\_3

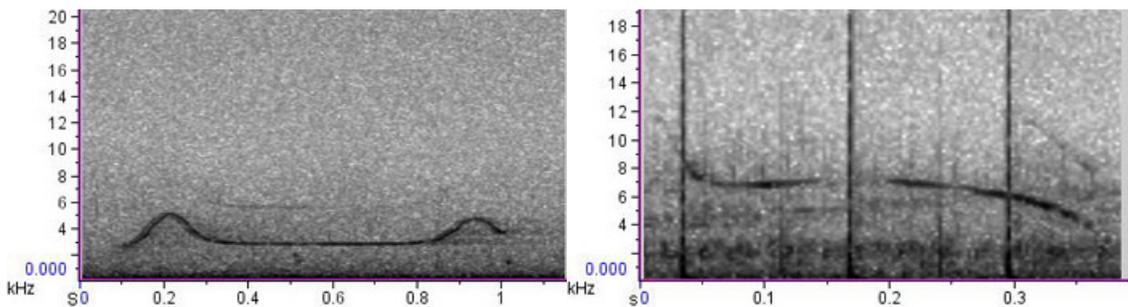


Figure 3.7. Examples of whistle pairs rated (a) identical and (b) different during the online comparisons.

Two naïve individuals (participants # 17 and # 152) were removed from the whistle data because of the high deviations of their ratings from the modal ratings of the first ten comparisons (Figure 3.8, Appendix III). Their removal left 90 naïve participants and 8,806 comparisons for subsequent whistle analyses (Table 3.2).

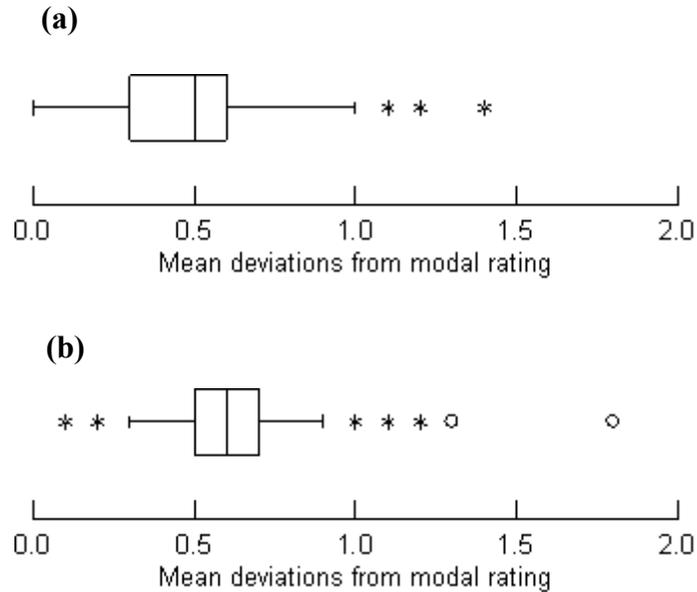


Figure 3.8. Box-and-whisker plots of mean participant deviations from the modal ratings of the first ten comparisons for (a) pulsed calls and (b) whistles. The center vertical line in a box-and-whisker plot marks the median of the sample. The length of each box shows the range within which the central 50% of the values fall (interquartile range). The whiskers show the range of observed values that fall within 1.5 times the interquartile range (Sokal and Rohlf 1995). The far outliers in (b) (designated by empty circles) were removed for subsequent analyses.

### *Pulsed Calls*

Naïve and experienced groups were highly consistent with each other when the average ratings of the first ten pulsed call pairs were compared across experience levels ( $r = 0.983$ ). The average ratings of naïve subgroups also strongly agreed with each other and with the experienced subgroups (Table 3.3). The mean ratings of the two experienced groups were almost perfectly correlated ( $r = 0.997$ ). When all of the ratings made by all participants were individually correlated, the agreement between individuals was, on average, still fairly high ( $r = 0.789$ ). When examined by experience level, naïve participants were slightly less consistent with each other than with experienced

participants (Table 3.4). Experienced participants were most in agreement with each other ( $r = 0.813$ ). Human perception of pulsed call similarity thus appears to be highly consistent between and within naïve and experienced groups, although experienced individuals tend to be more in agreement with each other than are naïve participants.

Table 3.3. Correlation coefficients and significance values for matrix correlations between both pulsed call and whistle perceptual and statistical similarity matrices. Each value within the perceptual similarity matrices is the mean similarity score of all participant ratings. Only the first ten comparisons for each call class, which were rated by every participant, were considered.

<b>Data Set</b>	<b>Matrix Correlation</b>	<i>Pulsed Calls</i>		<i>Whistles</i>	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Average ratings of first ten comparisons	Participants x measured	0.297	0.404	0.846	0.002
	Experienced x measured	0.295	0.407	0.863	0.001
	Naïve x measured	0.297	0.404	0.831	0.003
	Naïve x experienced	0.983	< 0.001	0.982	< 0.001
	Naïve 1 x naïve 2	0.986	< 0.001	0.974	< 0.001
	Experienced 1 x experienced 2	0.997	< 0.001	0.988	< 0.001
	Naïve 1 x experienced 1	0.979	< 0.001	0.982	< 0.001
	Naïve 1 x experienced 2	0.974	< 0.001	0.987	< 0.001
	Naïve 2 x experienced 1	0.985	< 0.001	0.965	< 0.001
	Naïve 2 x experienced 2	0.979	< 0.001	0.953	< 0.001

Table 3.4. Mean correlation coefficients for both whistles and pulsed calls for each possible series of matrix correlations. All of the ratings from each participant were compared to all common ratings from other participants, and to the similarity values produced by statistical measures, in a series of pairwise correlations.

<b>Data Set</b>	<b>Series of matrix correlations</b>	<i>Pulsed Calls</i>	<i>Whistles</i>
		<i>r</i>	<i>r</i>
Individual ratings of all comparisons made	All participants x all measured	0.366	0.364
	All naïve x all measured	0.362	0.355
	All experienced x all measured	0.375	0.380
	All participants x all participants	0.789	0.695
	All naïve x all naïve	0.784	0.672
	All naïve x all experienced	0.787	0.701
	All experienced x all experienced	0.813	0.752

### *Whistles*

Naïve and experienced groups were also highly consistent with each other when the average ratings of the first ten whistle pairs were compared across experience levels ( $r = 0.982$ ). The average ratings of naïve subgroups also strongly agreed with each other and with the experienced subgroups (Table 3.3). The mean ratings of the two experienced groups were the most strongly correlated ( $r = 0.988$ ). When all of the ratings made by all participants were correlated separately, individuals were still, on average, fairly consistent with each other ( $r = 0.695$ ), although less so than when rating pulsed calls (Table 3.4). When examined by experience level, naïve observers were less consistent with each other than with experienced participants (Table 3.4), and experienced individuals were in the highest agreement with each other ( $r = 0.813$ ). Human perception of whistle similarity thus appears to be highly consistent between and within naïve and experienced groups, although experienced individuals are slightly more in agreement with each other than are naïve participants. Individuals also appear to be slightly more consistent when rating pulsed calls than when rating whistles, regardless of experience level.

### **3.3.3 Statistical Measures vs. Perceptual Measures**

#### *Pulsed Calls*

The similarities between pulsed calls based on human perception and statistical measures were not more correlated than what is expected by random chance when considering the average ratings of the first ten comparisons ( $r = 0.297$ ,  $P = 0.404$ ), regardless of experience (Table 3.3). The results from the two methods showed a higher average correlation when the comparisons made by each participant were compared to the statistical measures ( $r = 0.366$ ). Experienced individuals produced ratings that were slightly more similar to the statistical measures than did naïve individuals (Table 3.4).

#### *Whistles*

Conversely, the similarities between whistles based on human perception and statistical measures were highly correlated when the average ratings of the first ten call comparisons were examined ( $r = 0.846$ ,  $P = 0.002$ ), and the experienced group was

slightly more comparable to the statistical measures than was the naïve group (Table 3.3). This high similarity was not maintained when all of the comparisons made by all participants were considered (Table 3.4). However, the mean correlation of all participant ratings to the statistical measures was still moderately high ( $r = 0.364$ ), and experienced individuals remained slightly more comparable to the statistical measures than the naïve individuals (Table 3.4).

## **3.4 Discussion**

### **3.4.1 The Perceptual Method**

The results of this study show that the perceptual method is a viable but inefficient technique for rating the similarity of pilot whale pulsed calls and whistles. Participants, especially those with previous experience in bioacoustics, were highly consistent with one another when comparing both sound classes, suggesting that the repeatability of the perceptual measures was robust. This is in agreement with studies on other delphinid species showing that inter-observer consistency of call-type rating is very high for whistles (Janik 1999, 2000) and pulsed calls (Deecke et al. 2000). The risk of observer bias, one of the main disadvantages of the perceptual method (Janik 1999), was reduced by limiting the amount of information available to participants, thereby ensuring that they were blind to the context of the calls and the identification of the callers (Milinski 1997). Over 200 observers participated in the study, which increased the number of call pairs that were rated and reduced the risk of producing idiosyncratic or irreproducible results (Jones et al. 2001). The results of only two participants were excluded from subsequent analyses due to their extremely high levels of inconsistency. That a few participants might produce highly anomalous results was not unexpected, as advertising the site publically introduced the risk that some participants would not take the comparisons seriously. However, both the whistle and pulsed call similarity matrices were very sparse, as it was logistically unfeasible to recruit enough participants to assess the large number of pairwise comparisons needed to successfully fill each matrix. Consequently, the perceptual method resulted in a significant loss of data, as many possible pairwise comparisons between calls were not rated, and thus not considered in subsequent analyses. Qualitatively rating calls with human observers is perhaps a feasible method for

smaller sample sizes, but when comparing large sample sizes (as was done here), sparseness of the data is a somewhat inevitable problem.

One of the main advantages of the perceptual method, however, is that it examines the overall pattern of the sound rather than disjunct pieces of it (Deecke et al. 1999). It has been shown to provide biologically meaningful results (e.g. Deecke et al. 1999, Yurk et al. 2002), and be highly reliable in detecting general similarities and differences of bird and humpback songs (Payne and McVay 1971, Podos et al. 1992, Price 1998). However, the perceptual method is based on the assumption that human perception and pilot whale perception of calls is the same, which may not be valid and has never been tested. It is also contingent on participants being able to successfully and consistently distinguish the similarities and differences of calls by their gestalt (Katz 1950, Deecke et al. 2000). The relative ability of human subjects to do this may be affected by the structure of the calls themselves. For instance, human classification has been shown to be one of the best methods of categorizing bottlenose dolphin whistles (e.g. Janik 1999). Conversely, Rendell and Whitehead (2003b) found that observer classification was the least useful method for studying sperm whale codas, as humans were unable to discriminate the naturally occurring groupings of the codas and were inconsistent with respect to each other.

Interestingly, in this study, participants displayed a wider range of individual deviations from the modal response when rating the first ten pairs of pulsed calls than whistles, suggesting that, at least initially, pulsed calls were more difficult to rate consistently. One can only speculate as to why this might be so, but one possibility is that it is more difficult at first to recognize the overall pattern of complex signals like pulsed calls. Due to technological limitations, there was no option in this study allowing observers to go back to previous ratings to recall or modify them. Because participants could not return to previous comparisons, there was no way to rectify erroneous similarity ratings from the beginning of the session, even once they were more comfortable with the highly variable structure of pulsed calls. Certainly, a useful feature for future interactive websites such as the one used here would be a method of returning to previous comparisons, to enable participants to check and modify their early assessments, and thus increase individual consistency across all comparisons and reduce

erroneous ratings. Alternatively, the first several comparisons made by each observer could be discarded, although given the sparseness of the data, it is difficult to justify excluding any information.

### **3.4.2 Human Perception of Pilot Whale Calls**

The mean matrix correlation coefficients between individual participant ratings in Table 3.4 suggest that the level of experience of a participant does not play a major role in determining their consistency with respect to other participants. While it is true that experienced individuals are, on average, more in agreement with each other than with naïve participants, the increased consistency observed is minimal. Other factors than experience with bioacoustics are likely influencing the differences observed between individuals. One such factor may be the weight individuals place on different parameters in their pattern recognition (Janik 1999, Jones et al. 2001). For instance, when comparing pulsed calls, some participants may have considered details such as duration and varying pulse repetition rates, while others may have looked more generally at the pulsed call contour.

Another possible cause is that individuals may have had slightly different frequency sensitivity ranges, and thus differential success hearing the higher frequency signals. The sound files of pulsed calls and whistles rated by human observers were not modified in any way in this study, as the range of human hearing (16 Hz – 20 kHz) theoretically covers the frequency range of the vocalizations included in the sample (Meijer 1992). Realistically, however, the useful bandwidth of the human hearing system is not much above 5 or 6 kHz, above which sensitivity drops rapidly, especially for elderly people (Meijer 1992). The maximum fundamental frequency of the whistles was on average 5 kHz ( $\pm 2$  kHz), which is at the higher end of the primary sensitivity range of human hearing. Because of the wide age range of participants (ages 18–76), it is likely that some individuals were unable to accurately hear the higher frequency whistles. However, the inclusion of spectrograms along with the sound files may have reduced the effects of this, as participants could examine the visual representation of each sound as well. This was unlikely an issue when comparing pulsed calls, as their primary energy is found, on average, at 3 kHz ( $\pm 1$  kHz).

### **3.4.3 The Statistical Method**

The statistical method proved to be a logistically feasible and repeatable technique for rating the similarity of pilot whale pulsed calls and whistles. It produced complete matrices that considered all possible pairwise comparisons between calls, and further had the advantage of being the least subjective method used (Clark et al. 1987, McCowan and Reiss 2001). I would add the caveat, however, that there remains an inherent subjectivity in the choice of which spectrographic parameters to measure, which could alter the entire picture of call similarity. This is the inherent pitfall of measuring only the physical properties of a signal with no information on how they are perceived (Deecke et al. 1999). The variables measured in this study were chosen to best reflect the frequency contour of the calls. For tonal signals, like the pilot whale whistles, contour is best measured by variables that reflect changes in the fundamental frequency of a call over time. For pulsed signals, such as the pulsed calls of pilot whales, contour is best described by changes in the pulse repetition rate (Deecke et al. 1999). Choosing representative measurements is rather challenging, as both the fundamental frequency of a whistle and the pulse repetition rate of a pulsed call vary considerably over the course of a call. The development of an automated procedure for extracting frequency contours, as has been developed for bottlenose dolphin whistles (McCowan 1995) and killer whale pulsed calls (Deecke et al. 1999), would be a valuable tool for future studies of pilot whale vocalizations.

### **3.4.4 Comparing Perceptual Measures with Statistical Measures**

For the most part, the whistle and pulsed call similarities produced through perceptual and statistical methods were only slightly correlated. This is in contrast to previous studies that found no substantial differences between visual and statistical methods of clustering bird song types (e.g. Podos et al. 1992) or killer whale pulsed calls (e.g. Ford 1984). However, unlike some bird songs (e.g. Price 1998) and killer whale pulsed calls (e.g. Ford 1987), pilot whale calls appear to be non-discrete and highly variable, which may increase the discrepancy between similarities based on the fine-scale measured variables considered in the statistical method and the more general contour of the calls used as the basis for the perceptual measures.

Perceptual ratings of pulsed calls were less in agreement with the statistical measures when the average ratings of the first ten pairs of calls only were considered than when the individual ratings of the entire set of comparisons were included. Participants may have experienced a learning curve while rating the first several pulsed calls, thereby further skewing their average similarity ratings away from those produced by the statistical measures for the first ten pairwise comparisons. Again, the ability to modify previous ratings in retrospect may negate this effect in future applications of this method. Conversely, the average ratings of the first ten pairs of whistles were highly comparable to the statistical measures, but this pattern was not maintained when the individual ratings of the entire set of comparisons were considered. This suggests that when a large number of people rate the similarity of a pair of whistles, as occurred for the first ten comparisons in this study, the average similarity value is nearly equivalent to that produced by multivariate statistics of measured variables. However, when only a few participants rate each pair of whistles (as occurred with the remainder of the comparisons in this study), their individual ratings are substantially less comparable to the statistical similarities, suggesting that individuals view whistle similarity from a different perspective than that indicated by statistical measures.

Call similarities were produced successfully by both the statistical measures and the perceptual measures. Individuals were more consistent with respect to each other than with the statistical measures. The two methods of rating call similarity compared in this study evaluate calls from different perspectives. However, based on the repeatability and relative objectivity of the statistical method, and the high inter-observer consistency of the perceptual method, both are likely to be useful in future studies of pilot whale vocalizations.

### **3.5 Summary**

The perceptual and statistical methods of rating call similarity produced results that were only moderately correlated. This may be a consequence of the different aspects of call structure considered by both methods. The statistical technique includes measurements of the fine-scale variability between calls, while the human participants are more likely considering the general contour of the calls. Naïve and experienced participants were

highly consistent with each other when rating both sound classes, indicating repeatability of the perceptual method. However, the statistical method was more efficient and considered all of the calls measured, while the perceptual method was restricted by the logistical challenge of rating all of the pairwise comparisons possible in such a large sample of calls. Both methods offer different perspectives on call similarity patterns within the pilot whale repertoire. Consequently, future studies that aim to analyze the similarity measures of pilot whale vocalizations in the context of social structure or behaviour should use the results of both methods, as conclusions supported by both are likely to be more robust.

## CHAPTER 4 – SOURCES OF VARIATION AND COMMUNICATIVE FUNCTIONS OF PILOT WHALE PULSED CALLS AND COMPLEX WHISTLES

### 4.1 Introduction

Signaling is an often dynamic process that can be greatly influenced by contextual factors, such as social or behavioural circumstances (King and Shanker 2003). Complex vocalizations, such as pilot whale (*Globicephala melas*) pulsed calls and complex whistles, are used in multiple contexts and thus likely evolved to serve multiple functions (Janik and Slater 1998). Identifying the behavioural and social contexts of such vocalizations is a crucial step in the study of the pilot whale communication system.

Variation in call structure within a species may be attributable to social structure (Ford 1991, Tyack 2000, Crockford et al. 2005). Animals living in fission-fusion societies seem to vary the contours or structural elements of their calls to facilitate individual recognition (e.g. McCowan and Reiss 2001, Sayigh et al. 2007). In cases where animals associate and interact in more permanent social units, variations in calls may be more indicative of group membership (e.g. Ford 1991, Crockford et al. 2005). The behavioural state of the caller may also play an important role in shaping call structure (Taruski 1979, Ford 1989, Weilgart and Whitehead 1990, Compton et al. 2001). For instance, bottlenose dolphins (*Tursiops truncatus*) may communicate behaviour-specific information in their vocalizations (Partan et al. 1988), and increasing arousal or “excitement” may result in extreme variations of the typical pulsed call types produced by resident killer whales, *Orcinus orca* (Ford 1989). The composition of the group being recorded can affect the structure or type of calls produced as well. The number of animals in a group of pilot whales significantly affects the type of whistles produced (Taruski 1979), and the presence of calves can introduce variation in call structure over time as the calves mature and modify their calls (Caldwell et al. 1990) and influence the structure of calls produced by adults within the group (e.g. Schulz 2007).

Calls may also be influenced by several contextual variables at the same time, and have multiple concurrent functions (Hebets and Papaj 2005). For instance, greater spear-

nosed bats (*Phyllostomus hastatus*) give highly distinctive group-specific foraging calls, from which individual bat calls are statistically indistinguishable (Boughman 1997), which reflect both the group membership and foraging behaviour of the sender. Female squirrel monkeys (*Saimiri*, spp.) produce variations of “chuck” calls that are thought to express a continuum of emotional states (Jürgens 1988), advertise location and movement direction of individuals (Boinski and Mitchell 1992) and coordinate activities such as foraging (Boinski and Mitchell 1997). In the Delphinidae, the discrete pulsed calls of resident killer whales are thought to function in group membership identification, group coordination during foraging, within-group bonding and possibly offer indications of individual identification through subtle variations in structure (see Ford 1989). Pilot whales are an extremely vocal species (Taruski 1979), using a combination of clicks, whistles and pulsed calls in a multitude of contexts. They are thought to have a complex social structure, in which animals live in kin-based long-term units that associate temporarily within larger groups (see Amos et al. 1993a, Ottensmeyer and Whitehead 2003), as described in Chapter 1. They display a variety of behaviour, including active behaviour such as foraging, travelling and socializing, as well as more restful states during which the animals move slowly at the surface (e.g. Weilgart and Whitehead 1990). Pilot whale groups off Cape Breton during the summer are composed of adults, juveniles and calves, as well as members of both sexes (Ottensmeyer and Whitehead 2000), and vary in size from 1-2 individuals to well over 100 (Bloch et al. 1993c, personal observation). However, few studies have explored the relationship of pilot whale calls over various contexts. Notable exceptions include Taruski (1979) and Weilgart and Whitehead (1990), both of whom investigated the differential production of pilot whale calls across behavioural categories. Their results suggest that complex whistles (Taruski 1979, Weilgart and Whitehead 1990) and pulsed calls (Weilgart and Whitehead 1990) are produced significantly more during active or “excited” behaviours, indicating a possible function in group cohesion. However, the variation in the structure of both pulsed calls and whistles across behavioural states has not previously been examined, and the social framework in which pilot whale communication takes place is still unresolved. In this chapter I describe possible sources of variation in pilot whale complex whistle and pulsed call structure by exploring the social, behavioural and group

composition contexts in which they occur, and attempt to interpret the potential communicative functions of these sounds.

## 4.2 Methods

### 4.2.1 Field Methods

#### 4.2.1.1 Field Sites

See field sites methods section 2.2.1 in Chapter 2.

#### 4.2.1.2 Encounters

An “encounter” was the base spatiotemporal unit used to delineate pilot whale associations (Ottensmeyer and Whitehead 2003). An encounter began when pilot whales were observed within 300m of the boat and ended 10 minutes after the last sighting of the group, when the whales moved further than 300m away from the boat or when the vessel captain decided to leave the area. All pilot whales within an encounter were assumed to have a high probability of interacting, and were thus considered associates (see Whitehead 1997, Whitehead and Dufault 1999). At the beginning of an encounter, the time and GPS location were recorded, along with an estimate of group size, the number of calves present and the modal behaviour of the animals (Table 4.1). This information was then collected every 10 minutes until the end of the encounter.

Table 4.1. Definitions of the four main categories of pilot whale behaviour, and examples of behavioural comments noted in log books.

<b>Behaviour</b>	<b>Definitions (Weilgart &amp; Whitehead 1990)</b>	<b>Examples of behav. comments</b>
Travelling	Coordinated, directed swimming by a group in a clearly defined direction	“all travelling in same direction, not surfacing often”
Socializing	No directional movement, short dives, active surface behaviour and body contact between individuals	“swimming upside down, lolling, spyhopping, splashing, body contact, tightly clustered”
Foraging	Prolonged dives, no directional movement, and little active surface behaviour, often feeding seabirds associated with the school’s location	“spread out, diving singly or in pairs, many surfacing”
Resting	Minimal movement, often essentially immobile at the surface (logging)	“staying at surface, side by side, logging, slow movement”

#### **4.2.1.3 Photographic Effort and Photo-Identification**

Photographic effort began when the whales were <50 m away from the boat and continued until all animals were no longer in range or until the end of the encounter, whichever occurred first. Photographs were taken opportunistically of either the right or left side of the dorsal fin, and all animals were photographed when possible with no regard to the presence or absence of marks on their dorsal fins. Photographs were taken from 1998-2000 on black and white Ilford Hp5 400 ASA film using a Canon EOS film SLR (300mm autofocus lens) with data-backs (time in hours and minutes), and on a Canon EOS 10D DSLR (200mm autofocus lens) in 2005, which produced digital colour images (2048 x 1360 pixels).

Individual pilot whales can be reliably distinguished based on acquired nicks and notches in the dorsal fin (Auger-Méthé and Whitehead 2007). All pilot whales included in this study were identified as described by Ottensmeyer and Whitehead (2003). In brief, a quality ( $Q$ ) assessment was assigned to each picture ( $Q1$ : poor -  $Q5$ : ideal), and all good quality photographs ( $Q \geq 3$ ) were then scored based on the number of nicks and inner corners of large notches along the fin edge, resulting in a total number of mark points (MP). Only well-marked individuals ( $MP \geq 3$ ) were considered for matching to reduce the risk of false identifications and increase the chances of reliably recognizing individuals after mark changes. Matching between encounters (1998-2005) was done using the string-matching function in the program Finscan (Araabi et al. 2000, Hillman et al. 2003), which uses the outline of the dorsal fin to match individuals. If there were no previous matches to individuals within the database, a new identification number was assigned to that animal.

#### **4.2.1.3 Recordings**

See recording of vocalizations methods section 2.2.2 in Chapter 2. Calls were only selected from recordings periods in which at least one pilot whale present was photographically identified. Vocalizations were recorded during a wide range of observable behaviours, such as travelling (slow and fast), foraging, resting and socializing, as described in Table 4.1.

### 4.2.2 Acoustic Analysis and Call Similarity Matrices

See methods section 3.2 and results section 3.3 in Chapter 3. Both the perceptual similarity matrices and the statistical similarity matrices of pulsed calls and whistles produced in Chapter 3 were used in the following analyses.

### 4.2.3 Assigning Social Units or Groups to Calls

Pilot whales off Cape Breton can be divided into social entities (both units, and groups of several units joined temporarily, as defined in Table 4.2) that represent sets of animals that associate more often with each other than with individuals from other groups or units (e.g. Ottensmeyer and Whitehead 2003). A social unit ID was assigned to each whistle and pulsed call included in the call similarity matrices. Calls were assigned a particular social unit if at least one member of that unit had been identified during the recording period. If members of more than one known social unit were identified in the same encounter, the calls were assigned to a mixed group (e.g. AF). It should be noted that there were often identified individuals not assigned to social units as well as non-photographed or non-identified individuals present in the encounters.

Table 4.2. Common terms describing pilot whale social structure and their definitions, as used in this study.

<b>Term</b>	<b>Definition (from Whitehead 2008)</b>
Social entities	Sets of animals within a population divided in such a way that many more interactions/associations occur within social entities than between them over the appropriate temporal scale.
Groups	Sets of animals that actively achieve or maintain spatiotemporal proximity (association) over any time scale (may be temporary) and within which most interactions occur.
Units	Sets of animals in nearly permanent mutual association.
Clusters	Sets of animals delineated by sequential additions of individuals (hierarchical cluster analysis) or divisions of a population (network analysis) that maximize the degree of associations within clusters and minimizes those between them. The target clusters, in the context of this research, represent social units.

Three main methods for delineating long-term pilot whale social units were considered, all of which use the same initial measure of association but differ in the importance they place on various aspects of relationships. The measure of association used by all three methods was presence in the same group during an encounter (using a chain rule of individuals within at least 200m of another group member, as described in Ottensmeyer and Whitehead 2003). The methods considered, described in more detail below, were the identification of key individuals and constant companions (Ottensmeyer and Whitehead 2003), a Bayesian hierarchical mixture model (Jankowski 2005), and a network modularity technique (see Lusseau et al. 2008). Social unit IDs were retained from these studies and subsequent analyses were repeated using the three different sets of social unit designations.

#### **4.2.3.1 Key Individuals and Constant Companions Method (KIN)**

Ottensmeyer and Whitehead (2003) used pilot whale photographs from 1998-2000 off Cape Breton to identify seven long-term social units (Appendix IV). Relationships were measured by the number of associations between individuals separated by a time lag and only incorporated presence data (i.e. when two animals are seen together). More specifically, social units were identified through the use of “key individuals”, sighted on at least four different occasions at least 30 days apart, and their “constant companions”, associates that were identified on the same day as a key individual on at least three occasions separated by at least 30 days, as described in Ottensmeyer and Whitehead (2003). Each social unit was comprised of key individuals and all of their constant companions.

#### **4.2.3.2 Bayesian Hierarchical Mixture Model (BAY)**

Jankowski (2005) used pilot whale photographs from 1998-2003 off Cape Breton to identify 18 social units (Appendix IV) by employing a hierarchical mixture model within a Bayesian statistical framework. This method attempts to model the variability in individual sighting probabilities, with social clusters treated as sub-populations within which individual sighting probabilities have a similar pattern over time (Jankowski 2005). Individuals are, therefore, assigned to clusters based on the temporal patterning of associations, as described in Jankowski (2005). This model is based on the assumption

that animals that form stable social clusters will have similar sighting histories (Gelman et al. 2004).

#### **4.2.3.3 Network Modularity Technique (NET)**

Lusseau (unpublished)<sup>2</sup> used pilot whale photographs from 1998-2006 off Cape Breton to identify 23 social units (Appendix IV) using the network modularity technique described in Newman (2006) and Lusseau et al. (2008). A network, in this case, is defined by weighted links between all pairs of individuals representing the half-weight association index between them. Different association indices, which estimate the proportion of time that a pair of individuals are associated, can be used in different circumstances, but the half-weight association index is less biased in situations where individuals are more likely to be seen apart than together (discussed in Whitehead 2008). It is thus well-suited for studies of pilot whale social structure as it is often not possible to observe all individuals in an area, creating a bias toward seeing individuals apart more often than together.

The maximum modularity method attempts to find a parsimonious division of the network that both maximizes the weights of edges within clusters and minimizes the weights of edges between them. Good cluster divisions contain strongly-weighted links within clusters but weak links between individuals in different clusters. The success of a division can be quantified by the modularity coefficient (Newman and Girvan 2004). The modularity coefficient,  $Q$ , is the proportion of total association within clusters minus the expected proportion when individuals associate at random (Lusseau et al. 2008, Whitehead 2008). Consequently, a higher  $Q$  indicates a clearer clustering of a network. Lusseau (unpublished) applied an aggregative clustering algorithm to the pilot whale data using the modularity method that iteratively split clusters until the maximum modularity coefficient was reached (see Newman 2006, Lusseau et al. 2008). The maximum modularity in this case,  $Q = 0.499$ , is well above Newman's (2004) suggested threshold of 0.3 for a useful clustering, strongly confirming that pilot whale society is well segmented. Unlike the two other methods considered, the network method of identifying unit membership assigns each identified individual within the population to a unit.

---

<sup>2</sup> Unpublished analysis by D. Lusseau, University of Aberdeen

#### **4.2.4 Assigning Contextual Information to Calls**

The modal behavioural state of the pilot whales and estimates of the average group size and number of calves present during each recording period were also noted for every whistle and pulsed call, as well as the year and encounter in which the recordings were made. Whenever possible, behavioural state was categorized as travelling (T), socializing (S), foraging (F) or resting (R) based on the closest 10-minute record (see Table 4.1 for definitions of behavioural categories). If no behaviour was mentioned for the recording period in the logs, I read through the detailed comments associated with each encounter and designated a behaviour based on the descriptions (see Table 4.1). The average group size was categorized as (1) < 10 whales, (2) 10-20 whales or (3) > 20 whales. Group size was calculated as the mean recorded group size observed during the recording period. The number of calves visible was categorized as 0 calves, 1 calf or  $\geq 2$  calves, and was the average number observed during the recording period. Calves were distinguished by their grey colour and small size.

#### **4.2.5 Statistical Analysis**

The three sets of social unit designations (from the KIN, BAY and NET methods), the behaviour of the group during recording, the average group size and number of calves, and the encounter and year in which recordings were made were transformed into binary similarity matrices (same = 1, different = 0) all describing the same calls, using MATLAB (ver. R2006b) (see Table 4.3). When producing the social similarity matrices, calls were considered to be from the same social group if at least one of the units present when the calls were recorded was common between them. For instance, a call from group ABC and a call from group AD would be given a similarity value of 1, as individuals from unit A were present during both recordings. Separate matrices were also produced that were restricted to calls made when only one social unit was identified as present (see Table 4.3).

Table 4.3. Names and descriptions of the social and contextual similarity matrices produced for both whistles and pulsed calls.

	<b>Matrix name</b>	<b>Description</b>
Social matrices	NET	Calls with at least one common social unit (as defined by the NET method) were given a 1 (same), calls with no common social units were given a 0 (different)
	KIN	Calls with at least one common social unit (as defined by the KIN method) were given a 1 (same), calls with no common social units were given a 0 (different)
	BAY	Calls with at least one common social unit (as defined by the BAY method) were given a 1 (same), calls with no common social units were given a 0 (different)
	NET – 1 unit	Same as above, but only calls with members of one social unit (as defined by the NET method) identified were included in the matrix.
	KIN – 1 unit	Same as above, but only calls with members of one social unit (as defined by the KIN method) identified were included in the matrix.
	BAY – 1 unit	Same as above, but only calls with members of one social unit (as defined by the BAY method) identified were included in the matrix.
Contextual matrices	encounter	Calls from the same encounters were given a 1 (same), calls from different encounters were given a 0 (different)
	year	Calls from the same year were given a 1 (same), calls from different years were given a 0 (different)
	behaviour	Calls made during the same behavioural state were given a 1 (same), calls made during different behavioural states were given a 0 (different)
	group size	Calls from the same average group size category were given a 1 (same), calls from different average group size categories were given a 0 (different)
	calves	Calls made when the same number of calves were observed were given a 1 (same), calls made when different numbers of calves observed were given a 0 (different)

#### **4.2.5.1 Relationships between Statistical Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts**

##### *Mantel tests*

One-tailed, partial Mantel tests were performed between the matrices of statistical similarity between pairs of calls produced in Chapter 3 and all social and contextual matrices to test the null hypothesis that calls produced within the same social units, or with the same behaviours, group sizes, number of calves or years were no more similar than calls from different social units or contexts. These partial Mantel tests controlled for similarity of encounter number to remove the effects of temporal similarities in call type. A Mantel test examines the association between two independent dissimilarity or similarity matrices describing the same set of entities (in this case calls) and tests whether the association is stronger than one would expect from chance (Sokal and Rohlf 1995). Statistical significance was tested using 1000 random permutations.

##### *Analyses of variance*

Distance-based analyses, such as the Mantel test described above, use similarities, dissimilarities or distances between samples in multivariate space. However, variable-based statistics can also be applied to multivariate data, and are instead a function of summary statistics that have been produced for each variable (Warton and Hudson 2004). Studies have shown that MANOVAs are at least as powerful as distance-based statistics, but may give different results and reveal alternative patterns in the data (Warton and Hudson 2004). MANOVAs examine consistent differences in measured variables between factor levels (in this instance, issues such as frequency shifts in calls with behavioural state), whereas distance-based measures look for clustering of calls with similarity of the factor.

Multivariate nested analysis of variance (MANOVA) models were used to analyze the relationship between the measurement data and social, behavioural and group composition contexts. It should be noted that mixed groups with at least one common unit between them were considered the same in the Mantel tests, but the MANOVAs were unable to differentiate the specific units within a mixed group, and thus considered

them different from one another regardless of which units they were composed of. The MANOVAs were also repeated for only encounters with single social units identified. For all analyses of variance, it was assumed that the calls from different encounters were independent of one another. It was thus important that encounter be nested within the categorical independent factors. MANOVAs were repeated to explore each independent factor separately, namely the three different unit designations (KIN, BAY and NET), the main behavioural state observed during each recorded encounter, the average group size present during recordings, the average number of calves present during recordings, and the year and encounter in which the recordings were made. The variables measured from the spectrograms (pulsed calls: number of elements, segments, and inflection points, SBI start, middle and end, total call duration, highest/lowest/ start/end frequencies and the fundamental frequency; whistles: number of inflection points, steps, parts, whistle duration, and highest/lowest/start/mid/end frequencies) were the dependent variables. Separate ANOVAs were performed on each dependent variable to explore the more fine-scale differences in call similarity between social units, behavioural states, group sizes, number of calves, years and encounters. Wilks' lambda tests were used to determine significance. All nested MANOVAs, ANOVAs and Wilks' lambda tests were run using R (ver. 2.8.0, R Development Core Team 2005).

The assumptions of normality, homoscedasticity and independence underlying analyses of variance were also investigated. A Lilliefors test was performed on the measurement variables to test for normality, which standardizes each variable and compares the new standardized variable to a normal distribution. All data were tested for homogeneity of variances using the Levene statistic, which tests for equality of group variances without assuming normality (Manly 1994). The Durbin-Watson D statistic was used to investigate autocorrelation of the data (calls were arranged in the data set by date and time of recording), and a value of 1-2 was considered to indicate little to no autocorrelation, while any values below 1 indicated that autocorrelation existed within the data (Durbin and Watson 1951). All tests were run on SPSS (ver. 12). Any variables that violated the assumptions of normality or homoscedasticity were transformed using standard data transformation techniques. Square-root transformations were applied to counts and log transformations were applied to the remainder of the variables (Wilkinson

et al. 1996). Although the assumptions were not satisfied for the most part, even after transformations, the MANOVAs and ANOVAs were still run with the transformed data because it often better satisfied the MANOVA assumptions. Unfortunately, non-parametric tests could not be used due to the necessity of nesting encounters within the independent variables, which cannot be taken into account by equivalent non-parametric tests. However, analyses of variance are generally robust to violations of normality and homogeneity (Miller 1986, Sokal and Rohlf 1995, Gupta and Richards 1997) and so were still used to examine the data. However, results from data which violated the underlying assumptions of the analyses of variance should be interpreted with caution.

#### **4.2.5.2 Relationships between Perceptual Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts**

Due to the sparseness of the perceptual matrices, similarity values were combined into broad similarity/dissimilarity categories in three different ways: (1) any similarity values  $\geq 3.0$  were clustered together as “highly similar” and  $< 3.0$  were considered “dissimilar”, (2) any similarity values  $\geq 4.0$  were clustered together as “highly similar” and  $< 4.0$  were considered “dissimilar”, and (3) any similarity values = 5.0 were clustered together as “highly similar” and  $< 5.0$  were considered “dissimilar”. This allowed the similarity of calls to be investigated at different levels, as some patterns may be evident when calls that are only slightly similar ( $\geq 3.0$ ) are included, while others may become obvious only when the most similar calls (= 5) are considered.

Mantel tests could not be used to investigate the data in the case of perceptual similarity as there were too many missing values in the matrices (the majority of pairs of calls were not compared, see Chapter 3, section 3.3.2). Instead, Kruskal-Wallis tests were used to compare the perceptual similarities to all social and contextual similarities from dyadic outputs produced in SOCPROG which allowed the removal of any missing values. The Kruskal-Wallis test investigates whether the similarities in each matrix are identically distributed (Sokal and Rohlf 1995). Because the grouping variable (highly similar or dissimilar) only had two levels, the Mann-Whitney U statistic was reported. Only calls from separate encounters were compared, as they were assumed to be independent from each other. Although there remains a potential violation of the independence assumption of the Mann-Whitney test as individual calls were used in

several comparisons, this violation should be of minor consequence as comparisons were made by different raters.

## **4.3 Results**

### **4.3.1 Statistical Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts**

#### **4.3.1.1 Testing MANOVA Assumptions**

The assumption of normality underlying the analyses of variance was not often satisfied by the data, even after standard transformations (Tables 4.4 and 4.5). The assumption of homogeneity of variances was also violated, as most Levene's tests were significant ( $P < 0.001$ ), indicating heteroscedasticity. However, the analyses of variance are still presented below, as they are generally robust to violations of assumptions and thus likely valid (Miller 1986, Sokal and Rohlf 1995, Gupta and Richards 1997). All data were assumed to be independent between encounters, and this was supported by the Durbin-D Watson statistics, all of which were above 1 indicating little to no autocorrelation of the data. See Tables 4.4 and 4.5 for a representative selection of Levene's and Durbin-D Watson test statistics.

#### **4.3.1.2 Call Similarity and Encounter**

Calls were predictably more similar within encounters than between them when investigated using Mantel tests, although this was more obvious for pulsed calls than whistles (see Figure 4.1, Table 4.6). Thus, all subsequent Mantel tests were partial tests, controlling for encounter number to remove the effects of temporal similarities in call type.

#### **4.3.1.3 Call Similarity and Social Unit Membership**

##### *Pulsed calls*

Pulsed call similarity was not significantly correlated with social unit similarity (partial Mantel tests,  $P > 0.05$ ), regardless of the method used to determine unit membership (Table 4.6).

Table 4.4. Lilliefors tests for normality, Levene's test statistics for homoscedasticity and Durban Watson D statistics of all measured pulsed call variables before and after standard transformations. Significance values of  $P < 0.05$  indicate non-normality and heteroscedasticity. Durban Watson D values between 1 and 2 indicate little to no autocorrelation of the data.

<i>Pulsed Calls</i>					
<b>Variable</b>	<b>Lilliefors</b>	<b><i>P</i></b>	<b>Levene's</b>	<b><i>P</i></b>	<b>Durban-Watson D</b>
Number of elements	0.28	< 0.001	4.00	< 0.001	
Number of segments	0.54	< 0.001	9.79	< 0.001	
Number of inflection pts	0.22	< 0.001	2.39	< 0.001	
SBI start	0.09	< 0.001	2.88	< 0.001	
SBI mid	0.09	< 0.001	2.95	< 0.001	
SBI end	0.11	< 0.001	9.14	< 0.001	
Total call duration	0.08	< 0.001	2.57	< 0.001	
Highest frequency sideband	0.17	< 0.001	3.03	< 0.001	
Lowest frequency sideband	0.05	0.032	4.21	< 0.001	
Start frequency	0.10	< 0.001	4.19	< 0.001	
End frequency	0.11	< 0.001	4.34	< 0.001	
Fundamental frequency	0.10	< 0.001	2.80	< 0.001	
SQRT(Number of elements)	0.27	< 0.001	4.17	< 0.001	1.38
SQRT(Number of segments)	0.53	< 0.001	9.56	< 0.001	1.96
SQRT(Number of inflection pts)	0.16	< 0.001	1.45	0.040	1.78
LOG(SBI start)	0.08	< 0.001	3.27	< 0.001	1.40
LOG(SBI mid)	0.09	< 0.001	3.74	< 0.001	1.43
LOG(SBI end)	0.05	0.059	5.89	< 0.001	1.93
LOG(Total call duration)	0.07	< 0.001	2.84	< 0.001	1.76
LOG(Highest frequency sideband)	0.15	< 0.001	2.71	< 0.001	1.65
LOG(Lowest frequency sideband)	0.12	< 0.001	4.21	< 0.001	1.86
LOG(Start frequency)	0.05	0.046	3.45	< 0.001	1.85
LOG(End frequency)	0.05	0.015	3.71	< 0.001	1.71
LOG(Fundamental frequency)	0.04	0.163	3.24	< 0.001	1.81

Table 4.5. Lilliefors tests for normality, Levene's test statistics for homoscedasticity and Durban Watson D statistics of all measured whistle variables before and after standard transformations. Significance values of  $P < 0.05$  indicate non-normality and heteroscedasticity. Durban Watson D values between 1 and 2 indicate little to no autocorrelation of the data.

<i>Whistles</i>					
<b>Variable</b>	<b>Lilliefors</b>	<b><i>P</i></b>	<b>Levene's</b>	<b><i>P</i></b>	<b>Durban-Watson D</b>
Number of inflection pts	0.24	< 0.001	6.48	< 0.001	
Number of steps	0.31	< 0.001	3.35	< 0.001	
Number of parts	0.53	< 0.001	15.75	< 0.001	
Total call duration	0.13	< 0.001	4.74	< 0.001	
Highest frequency point	0.15	< 0.001	4.91	< 0.001	
Lowest frequency point	0.11	< 0.001	6.59	< 0.001	
Start frequency	0.12	< 0.001	3.35	< 0.001	
Middle frequency	0.11	< 0.001	5.11	< 0.001	
End frequency	0.15	< 0.001	4.58	< 0.001	
SQRT(Number of inflection pts)	0.18	< 0.001	3.82	< 0.001	1.57
SQRT(Number of steps)	0.31	< 0.001	4.32	< 0.001	1.84
SQRT(Number of parts)	0.52	< 0.001	23.03	< 0.001	1.01
LOG(Total call duration)	0.06	< 0.001	2.42	< 0.001	1.81
LOG(Highest frequency point)	0.07	< 0.001	4.48	< 0.001	1.76
LOG(Lowest frequency point)	0.06	< 0.001	5.35	< 0.001	1.66
LOG(Start frequency)	0.04	0.005	4.87	< 0.001	1.76
LOG(Middle frequency)	0.03	0.152	5.25	< 0.001	1.67
LOG(End frequency)	0.05	< 0.001	3.06	< 0.001	1.83

Table 4.6. The matrix correlation coefficients and significance values (1000 permutations) of all possible partial Mantel tests for both pulsed calls and whistles, controlling for encounter number. Matrix 1 contains the Mahalanobis multivariate distances between all pairs of calls, transformed into similarity values (see Chapter 3, section 3.2.4.2). Significant values ( $P < 0.05$ ) are indicated by an asterisk (\*).

matrix 1	matrix 2	<i>Pulsed calls</i>			<i>Whistles</i>		
		N	matrix <i>r</i>	<i>P</i>	N	matrix <i>r</i>	<i>P</i>
call similarity	NET	318	-0.015	0.737	569	-0.004	0.518
call similarity	KIN	118	-0.109	0.999	317	0.022	0.200
call similarity	BAY	162	-0.089	0.998	286	-0.036	0.941
call similarity	NET – 1 unit	150	-0.028	0.767	184	0.010	0.477
call similarity	KIN – 1 unit	76	-0.172	0.999	214	-0.012	0.680
call similarity	BAY – 1 unit	72	0.007	0.435	123	0.006	0.518
call similarity	encounter <sup>†</sup>	370	0.101	< 0.001*	637	0.045	< 0.001*
call similarity	year	370	0.005	0.350	637	0.006	0.193
call similarity	behav	370	0.110	< 0.001*	637	0.008	0.354
call similarity	group size	370	-0.051	0.999	637	0.073	0.001*
call similarity	# calves	370	0.061	< 0.001*	637	0.017	0.100

<sup>†</sup> A full Mantel test was performed when correlating the call similarity and encounter similarity matrices.

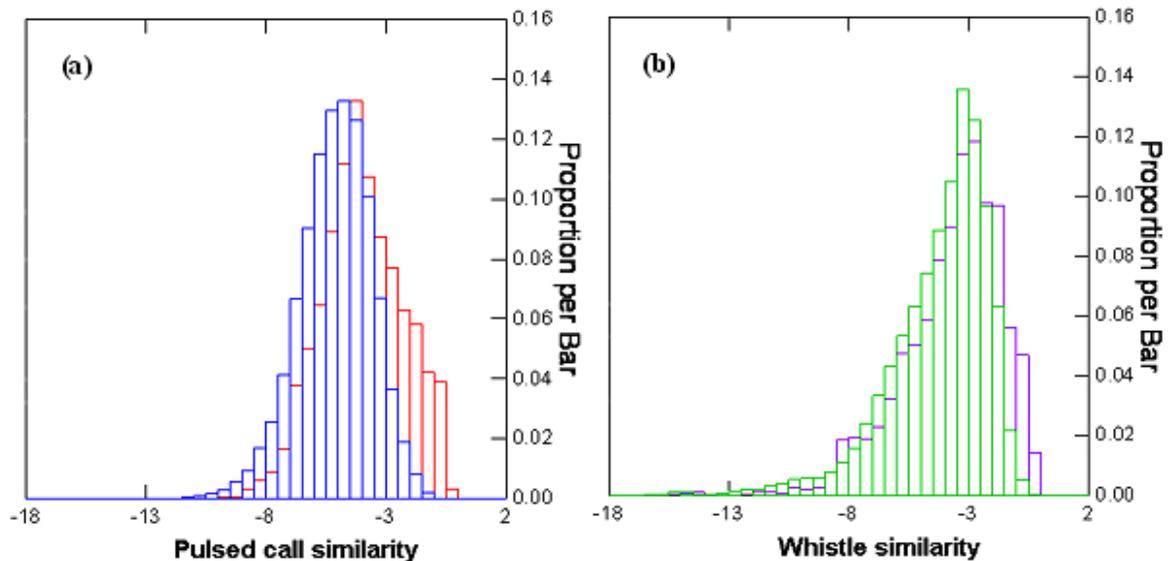


Figure 4.1. Histograms illustrating the statistical similarity of calls between (blue and green) and within (red and purple) encounters for (a) pulsed calls and (b) whistles. Calls were significantly more similar within an encounter than between them for both pulsed calls and whistles (Mantel tests,  $P < 0.001$ ).

This suggests that similar pulsed calls made by the same social unit do not form tight clusters. Histograms were produced to further investigate patterns in the data, and only those using social units defined by the NET method will be discussed in detail here, as they incorporate almost all calls measured. See Appendix IV for histograms using the KIN and BAY methods. As can be seen in Figure 4.2a, it appears that pulsed calls from different encounters are slightly more similar within social units than between them. When only calls made during encounters in which single (unmixed) units were present are considered, this pattern is less obvious (Figure 4.2c). It should be noted that even in encounters when only a single social unit was identified, there were always unidentified whales present that could not be ascribed to a unit.

The MANOVAs, on the other hand, were highly significant for all definitions of social units (Table 4.7), indicating that the means of the different call variables vary between social units. When examined more closely through the use of ANOVAs, the means of each pulsed call variable varied significantly across NET-defined social units when both mixed groups and single units were considered (Figures 4.3 and 4.4). Similar patterns were observed for all definitions of social units.

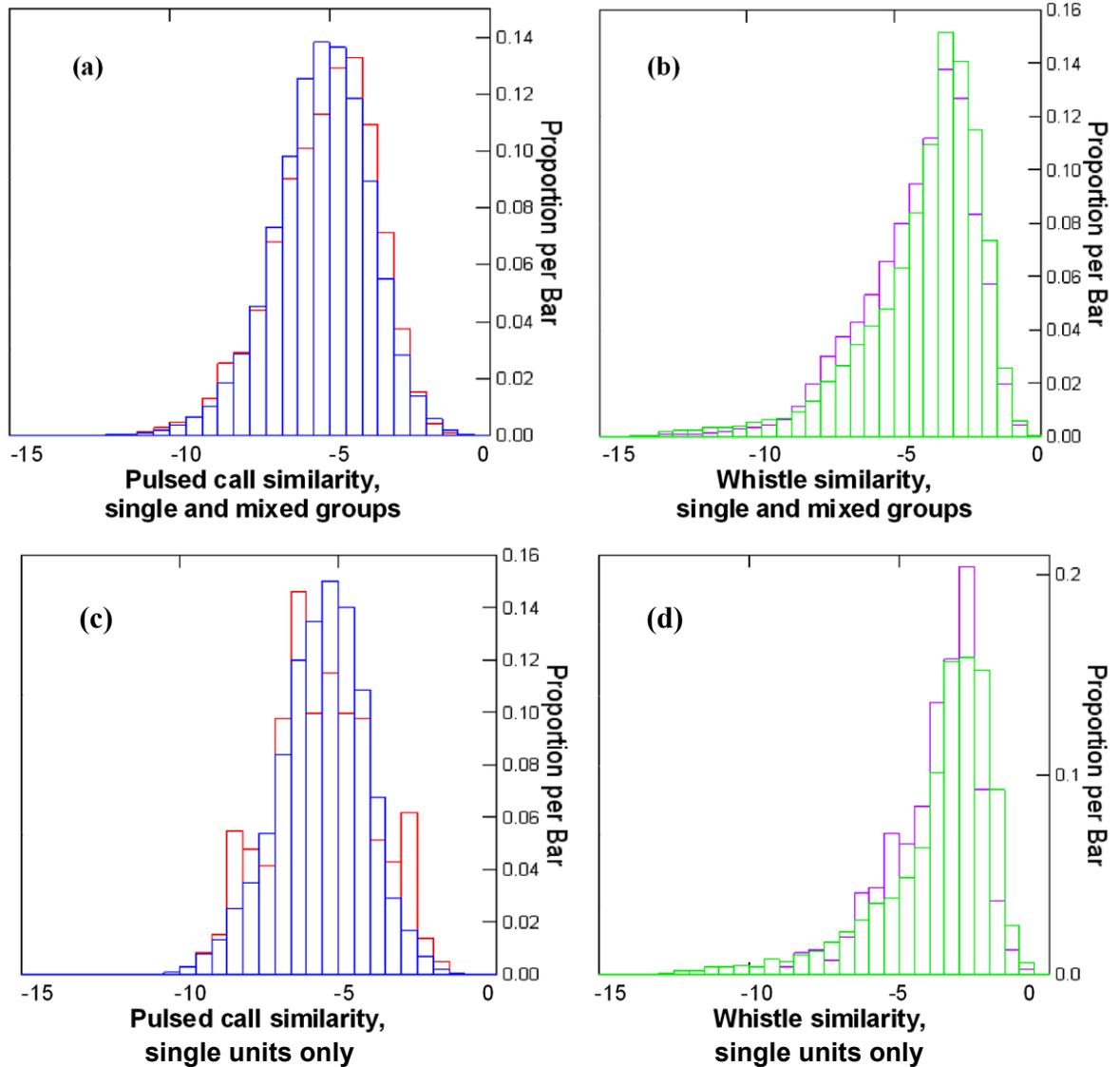


Figure 4.2. Histograms illustrating the statistical similarity of calls from different encounters between (blue and green) and within (red and purple) NET defined social groups for (a) pulsed calls and (b) whistles. Note that pulsed calls are slightly more similar within social groups than between them, while whistles appear to be less similar within groups than between them. This pattern is not as obvious for either pulsed calls (c) or whistles (d) when only single units are included.

Table 4.7. Summary of MANOVA results comparing statistical measures of pulsed calls across social units, years, behaviours, group sizes and numbers of calves present during the recording period. The dependent variables included were sqrt(number of elements), sqrt(number of segments), sqrt (number of inflection points), log(SBI start), log (SBI mid), log(SBI end), log(duration), log(highest frequency sideband), lowest frequency sideband, log(start frequency), log(end frequency), and log(fundamental frequency).

<i>Pulsed Calls</i>					
<b>Effect</b>	<b>Nested</b>	<b>Wilks' lambda</b>	<b>F-ratio</b>	<b>df</b>	<b>P</b>
NET	Encounter	0.020	3.41	372, 3045	< 0.001
KIN	Encounter	0.094	2.46	108, 689	< 0.001
BAY	Encounter	0.035	2.46	216, 1333	< 0.001
NET – 1 unit	Encounter	0.013	6.11	120, 985	< 0.001
KIN – 1 unit	Encounter	0.158	2.11	60, 261	< 0.001
BAY – 1 unit	Encounter	0.021	2.81	96, 347	< 0.001
Year	Encounter	0.458	7.84	36, 934	< 0.001
Behaviour	Encounter	0.479	7.34	36, 934	< 0.001
Group size	Encounter	0.585	8.11	24, 632	< 0.001
Calves	Encounter	0.487	11.42	24, 632	< 0.001

As the NET method includes the most data, only the results from the NET method will be presented here. See Appendix V for the ANOVA results using the KIN and BAY social units.

Figure 4.3 illustrates the mean values for all measurement variables across mixed groups and single units. While it is obvious that there is a wide variation in the pattern of call structures between the groups, it is difficult to tease apart any particular trends. Some groups, however, appear to preferentially produce more complex calls, while others tend to favor relatively simple ones. Similarly, it appears that the frequencies of calls vary widely between combinations of social groups.

When the pulsed call structures from units recorded alone are examined (Figure 4.4), however, several interesting patterns emerge. An important caveat is that the number of calls recorded from each unit varied widely, from a maximum of 39 from unit N to only one from unit V. However, when looking at social units from which at least 2 calls were measured, some consistently produced calls that were more complex than others, with higher numbers of elements, inflection points and segments.

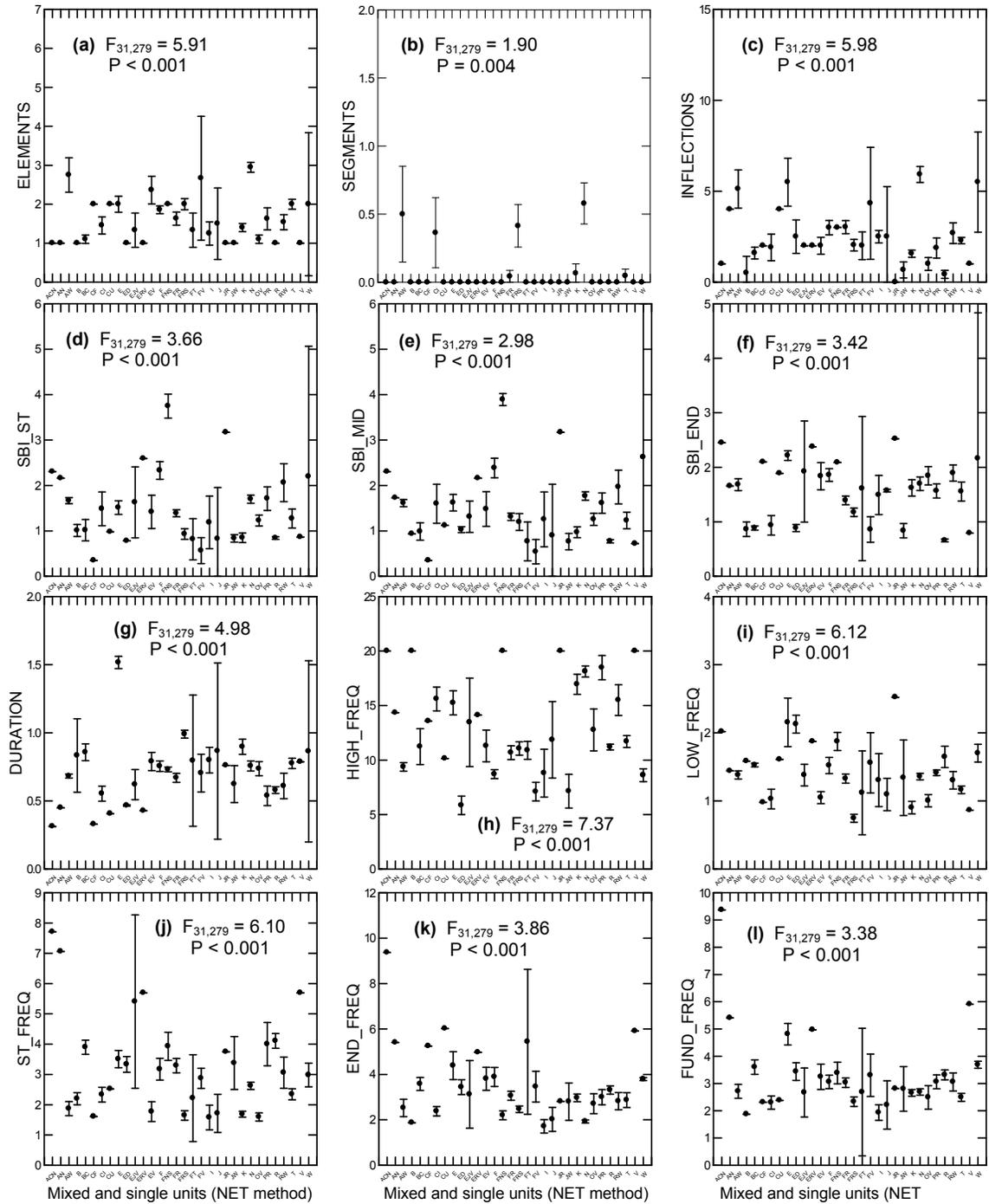


Figure 4.3. Means of each pulsed call measurement variable ( $\pm 1$ SE) for mixed and single social units (from the NET method), with associated ANOVA  $F$ -statistics and significance values.

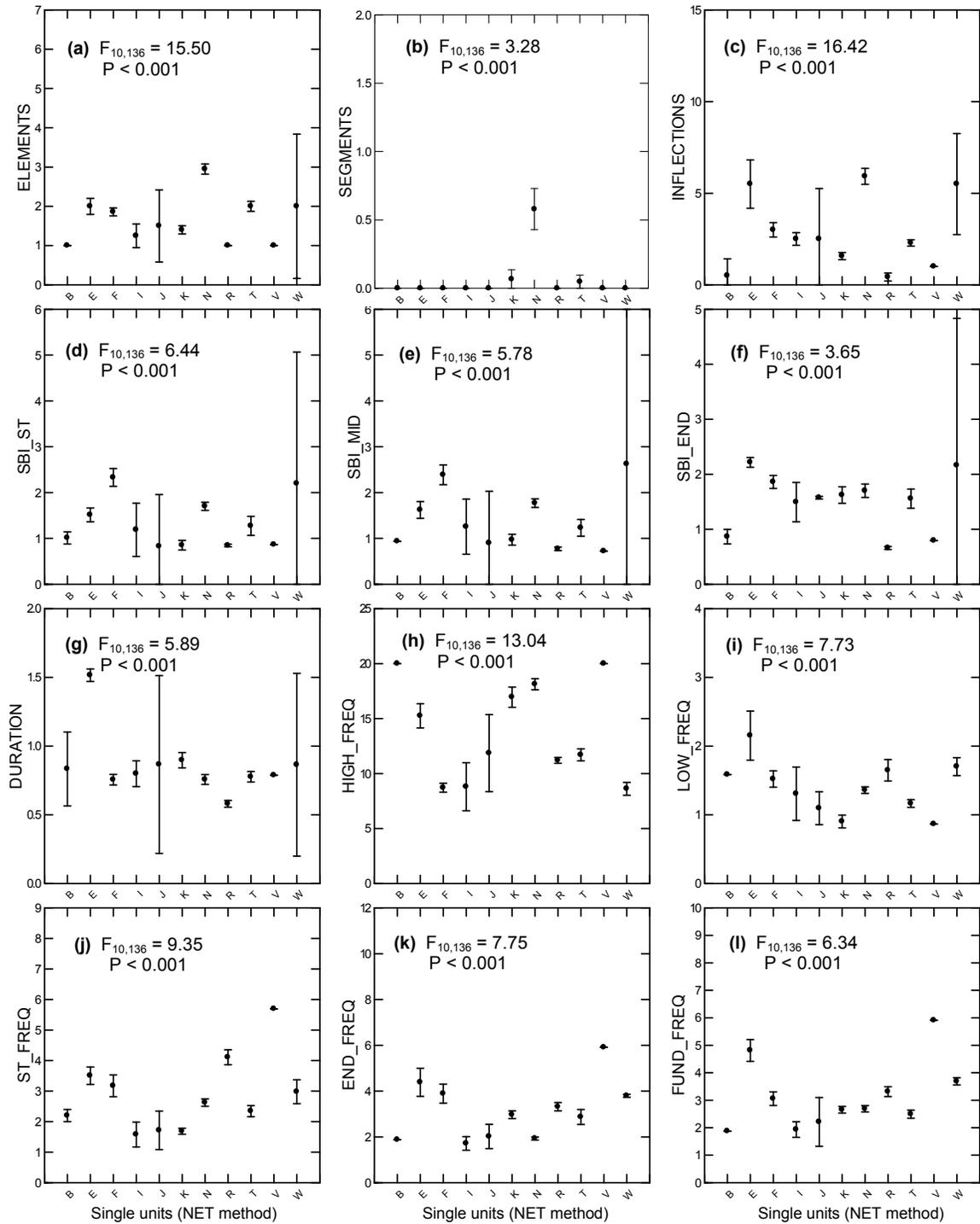


Figure 4.4. Means of each pulsed call measurement variable ( $\pm 1$  SE) for single social units only (from the NET method), with associated ANOVA  $F$ -statistics and significance values.

The frequencies of calls between the units also diverged widely, with a number of units producing calls with higher frequency measurements, and others with low or intermediate frequencies. Unit N, for instance, produced some of the most complex calls, composed of a high number of elements and inflection points and significantly more segmented than calls from any other group. They were also among the lowest frequency calls for start, end and fundamental energy measurements. Unit R, on the other hand, produced relatively simple calls with few elements or inflections points, but moderately high frequency values. Some social units produced similar calls to each other, but which varied significantly from those produced by other units. For instance, units I and J produced calls that could not be distinguished from each other based on any of the measured variables, but which were different from many other units. Duration did not vary widely between units, with the exception of unit E, which produced pulsed calls that were consistently over 0.5sec longer than most other units (Figure 4.4).

### *Whistles*

Mantel tests also suggested that whistle similarity was not significantly correlated with social unit similarity, regardless of the method used to determine unit membership (Table 4.6), indicating that overall whistles were not perceived as more similar when produced by the same units. As with pulsed calls, histograms were plotted to further investigate patterns in the data and only those with NET social units will be discussed here (see Appendix IV for histograms using KIN and BAY methods). From the histograms, it appears that whistles are actually slightly less similar within groups than between them (Figure 4.2b,d).

Similarly to the pulsed call data, the MANOVAs were highly significant for all definitions of social units (Table 4.8), showing that the means of the different call variables varied significantly between social units. The ANOVAs performed for each variable allowed a more detailed look at how aspects of whistle structure varied across both mixed groups and single units (Figures 4.5 and 4.6). See Appendix V for the ANOVA results using the KIN and BAY social units. Figure 4.5 illustrates the mean values for all whistle measurement variables across mixed groups and single units.

Table 4.8. Summary of MANOVA results comparing statistical measures of whistles across social units, years, behaviours, group sizes and numbers of calves present during the recording period. The dependent variables included were sqrt(number of inflection points), sqrt(number of steps), sqrt (number of parts), log(duration), log(highest frequency), log(lowest frequency), log(start frequency), log(middle frequency), and log(end frequency).

<i>Whistles</i>					
<b>Effect</b>	<b>Nested</b>	<b>Wilks' lambda</b>	<b>F-ratio</b>	<b>df</b>	<b>P</b>
NET	Encounter	0.064	3.74	432, 4452	< 0.001
KIN	Encounter	0.156	6.14	99, 2014	< 0.001
BAY	Encounter	0.037	4.54	216, 2067	< 0.001
NET – 1 unit	Encounter	0.094	4.42	99, 1098	< 0.001
KIN – 1 unit	Encounter	0.270	5.19	54, 958	< 0.001
BAY – 1 unit	Encounter	0.023	4.78	99, 667	< 0.001
Year	Encounter	0.614	11.10	27, 1648	< 0.001
Behaviour	Encounter	0.704	7.80	27, 1648	< 0.001
Group size	Encounter	0.674	13.22	18, 1092	< 0.001
Calves	Encounter	0.785	7.79	18, 1092	< 0.001

Again, there is observable variation in the pattern of whistle structures between the groups, although it remains difficult to distinguish any particular trends. An interesting difference, though, is that the variation in whistle structures across social groups appears to be far less extreme than was observed for pulsed calls. In fact, the majority of groups have mean measurements with overlapping standard errors, while only a few stand out as being widely divergent.

By examining the whistle structures produced by units recorded alone (Figure 4.6), it was possible to discern one interesting pattern. Again, a major caveat is that the number of calls recorded from each unit varied widely, from a maximum of 41 from unit F to only one from unit I. However, when looking at social units from which at least 2 calls were measured, some consistently produced calls that were higher frequency than others. For instance, unit M had consistently higher frequency measurements than most other social units, while unit P produced whistles with some of the lowest frequency values. The number of parts of a whistle was not significantly different between units, as the majority of whistles measured were composed of only one part (Figure 4.6).

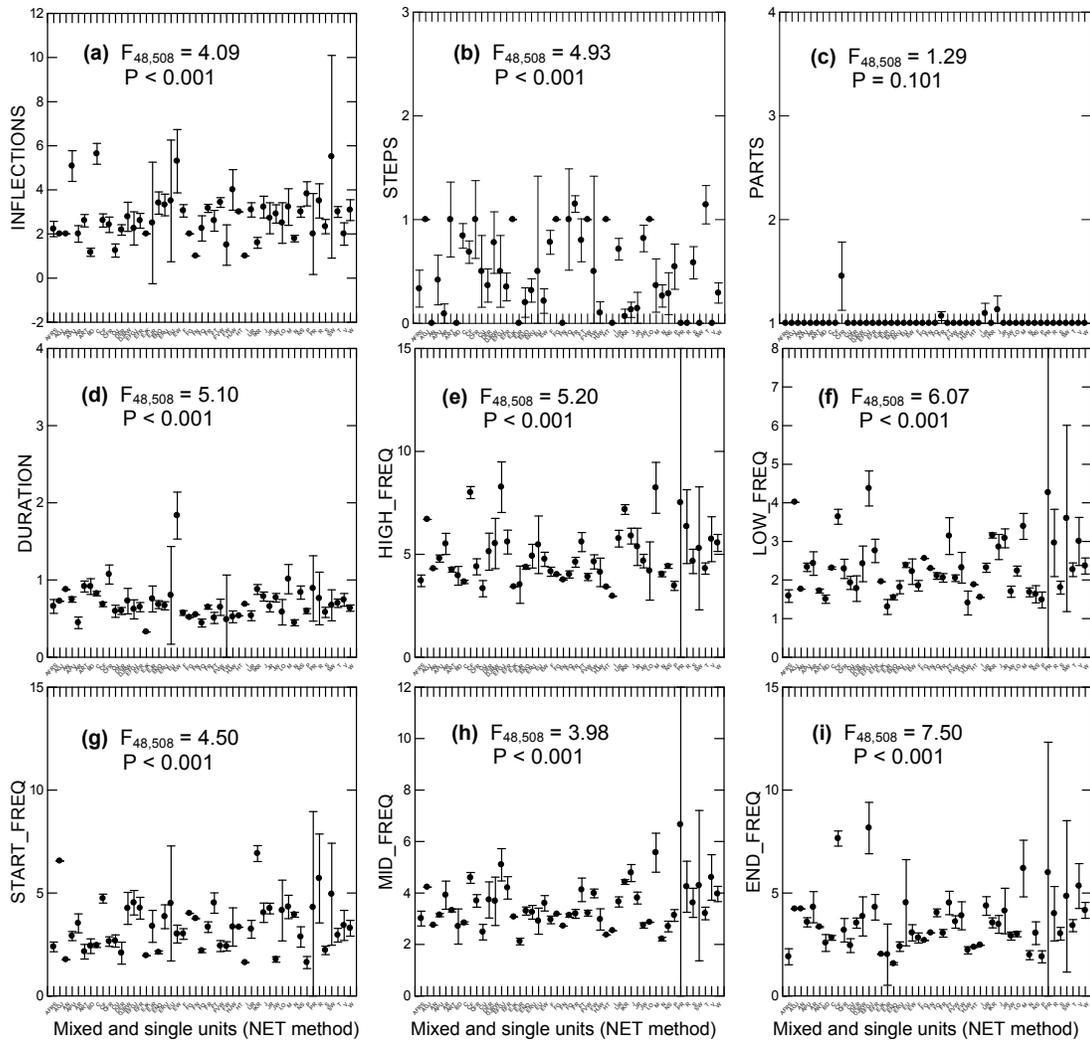


Figure 4.5. Means of each whistle measurement variable ( $\pm 1$ SE) for mixed and single social units (from the NET method), with associated ANOVA  $F$ -statistics and significance values.

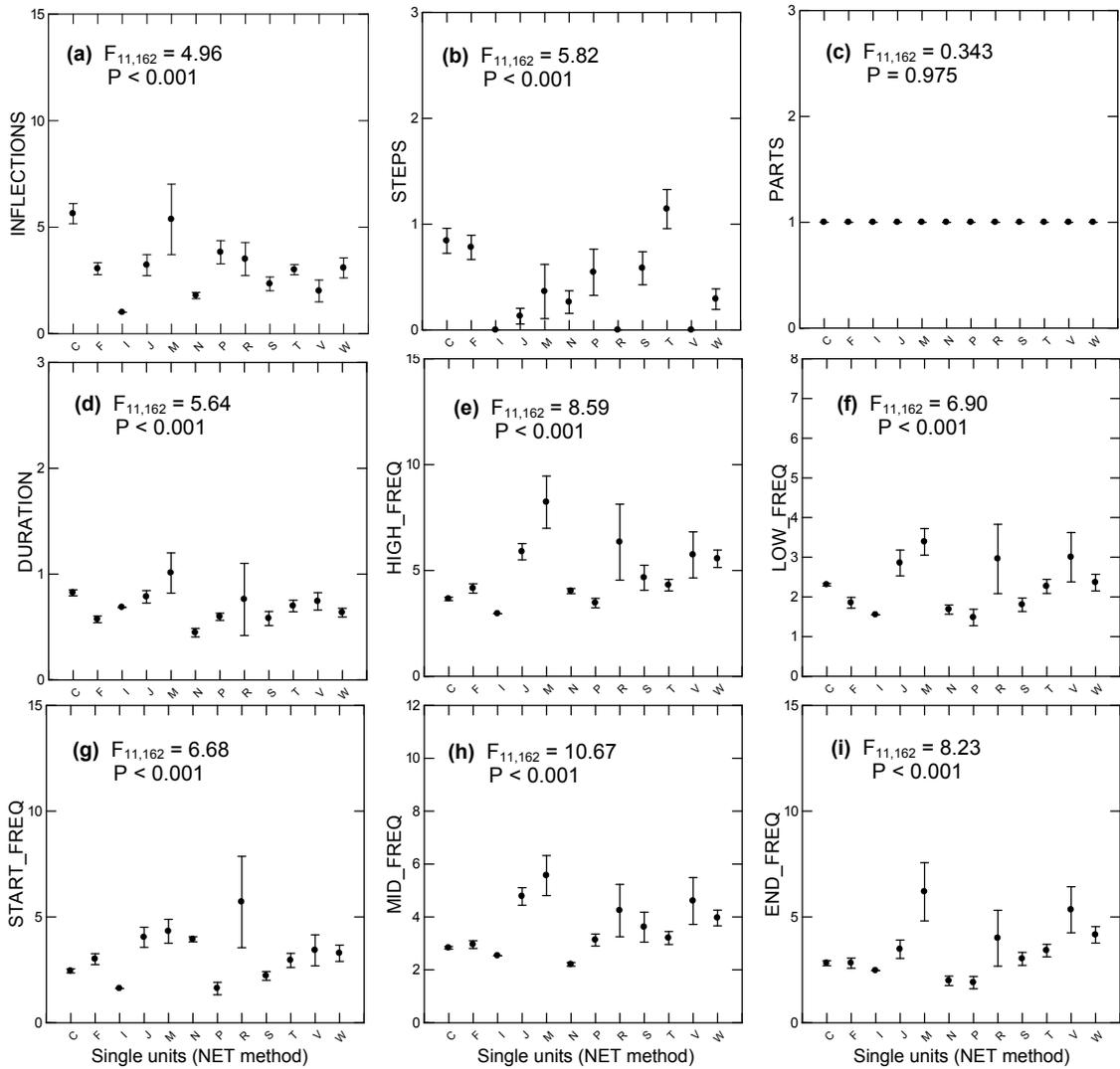


Figure 4.6. Means of each whistle measurement variable ( $\pm 1$  SE) for single social units only (from the NET method), with associated ANOVA  $F$ -statistics and significance values.

#### 4.3.1.4 Call Similarity and Behavioural State

##### *Pulsed calls*

Pulsed call similarity was found to be significantly correlated with behavioural similarity (partial Mantel test,  $P < 0.001$ , Figure 4.7a), suggesting that pulsed calls are tightly clustered together by behavioural state in multivariate space, with little variation between them. This was further supported by the MANOVA ( $F_{36,934} = 7.34$ ,  $P < 0.001$ ), indicating that the structure of pulsed calls varied significantly among behaviours. It should be noted, however, that there was only one pulsed call recorded during resting behaviour. The ANOVAs performed for each variable allowed a more detailed look at how aspects of pulsed call structure varied across behavioural states (Figure 4.8). The most obvious pattern observed is that calls made while socializing are generally more complex than those produced during other behavioural states, with the most elements, segments and inflection points of all calls measured. Calls made while foraging and travelling generally had similar frequency measurements and comparable numbers of elements, segments and inflection points, while those made during travel had the largest SBIs (Figure 4.8).

##### *Whistles*

Complex whistle similarity was not found to be significantly correlated to behavioural similarity (partial Mantel test,  $P = 0.354$ , Figure 4.9a), suggesting that the overall structures of complex whistles are not highly similar within each behavioural state. However, the MANOVA ( $F_{27,1648} = 7.80$ ,  $P < 0.001$ ) indicated that the mean measurements of the variables describing whistle structure varied significantly between behavioural states. The ANOVAs performed for each variable allowed a more detailed look at how features of whistle structure varied across behavioural states (Figure 4.10). The principal pattern observed was that whistles produced while the whales were socializing and travelling generally had the highest frequency measurements, while those produced while resting at the surface appeared to be slightly lower frequency (Figure 4.10).

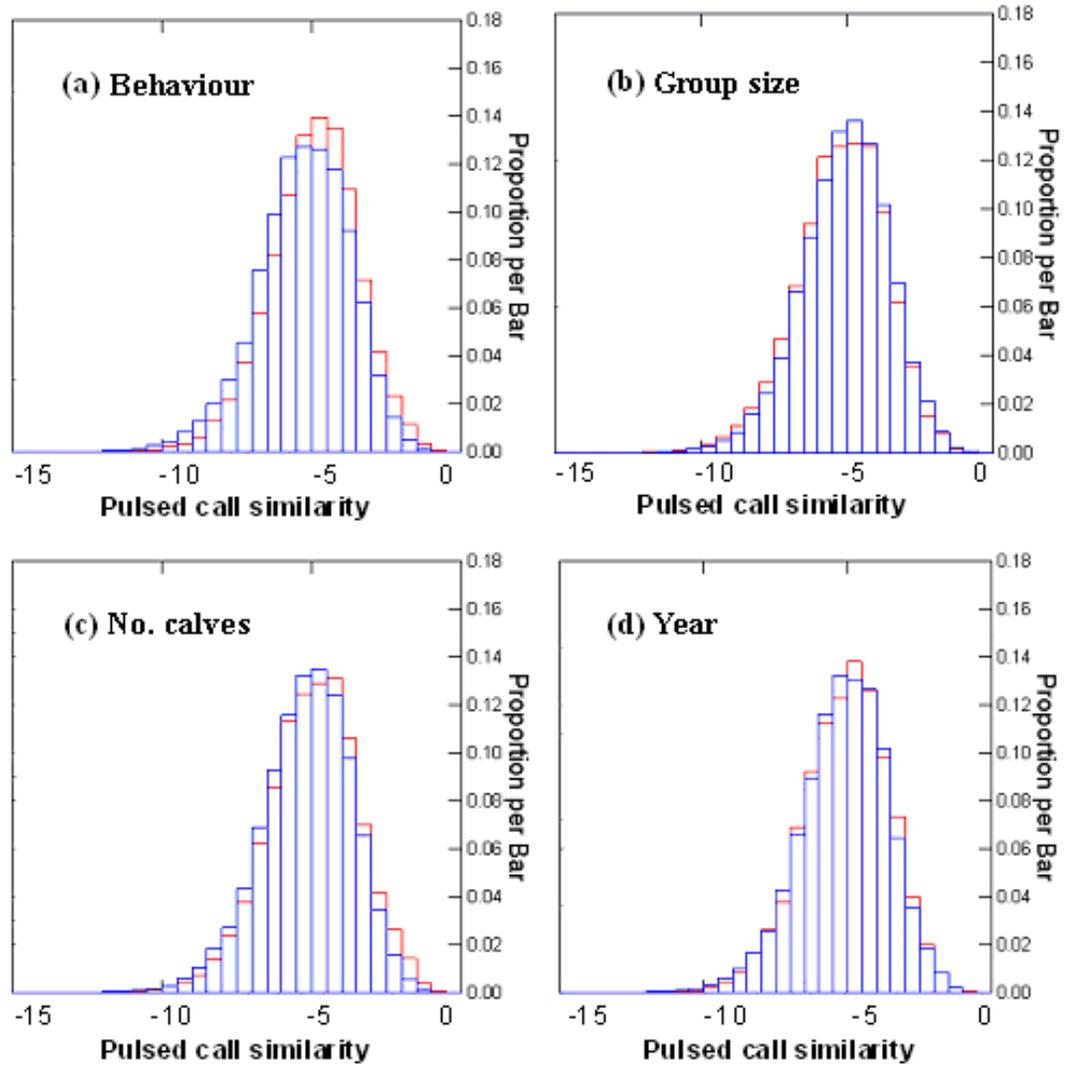


Figure 4.7. Histograms illustrating the statistical similarity of calls from different encounters between (blue) and within (red): (a) behavioural categories, (b) average numbers of whales present, (c) average numbers of calves observed, and (d) recording years. Pulsed calls similarity was significantly correlated with behaviour and the number of calves observed (partial Mantel tests,  $P < 0.001$ ).

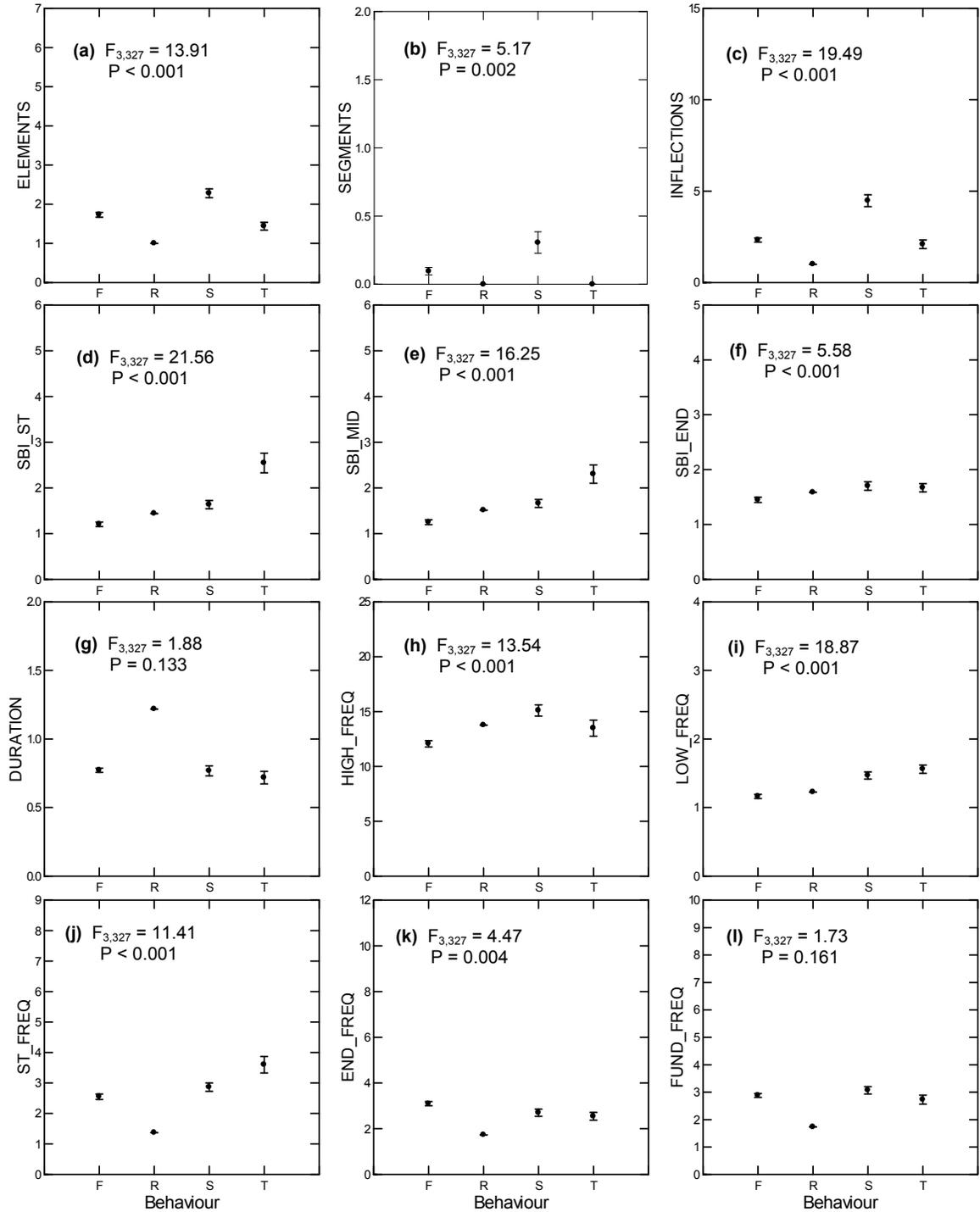


Figure 4.8. Means of each pulsed call measurement variable ( $\pm 1$  SE) across behavioural categories, where F = foraging, R = resting, S = socializing, and T = travelling. Also shown are the associated ANOVA  $F$ -statistics and significance values.

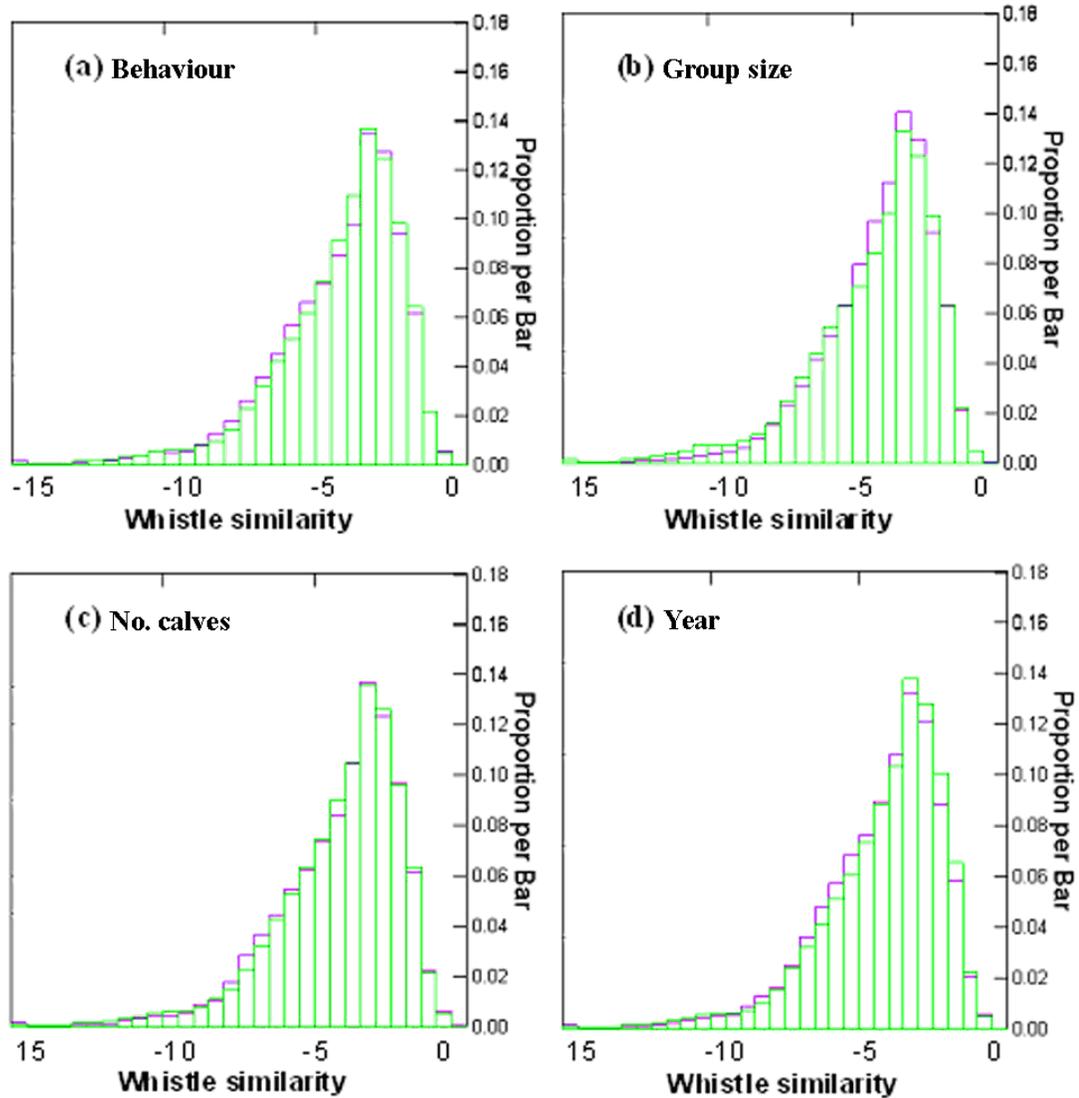


Figure 4.9. Histograms illustrating the statistical similarity of whistles from different encounters between (green) and within (purple): (a) behavioural categories, (b) average numbers of whales present, (c) average numbers of calves observed, and (d) recording years. Complex whistle similarity was found to be significantly correlated with the average group size (partial Mantel test,  $P = 0.001$ ).

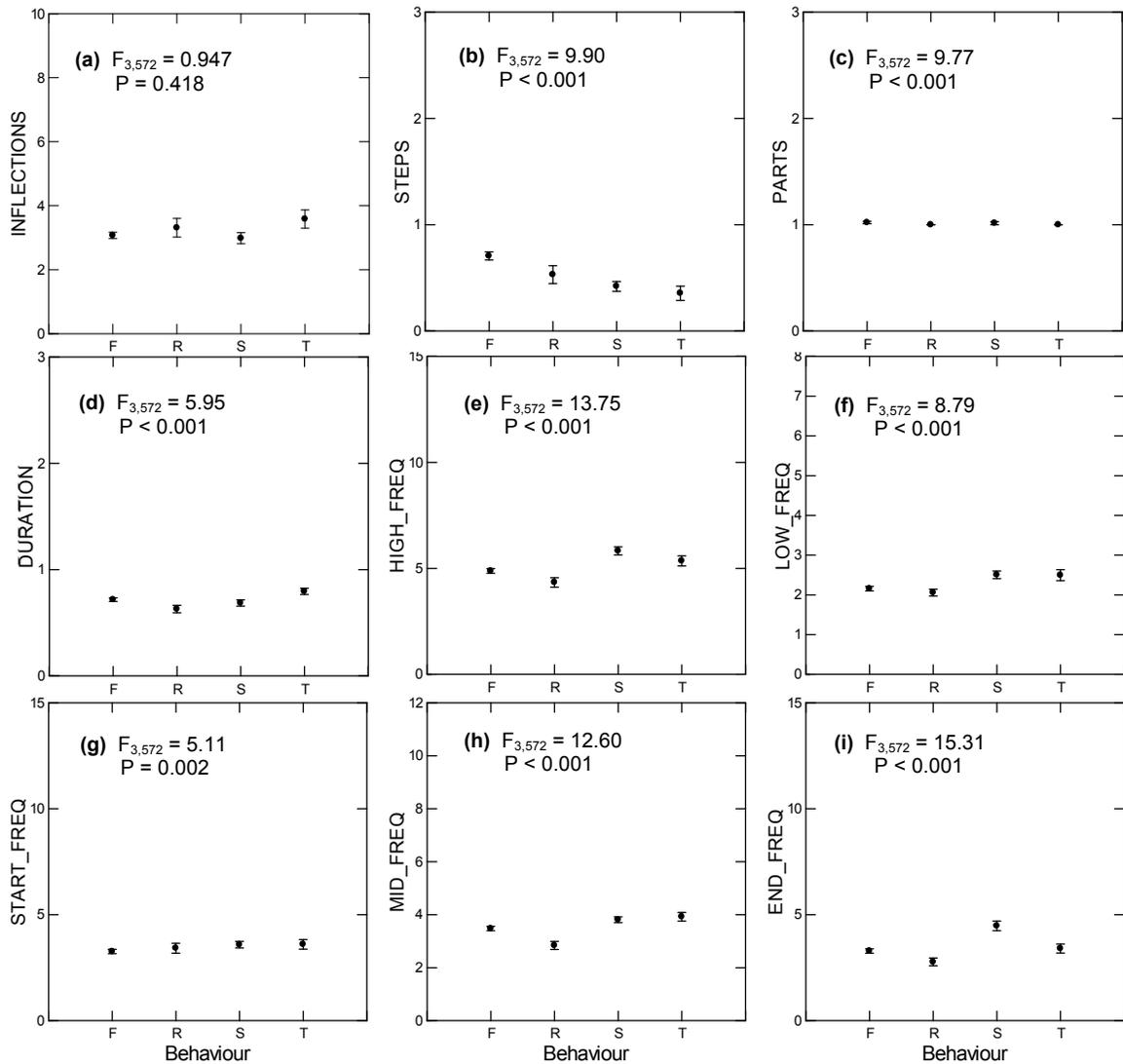


Figure 4.10. Means of each whistle measurement variable ( $\pm 1$  SE) across behavioural categories, where F = foraging, R = resting, S = socializing, and T = travelling. Also shown are the associated ANOVA  $F$ -statistics and significance values.

#### 4.3.1.5 Call Similarity and Average Group Size

##### *Pulsed calls*

Pulsed call similarity was not significantly correlated to group size (partial Mantel test,  $P = 0.999$ , Figure 4.7b), suggesting that overall pulsed call structure is not more similar when the same average number of whales are present. However, the MANOVA ( $F_{24,632} = 8.11$ ,  $P < 0.001$ ) indicated that the variables describing pulsed call structure varied significantly between average group size categories. The ANOVAs performed for each variable allowed a more in-depth look at how pulsed call structure varied across group sizes (Figure 4.11). The most apparent trend was that calls produced when 10-20 whales were present were the most complex, with the highest number of elements and inflection points. Calls produced when less than 10 animals were observed appeared to have slightly higher frequencies than those produced by groups of more than 20 whales (Figure 4.11).

##### *Whistles*

Whistle similarity was found to be significantly correlated with average group size (partial Mantel test,  $P < 0.001$ , Figure 4.9b), suggesting that complex whistles are more similar when produced by the same average number of whales. This was further supported by the MANOVA ( $F_{18,1092} = 13.22$ ,  $P < 0.001$ ), indicating that the mean measurements of whistle structure varied significantly between group sizes. The ANOVAs performed for each variable allowed a more detailed look at how whistle structure differed across group sizes (Figure 4.12). There was no clear pattern of variation between group sizes observed, although groups with less than 10 whales did produce calls with the highest number of parts and inflection points. However, there were few observable frequency variations between the group size categories (Figure 4.12).

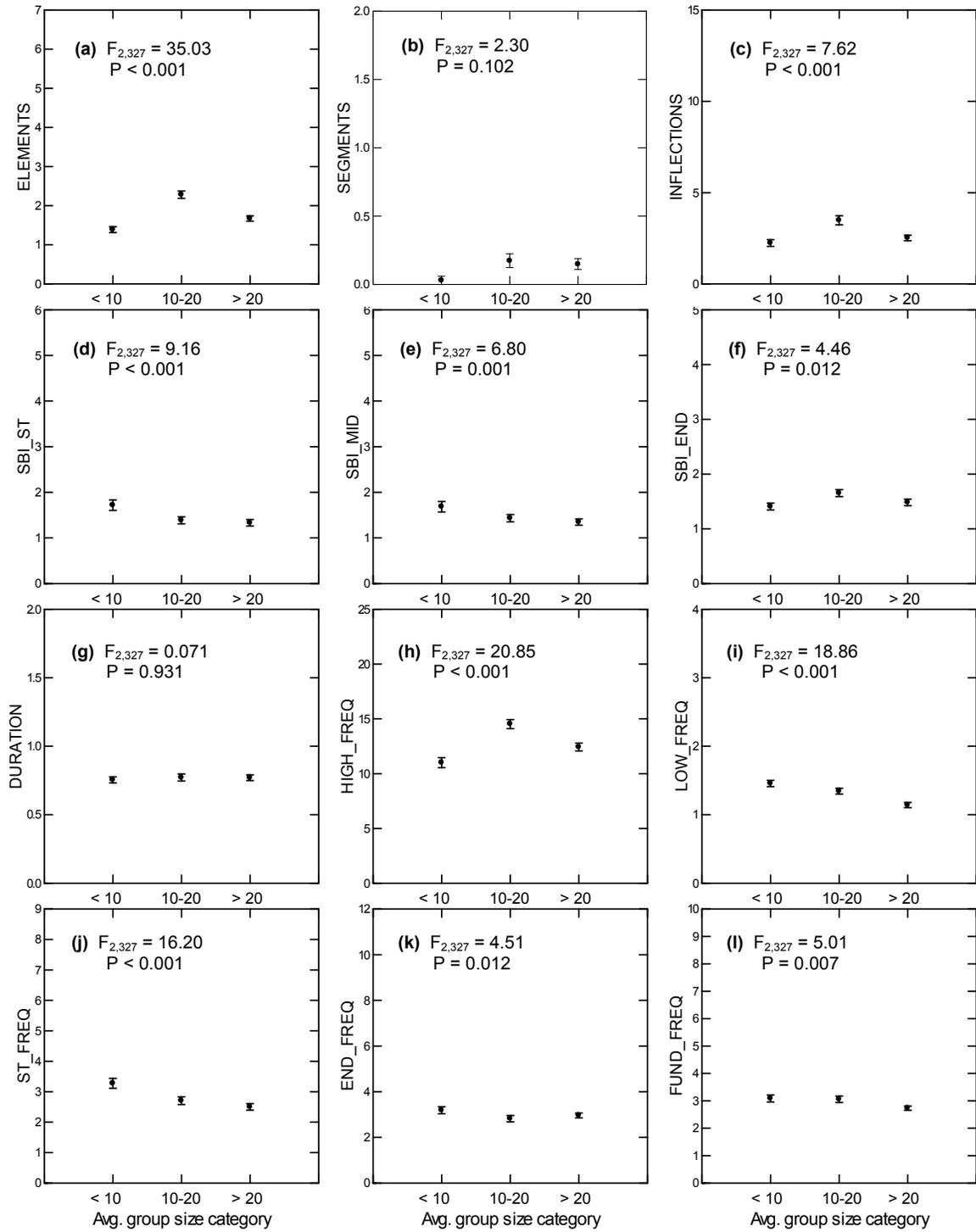


Figure 4.11. Means of each pulsed call measurement variable ( $\pm 1SE$ ) across average group size categories. Also shown are the associated ANOVA  $F$ -statistics and significance values.

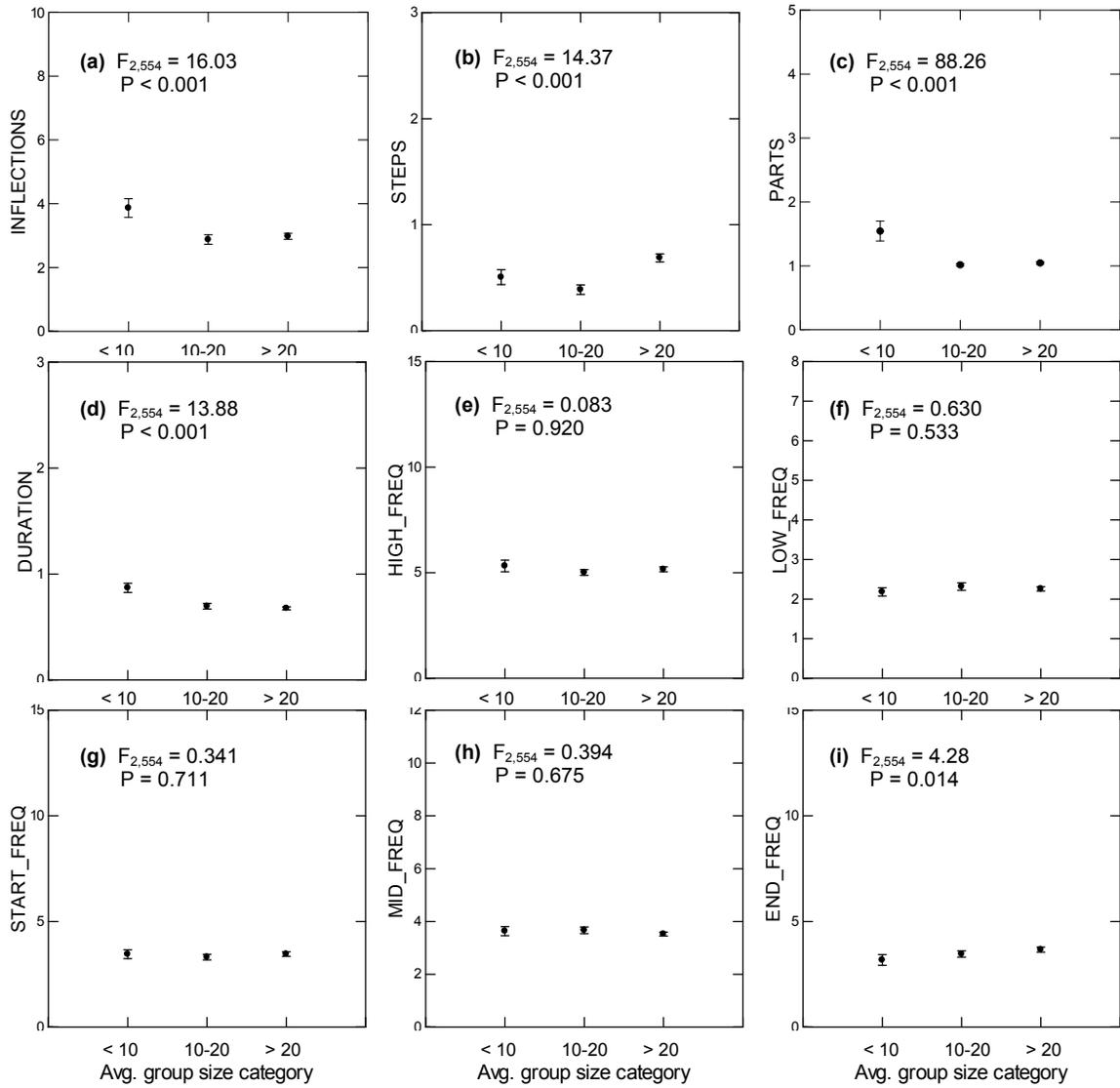


Figure 4.12. Means of each whistle measurement variable ( $\pm 1$  SE) across average group size categories. Also shown are the associated ANOVA  $F$ -statistics and significance values.

#### 4.3.1.6 Call Similarity and Average Number of Calves

##### *Pulsed calls*

Pulsed call similarity was found to be significantly correlated with the number of calves observed (partial Mantel test,  $P < 0.001$ , Figure 4.7c), suggesting that pulsed calls are more similar when the same number of calves are observed in a group. This was further supported by the MANOVA ( $F_{24,632} = 11.42$ ,  $P < 0.001$ ), indicating that the structure of pulsed calls varied significantly between the number of calves present. The ANOVAs run for each variable allowed a more fine scale look at how pulsed call structure varied between calf categories (Figure 4.13). For the most part, calls produced when either no calves or more than one calf was present had similar structures, with more elements and inflection points than when a single calf was observed, as well as larger SBIs and higher frequency minimum visible sidebands and start frequencies. Additionally, calls produced when more than one calf was observed were shorter and had a higher frequency maximum visible sideband than when fewer calves were present (Figure 4.13).

##### *Whistles*

Complex whistle similarity was not found to be significantly correlated with the number of calves present (partial Mantel test,  $P = 0.100$ , Figure 4.9c), suggesting that the overall structures of complex whistles are not more similar when the same number of calves are present in the recording period. However, the MANOVA ( $F_{18,1092} = 7.79$ ,  $P < 0.001$ ) indicated that the mean measurements of the variables describing whistle structure varied significantly between calf categories. The ANOVAs performed for each variable allowed a more detailed look at how aspects of whistle structure differed based on the number of calves observed (Figure 4.14). There was actually very little variation in whistle structure evident between the calf categories, although whistles appeared to have a higher final frequency when more than one calf was observed in the group than when there were fewer calves present (Figure 4.14).

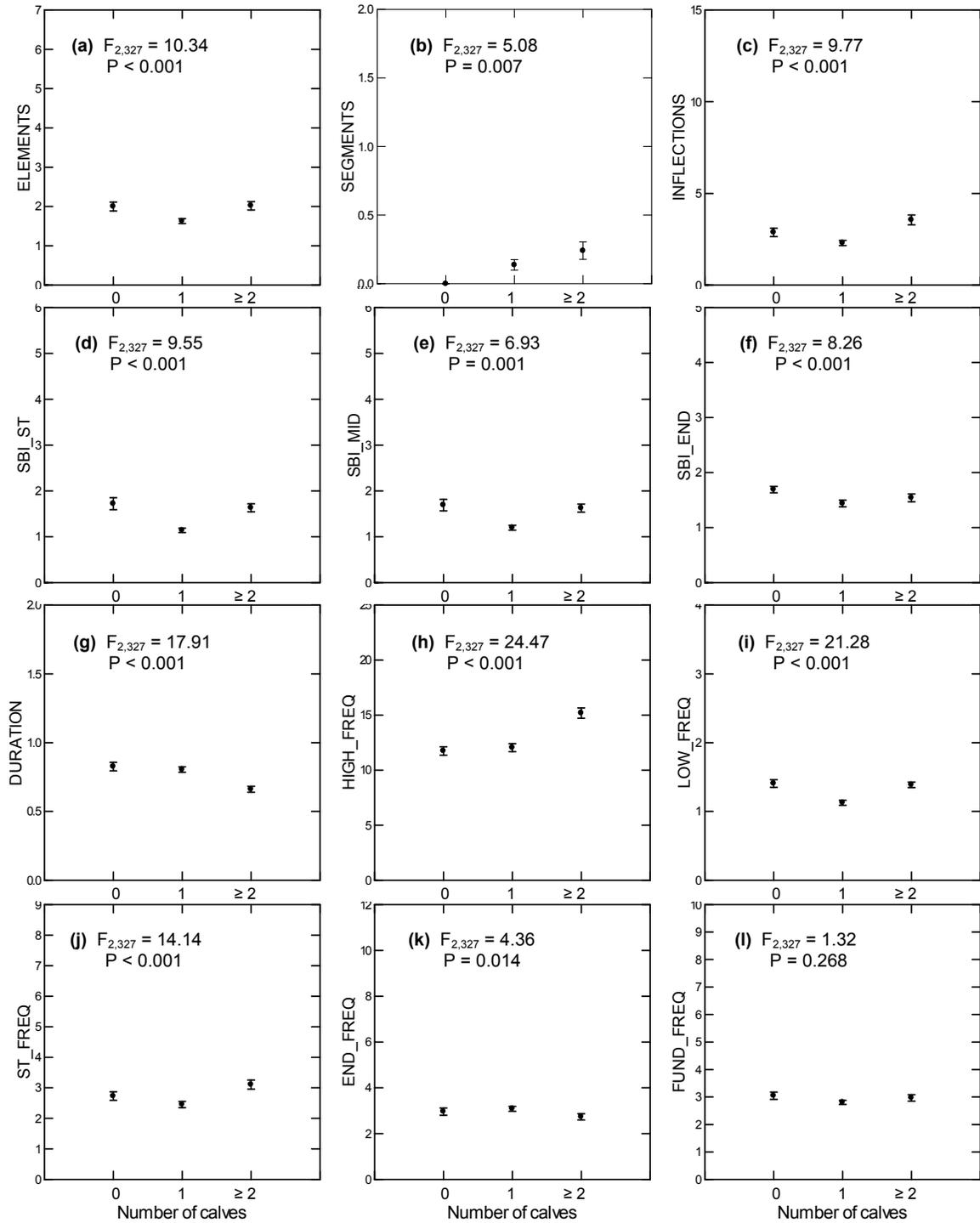


Figure 4.13. Means of each pulsed call measurement variable ( $\pm 1$ SE) across average number of calves categories. Also shown are the associated ANOVA  $F$ -statistics and significance values.

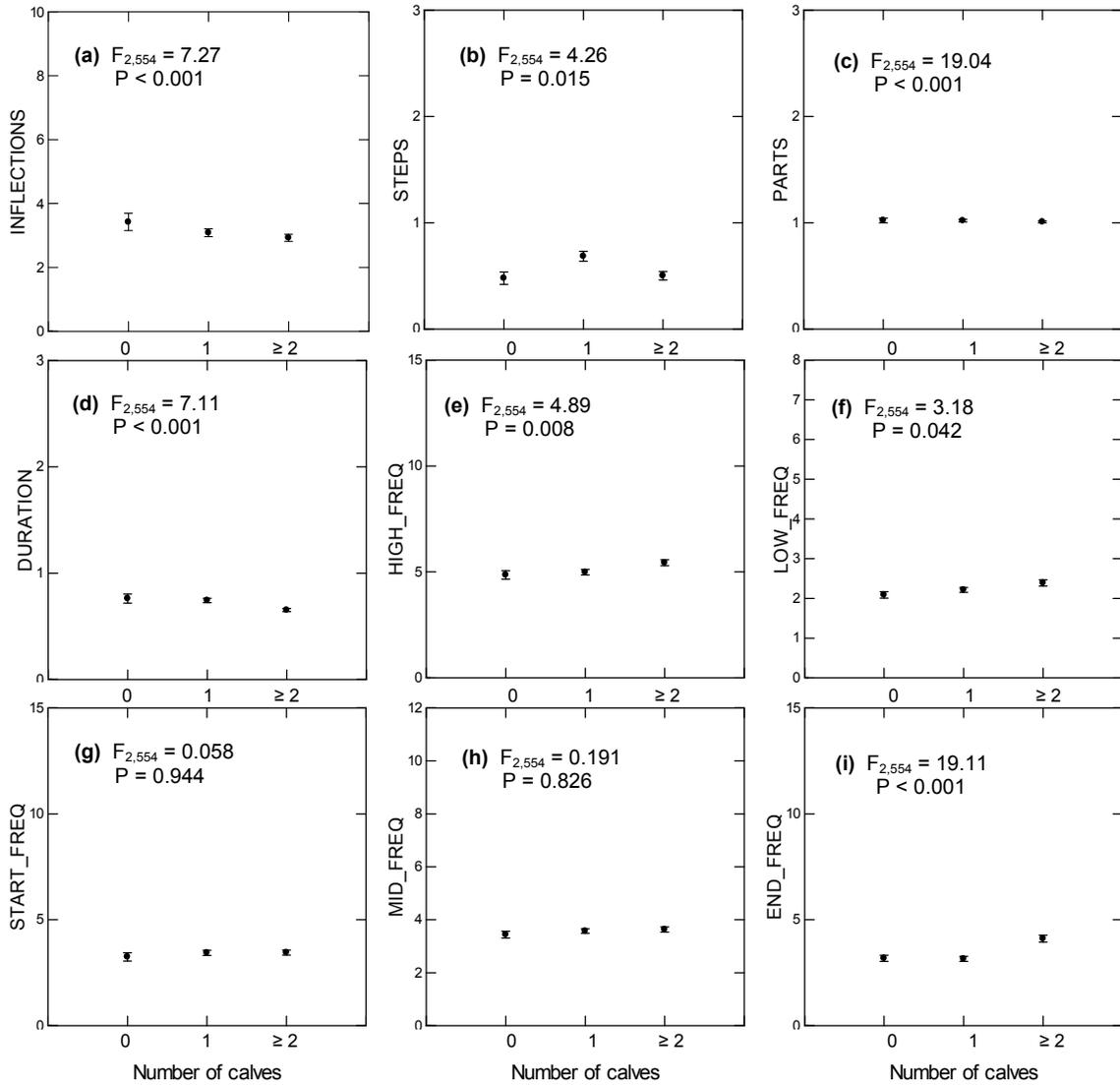


Figure 4.14. Means of each whistle measurement variable ( $\pm 1$  SE) across average number of calves categories. Also shown are the associated ANOVA  $F$ -statistics and significance values.

#### **4.3.1.7 Call Similarity and Year**

##### *Pulsed calls*

The overall structure of pulsed calls produced in the same year were not significantly more similar (partial Mantel test,  $P = 0.350$ , Figure 4.7d) than in different years. However, the mean measurements of the variables describing call structure appeared to vary significantly between years (MANOVA,  $F_{36,934} = 7.84$ ,  $P < 0.001$ ), suggesting that aspects of pulsed call structure vary over time. When examined more closely through the use of ANOVAs (Figure 4.15), there did not appear to be a consistent pattern of variation. The highest frequency visible sideband was the most variable over the years, being lowest in 2000, intermediate in 1998 and highest in 1999 and 2005 (Figure 4.15).

##### *Whistles*

The overall structure of whistles produced in the same year were not significantly more similar (partial Mantel test,  $P = 0.193$ , Figure 4.9d) than in different years. However, the mean measurements of the variables describing whistle structure appeared to vary significantly between years (MANOVA,  $F_{27,1648} = 11.10$ ,  $P < 0.001$ ), suggesting that aspects of whistle structure vary over time. When examined in more detail through the use of ANOVAs (Figure 4.16), there did not appear to be consistent patterns of variation, although the numbers of steps in a whistle appear to be declining over time (Figure 4.16).

#### **4.3.2 Perceptual Measures of Call Similarity and Social, Behavioural and Unit Composition Contexts**

##### **4.3.2.1 Call Similarity and Encounter**

Again, both whistles and pulsed calls were predictably more similar within encounters than between them (Table 4.9), thus all subsequent Kruskal-Wallis tests were restricted to only comparing calls from different encounters.

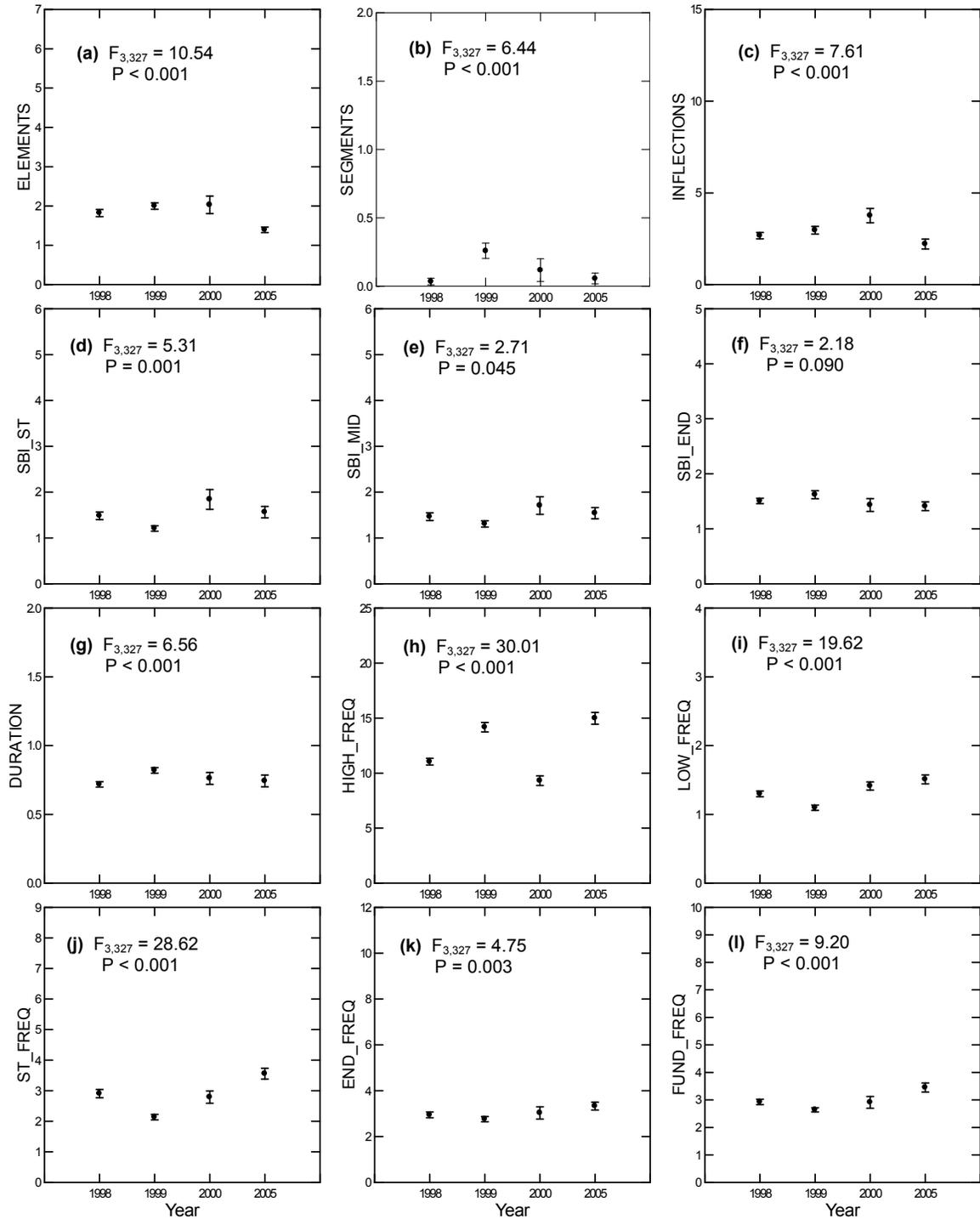


Figure 4.15. Means of each pulsed call measurement variable ( $\pm$  1SE) across years. Also shown are the associated ANOVA  $F$ -statistics and significance values.

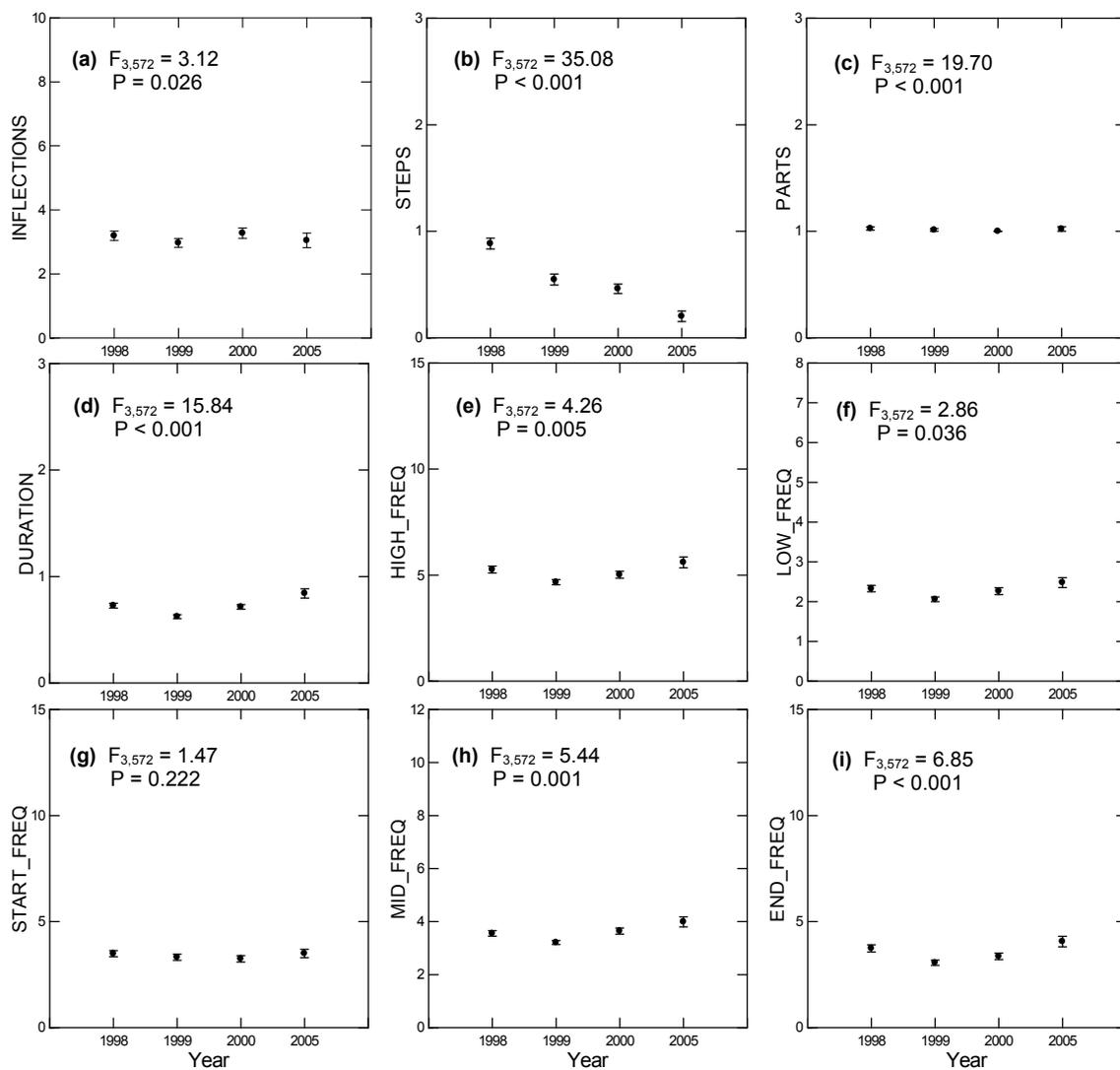


Figure 4.16. Means of each whistle measurement variable ( $\pm 1SE$ ) across years. Also shown are the associated ANOVA  $F$ -statistics and significance values.

#### **4.3.2.2 Call Similarity and Social Unit Membership**

##### *Pulsed calls*

Results from the Kruskal-Wallis tests suggest that pulsed calls from different encounters are more similar within social units defined by the NET method than between them, across all definitions of similarity (Table 4.9). This was further supported by a network depiction of a random subsample of calls produced by two social units (F and T), that generally showed that calls from the same social unit were more strongly linked to each other than to calls produced from a different unit (Figure 4.17). Spectrograms of the calls included in Figure 4.17 are shown in Appendix VII. Histograms further illustrate the distribution of similar calls from different encounters within and between social groups (Figure 4.18). This relationship was maintained when only single NET social units were considered as well for the first two definitions of call similarity ( $\geq 3$  and  $\geq 4$ ) (Table 4.9). There was no evidence that pulsed calls are more similar within units than between them when using either the KIN or BAY social unit designations (Table 4.9).

##### *Whistles*

Results from the Kruskal-Wallis tests suggest that whistles from different encounters are not more similar within social units than between them, regardless of which method was used to delineate social unit membership (Table 4.9). Whistle similarity was significantly associated with BAY social units only when similarity was defined as being a combination of human ratings that were greater than or equal to 3, although this was not maintained when the more strict definitions of similarity were applied (Table 4.9). Consequently, this result is ambiguous, as a rating of 3 suggests that calls are not particularly similar or dissimilar.

#### **4.3.2.3 Call Similarity and Behavioural State**

##### *Pulsed calls*

Pulsed calls from different encounters appear to be more similar within behavioural categories than between them, across all definitions of similarity.

Table 4.9. The results of the Kruskal-Wallis tests for pulsed call and whistle similarity across social groups and contexts. Similarity was defined by three different combinations of human ratings (either  $\geq 3$ ,  $\geq 4$  or  $= 5$ ). Because the grouping variable (similar or dissimilar) only had two levels, the Mann-Whitney U statistic is reported ( $df = 1$ ). Significance values ( $P < 0.05$ ) are indicated by an asterisk (\*), and significant associations that were maintained across all three definitions of similarity are bolded. Only calls from different encounters were compared to each other.

matrix 1	matrix 2	<i>Pulsed calls</i>		<i>Whistles</i>	
		n	p-value	n	p-value
call similarity $\geq 3$	NET	10276	< <b>0.001*</b>	10248	0.473
call similarity $\geq 3$	KIN	1180	0.770	2912	0.486
call similarity $\geq 3$	BAY	2534	0.738	2366	0.042*
call similarity $\geq 3$	NET – 1 unit	1868	0.002*	1054	0.924
call similarity $\geq 3$	KIN – 1 unit	430	0.076	1250	0.846
call similarity $\geq 3$	BAY – 1 unit	458	0.547	420	0.038*
call similarity $\geq 3$	encounter <sup>†</sup>	15326	< <b>0.001*</b>	13878	< <b>0.001*</b>
call similarity $\geq 3$	year	14080	< 0.001*	13166	<b>0.048*</b>
call similarity $\geq 3$	behaviour	14080	<b>0.018*</b>	13166	0.341
call similarity $\geq 3$	group size	14080	0.855	13166	0.181
call similarity $\geq 3$	calves	14080	< 0.001*	13166	0.554
call similarity $\geq 4$	NET	10276	< <b>0.001*</b>	10248	0.118
call similarity $\geq 4$	KIN	1180	0.429	2912	0.463
call similarity $\geq 4$	BAY	2534	0.265	2366	0.212
call similarity $\geq 4$	NET – 1 unit	1868	< 0.001*	1054	0.691
call similarity $\geq 4$	KIN – 1 unit	430	0.006*	1250	0.635
call similarity $\geq 4$	BAY – 1 unit	458	0.448	420	0.051
call similarity $\geq 4$	encounter <sup>†</sup>	15326	< <b>0.001*</b>	13878	< <b>0.001*</b>
call similarity $\geq 4$	year	14080	0.004*	13166	< <b>0.001*</b>
call similarity $\geq 4$	behaviour	14080	<b>0.004*</b>	13166	0.147
call similarity $\geq 4$	group size	14080	0.361	13166	0.012*
call similarity $\geq 4$	calves	14080	0.008*	13166	0.730
call similarity = 5	NET	10276	<b>0.001*</b>	10248	0.518
call similarity = 5	KIN	1180	0.839	2912	0.855
call similarity = 5	BAY	2534	0.720	2366	0.333
call similarity = 5	NET – 1 unit	1868	0.892	1054	0.239
call similarity = 5	KIN – 1 unit	430	0.233	1250	0.107
call similarity = 5	BAY – 1 unit	458	0.278	420	0.485
call similarity = 5	encounter <sup>†</sup>	15326	< <b>0.001*</b>	13878	< <b>0.001*</b>
call similarity = 5	year	14080	0.195	13166	<b>0.004*</b>
call similarity = 5	behaviour	14080	< <b>0.001*</b>	13166	0.047*
call similarity = 5	group size	14080	< 0.001*	13166	0.852
call similarity = 5	calves	14080	0.282	13166	0.283

<sup>†</sup> When testing call similarity with encounter similarity, Kruskal-Wallis tests were run comparing calls from both the same and different encounters.

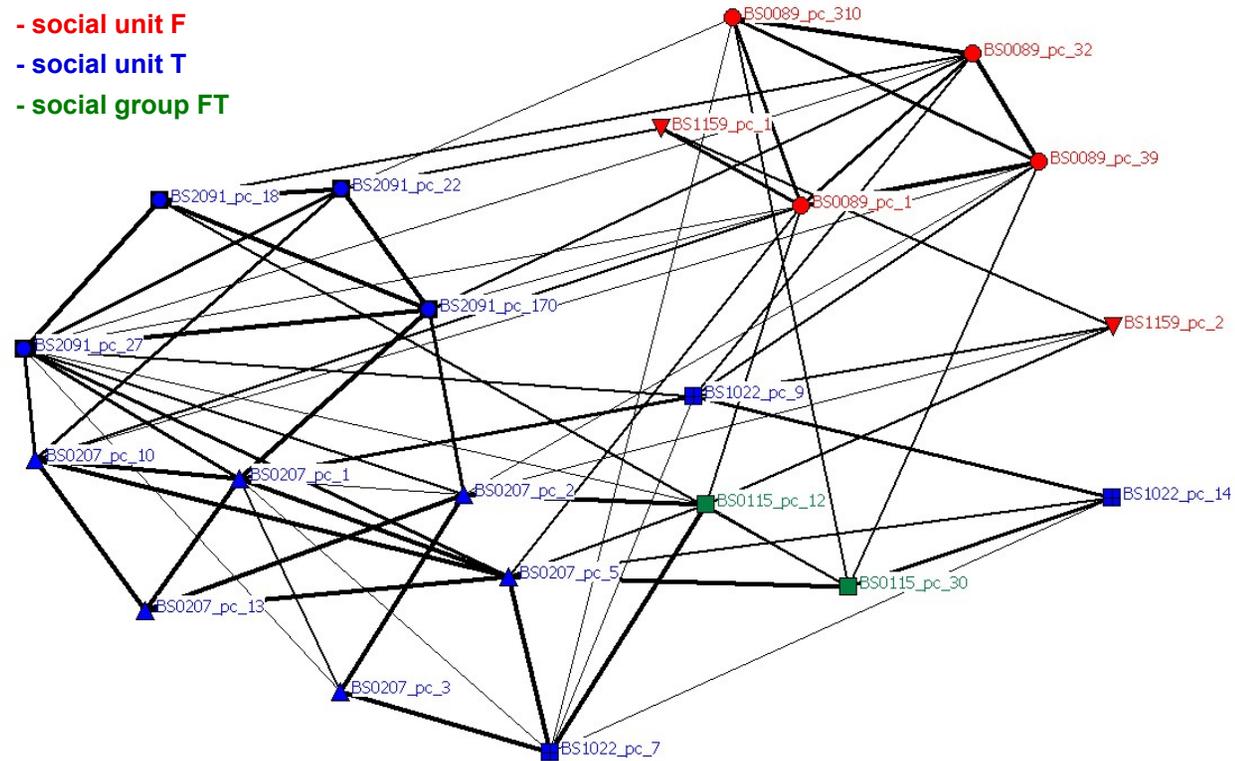


Figure 4.17. Network depiction of pulsed call similarity as rated by human observers, using a random subsample of calls ( $n = 21$ ) produced by two social units (defined using the NET method). Social units are colour coded (red: F, blue: T, green: FT), and different encounters are distinguished by node shape. The first 6 digits of each pulsed call name also indicate the encounter number. Line thickness reflects the degree of similarity between two compared calls. Unconnected pairs of calls were not compared. The initial position of calls was determined from multidimensional scaling and then moved interactively to improve clarity. The spectrogram of each call included can be found in Appendix VII. Drawn using NetDraw (ver. 2.083, Borgatti 2002).

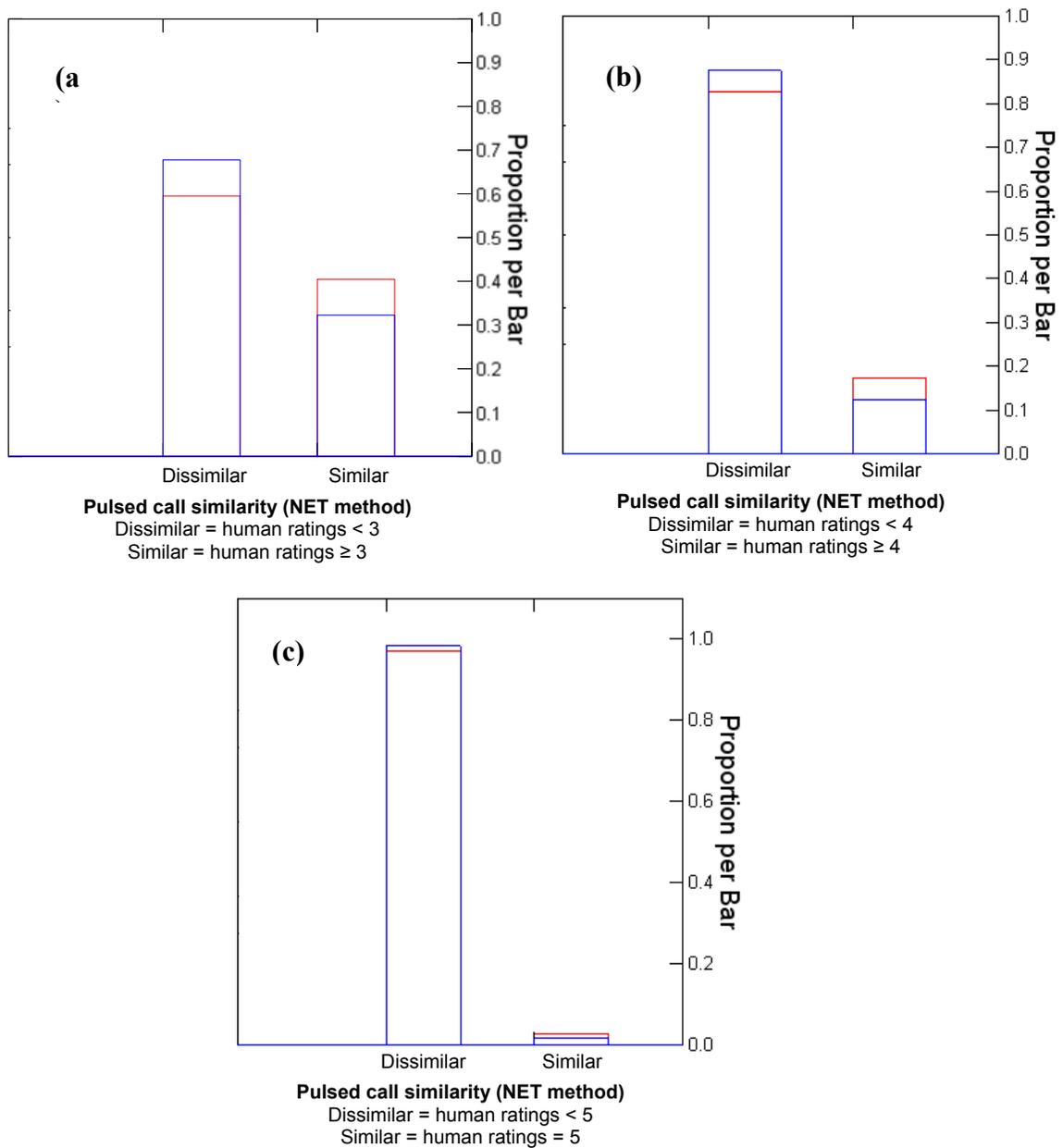


Figure 4.18. The distribution of dissimilar and similar pulsed calls recorded in different encounters from the same social units (red) and different social units (blue), as defined by the NET method, for all three similar/dissimilar category groupings. Pulsed calls were always significantly more similar when produced by the same social unit than when produced by different units (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how rigid the definition of “similar” was (a, b and c).

In fact, the strength of the association was more significant as the definition of similarity became more rigid (see Table 4.9). This was further supported by histograms illustrating the distribution of similar calls from different encounters within and between behaviours (Figure 4.19).

#### *Whistles*

Conversely, whistles do not appear to be more similar when produced during the same behaviour than during different ones (Table 4.9). There was, however, a borderline significant association between whistle similarity and behavioural similarity when similarity was defined as only ratings that equal 5 ( $P = 0.047$ ). This suggests that only the most similar complex whistles may be slightly associated with behaviour.

#### **4.3.2.4 Call Similarity and Average Group Size**

##### *Pulsed calls*

Pulsed calls do not appear to be more similar when produced from the same average group size than from different ones (Table 4.9). There was, however, a significant association between the similarities of pulsed call contour and group size when similarity was defined as only ratings that equal 5 ( $P < 0.001$ ), indicating that only the most similar pulsed calls may be associated with the average group size observed during the recording period.

##### *Whistles*

Complex whistles also do not appear to be more similar when produced from the same group size category than from different ones (Table 4.9). There was a significant association between the similarities of whistle contour and group size when similarity was defined as only ratings that were equal or greater than 4 ( $P = 0.012$ ), although this was not observed when either the more relaxed definition of similarity ( $\geq 3$ ) or the more rigid definition of similarity ( $= 5$ ) were applied, and thus may be spurious.

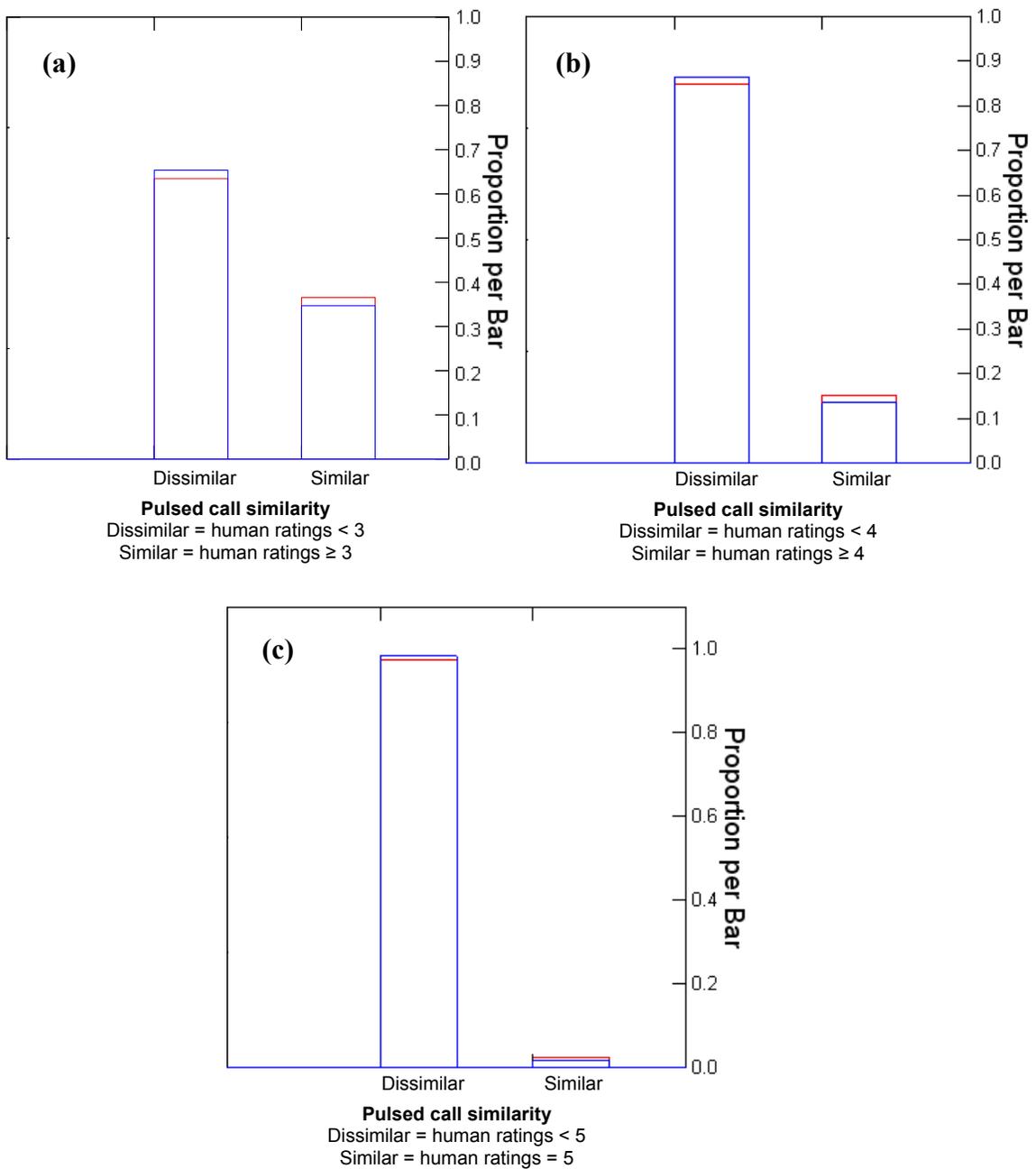


Figure 4.19. The distribution of dissimilar and similar pulsed calls recorded in different encounters with the same behavioural state (red) and different behavioural states (blue) for all three similar/dissimilar category groupings. Pulsed calls were always significantly more similar when produced during the same behavioural state than when produced during different behavioural states (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how rigid the definition of “similar” was (a, b and c).

#### **4.3.2.5 Call Similarity and Average Number of Calves**

##### *Pulsed calls*

Pulsed calls are likely more similar when produced from groups with the same number of calves than from those with different numbers of calves (Table 4.9), when using the first two definitions of similarity ( $\geq 3$  and  $\geq 4$ ). This was not maintained when the strictest definition of similarity ( $= 5$ ) was applied, suggesting that calls may only be generally more similar when the same number of calves are observed.

##### *Whistles*

Conversely, complex whistles are not more similar when produced from groups with the same number of calves than from those with different numbers of calves, regardless of the definition of similarity (Table 4.9).

#### **4.3.2.6 Call Similarity and Year**

##### *Pulsed calls*

Pulsed calls appear to be more similar when produced during the same year than different years (Table 4.9) when the first two definitions of similarity ( $\geq 3$  and  $\geq 4$ ) are applied. This was not maintained, however, when the strictest definition of similarity ( $= 5$ ) was used, suggesting that calls may only be slightly more similar within years than between them.

##### *Whistles*

Complex whistles, though, appear to be more similar within years than between them, regardless of the definition of similarity (Table 4.9). This was further supported by histograms illustrating the distribution of similar whistles from different encounters within and between years (Figure 4.20).

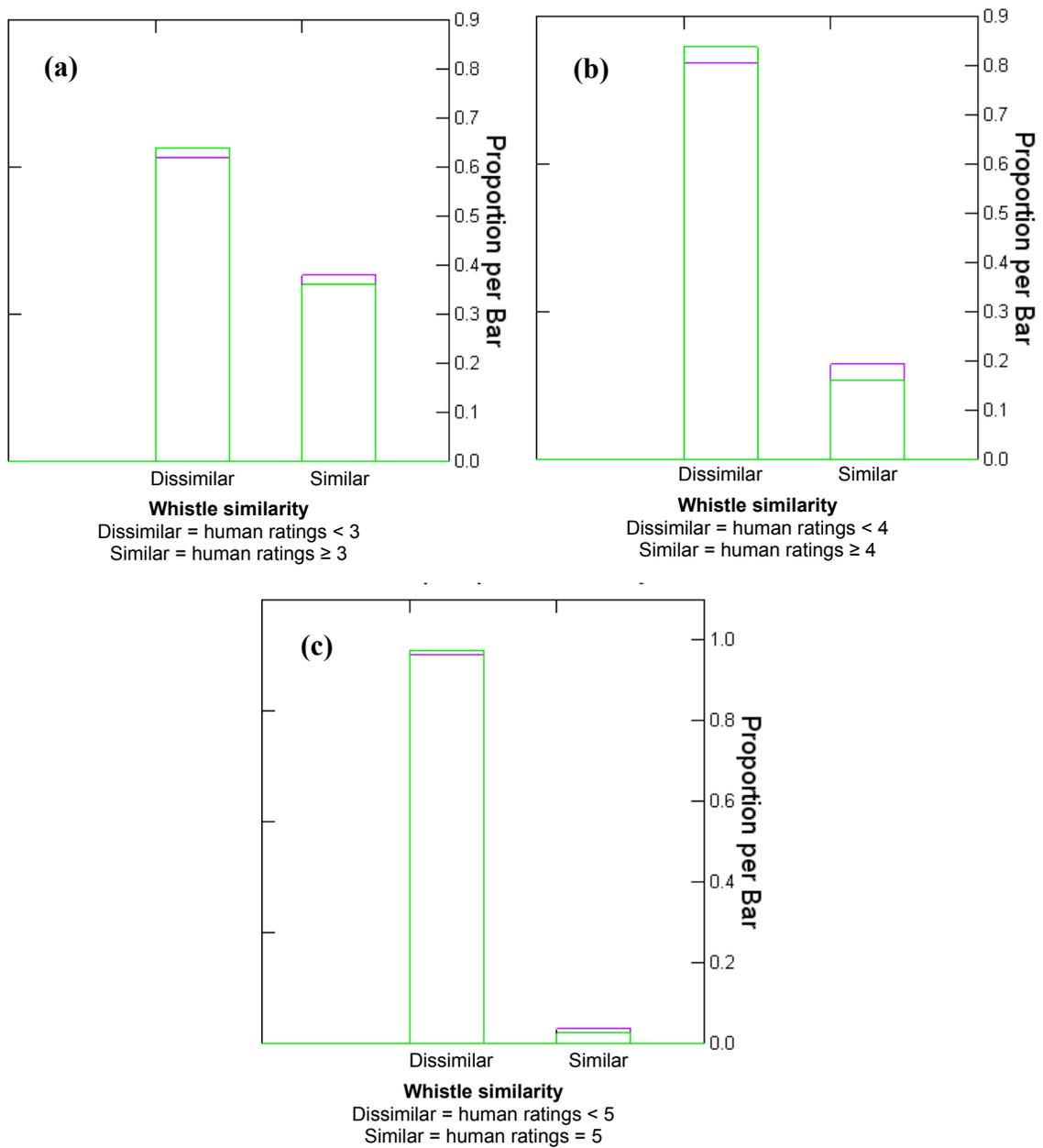


Figure 4.20. The distribution of dissimilar and similar whistles recorded in different encounters within the same year (purple) and different years (green) for all three similar/dissimilar category groupings. Whistles were always significantly more similar when produced in the same year than when produced in different years (Kruskal-Wallis tests,  $P < 0.05$ ), regardless of how strict the definition of “similar” was (a, b and c).

## **4.4 Discussion**

### **4.4.1 Investigating the Variability of Call Structure from Different Angles**

The methods used in this study all investigated the similarity of pilot whale whistles and pulsed calls across social, behavioural and group composition contexts. The techniques used different concepts of “similarity” and thus addressed the data from different perspectives. The techniques also had different strengths. Thus they sometimes appear to have given conflicting results. The statistical measures offered information on the structural characteristics of the calls and revealed both clusters of calls made in the same contexts and with similar structural features (using Mantel tests), and more specific patterns in the variation of aspects of call structure across units or contexts (using MANOVAs). The perceptual measures, on the other hand, assessed the more general contours of the calls and determined if they were then more similar within or between social units or contexts. The social unit designations themselves were retained from three separate studies using different methodologies in an attempt to tease apart any possible patterns. The network modularity (NET) method was the preferred method in the end, as it included the largest amount of data and allowed each individual to be assigned to a social unit. Although there may have been more misassignments compared with the more conservative KIN and BAY methods, this seems to have been more than compensated for by the much larger sample sizes. Thus, the similarity of calls was investigated from multiple angles, allowing alternative patterns within the data to emerge. Both statistical and perceptual methods have been used extensively with other species (see Chapter 3), and often offer rather different pictures of call classification and even usage patterns when applied to similar data sets (e.g. McCowan and Reiss 1995 and Janik 1999). For species such as the pilot whale in the wild, where an understanding of call production patterns is confounded by the difficulty of identifying the individuals or social groups making sounds (due to the presence of mixed groups, distant groups and unidentified individuals during recordings), and where calls appear to be non-discrete, it is often not possible to test the validity of the results from a particular method. Also, the presence of some statistical issues (such as false positives from multiple tests, non-normality in MANOVAs, and non-independence in Kruskal-Wallis tests) means that *p*-values and

effect sizes should be considered carefully. Consequently, support for patterns in the data comes mainly from relationships maintained by more than one method. Such results will be the focus of this discussion.

#### **4.4.2 What Governs Variability in Pulsed Calls?**

The results of this study indicate that variation in pulsed call structure is most clearly influenced by the social group producing the calls and by the behaviour of the group during recording, and support the hypotheses that pulsed calls are affected by, and may reflect, group membership and behavioural or arousal state. The average group size, number of calves and year of recording may also affect pulsed call structure, although likely not as strongly.

##### *Group membership*

Social group membership has been shown to play an important role in the vocalizations of many species, including birds (e.g. Price 1998), bats (Boughman 1997) and primates (e.g. Crockford et al. 2004). In the Cetacea, resident killer whales (Ford and Fisher 1983, Ford 1991) and sperm whales, *Physeter macrocephalus* (Weilgart and Whitehead 1997) have been shown to live in stable social units that exhibit strong, culturally-transmitted group-specific dialects, which can then be grouped into broader vocal clans of units that share some call types or codas (Ford 1991, Rendell and Whitehead 2003a). Unlike the discrete call types identified for both killer whales (Ford 1987) and sperm whales (Weilgart and Whitehead 1997), in my study pilot whale pulsed calls showed acoustic variability and graded differences in call structure between social groups. This variability is also observed in wild chimpanzee (*Pan troglodytes verus*) group-specific calls, where the animals appear to be using a narrow range from a wide range of possible graded pant hoot types in their vocal repertoire (Crockford et al. 2004). This is likely true for pilot whales as well, as aspects of the structure of pulsed calls vary significantly between social units and groups, when analyzed using both specific measurements and human perception of the contour of the calls. This strongly suggests that whales from different social units produce different features of their calls in stereotyped ways and thus use a specific range of variable signals.

From a structural perspective, particular measured variables vary widely between units, with some units consistently producing relatively complex calls with high numbers of elements, inflection points and segments, while others consistently produce simpler calls. I would add the caveat, however, that some of the observed pattern may be confounded by unmeasured factors, such as environmental conditions, and even measured factors such as the unit's behaviour during recording. However, when calls produced from units exhibiting the same behavioural state are compared, the differences between units are maintained. For example, all of the pulsed calls from both unit N and unit R were recorded during socializing behaviour and yet show widely divergent structural patterns. Whales in unit N consistently produced calls that were low frequency and highly complex, while animals from unit R produced calls that were higher frequency and substantially more simple, suggesting that whales tend to produce pulsed calls characteristic of their own unit.

Human perception of the general contour of pulsed calls also found greater similarity within social units than between them, and this trend was more obvious for mixed groups of units than single units. Together with the structural analysis which shows that the measured parameters of calls vary considerably between clusters of units, this supports the idea of larger, sympatric vocal clans, delineated by groups of social units with similarly structured or contoured pulsed calls (e.g. Ford 1991, Janik and Slater 2000). The formation of new pilot whale social units may result from the gradual splitting of older, larger pods, as is observed with killer whales (Bigg et al. 1990b, Ford 1989). Young whales within a unit likely learn their vocal repertoire from their parent or other kin group member rather than acquiring it genetically (see Tyack 1997, Ford 1989). Such vocal learning, defined as the modification of an animal's calls as a result of experience with those of other individuals (Tyack 2000), has been suggested to be the mechanism behind the maintenance of dialects in the repertoires of related killer whale pods (Ford 1989). When units of killer whales divide, group-specific variation in calls may occur gradually over generations, with newly formed sister units spending a substantial amount of time together and sharing most of the calls of the original ancestral group. However, cultural drift (Lynch 1996), improvisation (Marler and Peters 1982) and cultural diffusion (Slater et al. 1980) may lead to eventual call divergence between sister units who are no

longer in constant contact. Cultural drift results from copying errors of calls and the transmission of these changes across generations through vocal matching between the members of a unit. Such changes are usually adaptively neutral and non-directional, and are simply a consequence of the process of vocal learning (Ford 1989, Deecke et al. 2000). The improvisation of new elements or call structures may also produce novel sounds that are then imitated and distributed within a unit (Marler and Peters 1982). Cultural diffusion may also be an important source of variation. New call structures may be introduced into a social unit's repertoire through an immigrant's calls and its subsequent dispersion between individuals. At this point, it is impossible to say which mechanism, or combination of mechanisms, is behind the variation in pulsed call structure observed in the pilot whale population. We still do not have enough information of the similarity or difference of call structures within groups but between years, and the presence of unidentified individuals within encounters makes following individual dispersal between units difficult. However, if pilot whale social units are as stable and closed as we assume them to be (Amos et al. 1993a, Ottensmeyer and Whitehead 2003), cultural diffusion may only play a small role, if any, in the modification of calls between units (Yurk et al. 2001). Regardless, the similarities in pilot whale pulsed call structure and contour within mixed groups of units, and the apparent differences between them, is indicative of such a substructure within the population. Vocal clans may encompass social units that have split more recently than units of different clans (discussed in Ford 1991). For killer whales, this association between genetic and cultural relatedness has been confirmed (Barrett-Lennard 2000), but it has yet to be verified for pilot whales.

The function of group-specific dialects is a matter of speculation. Differences in call structure among social units may simply be the result of pure cultural drift between units that have divided (Bigg et al. 1990b), and serve no particular function. Pilot whales likely communicate mainly with individuals from their own social unit, which appear to be highly stable over time (Ottensmeyer and Whitehead 2003). As such, vocal learning of variations in structure due to cultural drift from members of their own unit would cause the observed differences between social units, even without any selection pressures for standardizing call structure or any function to advertize unit differences or affiliations. However, although selection may not have acted directly on the development of group-

specific dialects, this does not preclude the possibility that they have some functional significance (Ford 1991). There may be considerable selective pressure on individual whales to copy the unit-specific call structures of their social unit, in order to access the benefits of group-living (Ford 1991). It has been suggested that group-specific dialects play an important role in mediating apparently altruistic cooperative behaviour (Rendell and Whitehead 2003a) by acting as honest signals which reduce “cheating” by individuals who act like kin and receive benefits without returning the favour (see Dunbar 1999 and Fitch 2004 for reviews and discussion). For mobile individual animals that live within social groups, like pilot whales, a communication system that allows them to honestly maintain and regain contact with members of their group is necessary to obtain the fullest benefits of group living (Tyack 2000). Such benefits include improved food acquisition through cooperative foraging (e.g. Similä and Ugarte 1993, Wells et al. 1999), and increased offspring survival rates through allomaternal care (Whitehead 1996) and the avoidance of predation or cooperative defence (Wrangham 1983, Pitman et al. 2001). Animals within matrilineal groups may further use their calls to maintain and reinforce long-term bonds with other animals, as is seen through coda matching between sperm whales (Schulz et al. 2008) and pulsed call matching in killer whales (Miller et al. 2004), and avoid inbreeding costs by facilitating discrimination between kin and other conspecifics (Amos et al. 1993a, Barrett-Lennard 2000).

The next important steps in this research are to further investigate the structure of vocal similarities between different units, identify the specific groups of units that make up the various vocal clans, if such clans exist, and then investigate whether other behavioural and genetic traits can be correlated with clan membership. For instance, vocal clans of sperm whales in the South Pacific exhibit different foraging behaviours and are affected by the El-Niño/Southern Oscillation ocean climate phenomenon to different extents, resulting in differential feeding success across the clans (Rendell and Whitehead 2003a, Whitehead and Rendell 2004). There is the suggestion of variation in ecologically important behaviour between groups of pilot whales as well, although this has not yet been associated with variable acoustic behaviour or genetic relatedness. Sympatric groups of pilot whales in the Strait of Gibraltar have been found to possess some level of specialization of prey choice or foraging behaviour (de Stephanis et al.

2008). Carbon ( $^{13}\text{C}/^{12}\text{C}$ ) stable isotope signatures appear to indicate a difference in diet among the stable social units identified there, which may indicate that sympatric pilot whale social groups in the Strait of Gibraltar are apt to forage in different locations or depths along a bathymetric gradient (de Stephanis et al. 2008). If these divergent foraging strategies are shaped by cultural inheritance in pilot whales, there may be a potential fitness consequence of clan membership, as is observed for sperm whales (Marcoux et al. 2007). Future research on the genetic and acoustic relatedness of pilot whales in the Strait of Gibraltar and off Cape Breton is needed before this can be verified.

An important factor limiting the scope of the patterns observed here is the depth of our information regarding the pilot whale population off Cape Breton. The distinct social units and detailed genealogy identified for the population of resident killer whales off B.C. (Bigg et al. 1990b), for example, have not yet been properly resolved for pilot whales. Instead, we are currently able to identify 33.6% of the Cape Breton population of pilot whales (Ottensmeyer and Whitehead 2003). The entire population has also not yet been sampled, as suggested by Jankowski (2005), who found that more individuals were being identified in each succeeding field season, which is characteristic of an open population. As such, the recordings analyzed here offer an incomplete coverage of the population. Also, our understanding of pilot whale social structure comes largely from a combination of the extensive genetic studies conducted on the pilot whales hunted in the Faroese drive fishery (e.g. Amos et al. 1993a), as well as studies of the Cape Breton population using photo-identification (Ottensmeyer and Whitehead 2003, Jankowski 2005). The former study includes no observations of the behavior of living animals, and the latter no genetic, and so sex or kinship, information. As shown so clearly for killer whales (see Barrett-Lennard 2000, Yurk 2005), these two types of research complement each other and should be combined into one study. As such, we cannot yet relate the call similarities among groups observed in this study with any genetic information on the relatedness of individuals within the groups. A more resolved picture of the relationship between pilot whale social structure and acoustics will require continued monitoring and tracking of the Cape Breton population, along with genetic analyses and further acoustic analyses.

### *Behavioural state*

The structure and contour of pulsed calls are also strongly influenced by the behaviour of the animals producing them. This relationship between call structure and the behavioural state of the sender has been observed in many species, including terrestrial mammals (e.g. Boinski and Mitchell 1997) and cetaceans (e.g. Ford 1989, Murray et al. 1998). Weilgart and Whitehead (1990) observed the greatest number of pilot whale pulsed calls during surface active behaviours, and speculated that they may serve to maintain contact and coordination of the group during foraging. Interestingly, while the structure of pulsed calls was found to vary considerably between the different behavioural states in this study, many of the measured variables, such as frequency values and the number of elements, segment and inflection points, were often indistinguishable when the whales were foraging and travelling. Whales within a unit or group move at high speeds and may be spread out during both foraging and travelling. This suggests that the structure of pulsed calls produced during behavioural states with an increased need for maintaining contact with group members and coordination may be similar. An interesting parallel exists with the acoustic behaviour of certain resident killer whale pods. Their call usage patterns are also highly similar when both foraging and travelling, with an extremely high percentage of “discrete” calls and no statistical difference between the more specific call types produced during each behaviour (Ford 1989). Structural aspects of pilot whale pulsed calls further support the idea that they may serve as contact calls between separated individuals. Many of the calls contain high-frequency UFCs and undergo abrupt shifts in pitch, both of which enhance their recognition over long distances and may increase the potential for accurate localization (Brown 1982, Ford 1989, Miller 2006). Pilot whale pulsed calls may thus also function as contact calls, facilitating group cohesion during activities in which the members of a group are spread out and moving quickly (Weilgart and Whitehead 1990, Ford 1984).

Another interesting result is that pulsed calls made while socializing are the most complex, being composed of substantially higher numbers of elements, segments and inflection points than those produced during any other behavioural state. This is again similar to resident killer whale acoustic behaviour. While socializing, killer whales off B.C. produce the highest proportion of “variable” and “aberrant” pulsed calls, which have

highly variable structures and are distorted or modified versions of “discrete” calls, respectively. When looking at the spectrograms of such calls, it is clear that they are often more complex than the more typical versions of the same call type, with many more inflection points and modulations of the pulse repetition rate (see Figure 4.21, spectrograms in Ford 1989, 1991).

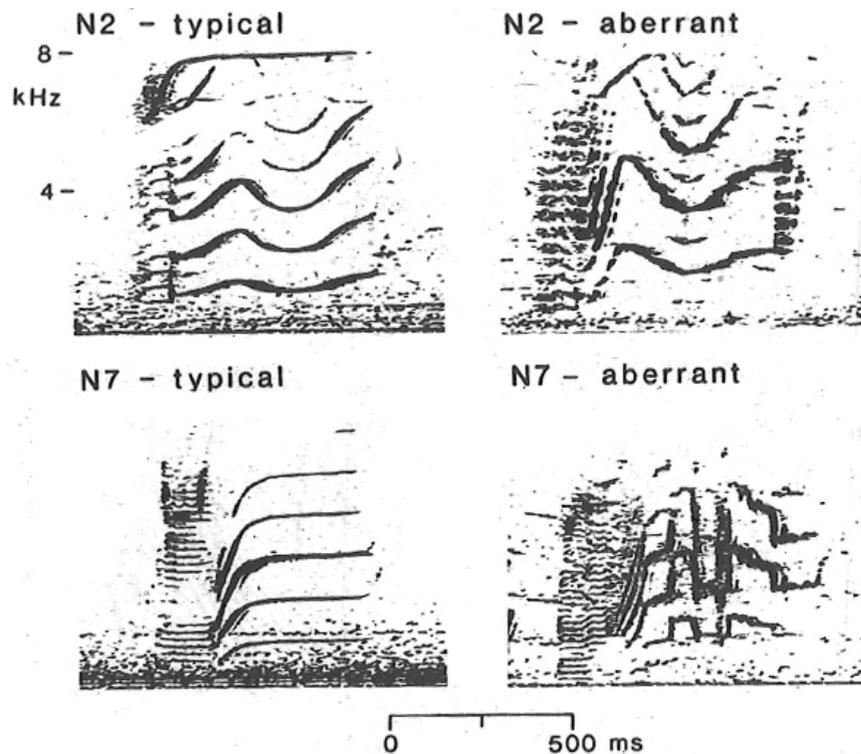


Figure 4.21. Spectrographic examples of resident killer whale (*Orcinus orca*) typical and aberrant versions of discrete call types N2 and N7 (from Ford 1989). Note the increased number of inflection points and elements in the aberrant versions.

Such structural complexity likely allows the calls to convey several pieces of information at one time (Hebets and Papaj 2005). Pilot whale socializing generally occurs when two or more groups join together (Auger-Méthé unpublished)<sup>3</sup>, and is the behavioural state during which animals strongly interact and sexual interactions are often observed (Amos et al. 1993a, personal observation). It is also a state of high energy output, with frequent aerial activities, such as breaching, spy-hopping and tail-slapping (Ford 1984, personal

<sup>3</sup> Unpublished analysis by M. Auger-Méthé, University of Alberta

observation). It is thus a behavioural state that may require individuals to communicate a large amount of information to the whales around them, such as arousal or “excitement” level (Ford 1989), motivation (Bradbury and Vehrencamp 1998, Compton et al. 2001) or social familiarity (Ford 1989, McCowan et al. 1998), as well as group membership, both to reduce the risk of inbreeding costs and to relocate members of their unit once the group dissolves (Tyack 2000). The increased complexity in call structure observed may reflect such high information exchanges.

#### *Other causes of variability*

The results of this study also suggest that the number of animals present and, more specifically, calves present may play a role in pulsed call structural variation. A number of studies have shown that bottlenose dolphin calves produce non-stereotyped calls at birth that gradually develop a more stereotyped structure as they mature (e.g. Caldwell et al. 1990). Adult sperm whales within social units have also been shown to alter their calls when a calf is present, which may reflect the increased necessity of a mother and calf being able to locate each other and ensure the efficient transfer of milk (e.g. Schulz 2007). Because I am unable to attribute specific calls to specific animals, there is no way to determine how the calls from calves differed from those of adults. However, the differences in pulsed call structure with group size and numbers of calves present are interesting results and warrants further investigation.

There also appears to be modifications to the structure of pulsed calls with time, although they were generally relatively minor modifications to multiple measured variables and did not appear to be strongly directional, showing no observable consistent trend over time. This degree of variation in pulsed call structure, although over a much larger time scale time, is also observed within and between groups of killer whales (Deecke et al. 2000), and may be a consequence of cultural drift shaping the structure of the calls. It has been suggested that an ever-changing dialect, mastered at an early age and modified over time through vertical and horizontal learning (Deecke et al. 2000), could still provide a reasonably reliable indication of kinship (Fitch 2004). Another possibility is that such year-to-year differences may, in fact, be simply due to the

differential presence of particular (or similar) clans in different sampling years, and thus more a consequence of chance than evidence of cultural drift over such a short time scale. Finally, the strong similarities observed between calls produced during the same encounters may be due to the presence of one or more highly vocal individuals within an encounter or call-matching between individuals (Janik 2000, Miller et al. 2004, Shulz et al. 2008). It is also likely a consequence of the behaviour and group composition contexts, which were often fairly consistent over the length of a recording. This emphasizes the need for representative samples of calls from social units across multiple encounters.

*Maturational effects, genetic differences or cultural drift?*

While it is tempting to attribute the variation observed here solely to culturally delineated units and behavioural state, other possible confounding factors may also explain some of the differences in call structure and need to be discussed. Such variation, while potentially a result of vocal learning, may also be caused by maturational effects or genetic differences (Janik and Slater 1997). The sexes and ages of members of each social unit are not at all resolved, and the additive effect of maturational processes affecting the vocalizations of different group members cannot be excluded as a cause of variation. However, one would expect that differences due to anatomical or physiological changes would affect all aspects of a particular measurement (such as start and end SBIs) equally over time, which was not always the case. As can be seen in Figure 4.15, for example, end SBIs are highest in 1999, but start SBIs are highest in 2000, although this may again be confounded by the different clans present between years. This suggests that whatever maturational processes may be affecting the vocalizations of whales of different sizes, ages or sexes, it is not a substantial cause of variation between units over time. It is currently impossible to rule out genetic differences between units of pilot whales off Cape Breton. However, evidence from the Faroese drive fishery indicates that male pilot whales rarely, if ever, mate successfully within their social unit or group (Amos et al. 1991, 1993a, 1993b), and thus genetic inheritance is unlikely to be the primary governing source of variation between units. It is possible, however, that, in contrast to killer whales (Barrett-Lennard 2000), mating could be occurring primarily within vocal clans, if

they exist, in which case genetic inheritance cannot be excluded as a contributing factor to call structure between clans.

Consequently, cultural drift, namely the modification of behaviours in a population over time and the subsequent fixation of the new variants by behavioural matching (Lynch 1996), is most likely the driving factor behind the variation we see in pulsed call structure between units. Cultural drift has been suggested as the cause behind the spreading of new syllables in the songs of honeyeaters, *Meliphaga virescens* (Baker et al. 2001), and the structural changes of discrete calls in resident killer whales over time (Deecke et al. 2000). Such structural modifications over time are likely introduced by random processes and thus not strongly directional (Deecke et al. 2000). Vertical and horizontal vocal learning is the most probable mechanism behind the maintenance of vocal traditions within social units or groups, allowing individuals to modify their pulsed calls in accordance with those of other members of their unit (Deecke et al. 2000), and has been observed in many species (Ford and Fisher 1983, Boughman 1997, Weilgart and Whitehead 1997, Price 1998, Crockford et al. 2004). Furthermore, cultural drift does not rule out a possible genetic component to variation, since learning often acts in conjunction with genetic factors in generating and maintaining patterns of variation in acoustic signals, as has been observed for some songbirds (e.g. Mundinger 1995). Further research into the variation in pulsed call structure *within* pilot whale social units between years is needed before the observed differences in call structure can be confidently attributed to cultural drift. The capacity for vocal learning has also yet to be demonstrated for pilot whales, although it has been established for other odontocete species (see Janik and Slater 1997).

#### **4.4.4 What Governs Variability in Complex Whistles?**

Unlike pulsed calls, there is little evidence from this study that pilot whale complex whistles are more similar within social units than between them. This is consistent with studies of resident killer whale whistles off Vancouver island, which were found to be similar regardless of the vocal clan from which they were recorded (Riesch et al. 2006). Complex whistle structure also does not appear to be more similar when produced during the same behavioural state than different ones. Previous studies of pilot whale whistles

have shown that whistle use varies between behaviours (Taruski 1979), and that the rate of complex whistle production increased during surface active behaviours, fast travel or “excited” states (Taruski 1979, Weilgart and Whitehead 1990). However, comparisons between the results of this study and others is complicated by the fact that only complex whistles were considered here and were not divided into discrete whistle types but were instead assumed to be graded (Taruski 1979). An important caveat is that there may be a sampling bias within the data, as the majority of whistles included in this analysis were recorded during socializing, foraging or travelling behavioural states, all of which are fairly active or “excited” behaviours. This supports the conclusions of Taruski (1979) and Weilgart and Whitehead (1990), as it was difficult to find many complex whistles during restful states, which were dominated by the production of simple whistles with no inflection points.

Instead, it appears that the structure of complex whistles is influenced most strongly by the average group size, while the general contours of whistles produced in the same year are more similar than those produced in different years. Complex whistles appear to cluster together based on the number of whales present during the recording period. This is generally consistent with Taruski (1979), who showed that the size of the herd (or group) significantly affected the types of whistles produced. Groups of less than 10 whales produced slightly more complex whistles, with the highest number of parts and inflection points. It is difficult to speculate on the significance of this, although it may indicate that whales somewhat simplify their whistles when surrounded by higher numbers of individuals. However, it is important to note that group size is a difficult measure to determine accurately, and thus such results must be interpreted with caution. There is also inter-annual variation between complex whistles, which appear to be more similar within years than between them. However, this is again not strongly directional, and may reflect that whistles are also not genetically fixed, and thus undergo slight parameter changes over time (Riesch et al. 2006). It may also, again, simply be a consequence of the differential presence of particular clans, with somewhat different whistle repertoires or behavioural repertoires, between sampling years. Finally, the strong similarities observed between whistles produced during the same encounters may be due to the presence of one or more highly vocal individuals within an encounter or call

matching, and may also be a consequence of average number of whales present, which remained fairly consistent over the length of a recording.

### *Communicative functions of complex whistles*

At this point, it is difficult to speculate on the possible communicative functions of complex whistles. Weilgart and Whitehead (1990) suggested that they play a role in group coordination and cohesion during foraging. While the structure of complex whistles specifically does not appear to vary between the behavioural states considered in this study, the majority of whistles recorded were produced during “active” behaviour, and thus a role in group coordination during fast or spread out behaviour cannot be excluded. Certainly, complex whistles have a relatively simple acoustic structure which is likely to suffer less from degradation during long-range transmission than the more complicated pulsed calls. Thus, they may be effective signals for facilitating coordination during active behaviours or over vast distances (Wiley and Richards 1982, Naguib and Wiley 2001) by, for instance, accurately advertising the sender’s location (Caldwell et al. 1990, Naguib et al. 2002). Whistles produced by several other Delphinid species appear to serve as individually-specific signatures (reviewed in Sayigh et al. 2007; but see McCowan and Reiss 2001). However, many dolphin species live in fission-fusion societies with highly stable associations with at most one or two other individuals, and identifying specific animals is highly important (Tyack 1986, 2000). In contrast, pilot whales form stable units that are likely matrilineal (Amos et al. 1993a), and identifying members of the unit or larger groups of related units is likely more important than identifying particular individuals (Tyack 1986, 2000). Given the apparent role of pulsed calls in identifying members of the same units, it is thus unlikely that complex whistles act as signature whistles. However, it is possible that subtle variations in pilot whale whistle structure may carry information on the caller’s identity (McCowan and Reiss 2001, McCowan and Hooper 2002). However, because I am unable to ascribe particular whistles to individual whales at this time, this cannot be tested. The lack of complex whistle similarity within social units or behavioural states may instead indicate a population-wide function, perhaps facilitating association and affiliation between members of different clans (discussed in Riesch et al. 2006). This is supported by the

increased simplicity of whistles when produced by groups larger than the average unit size (>10 animals), as whales may be modifying their whistles to facilitate interactions with other individuals when several units meet. However, the detailed acoustic behaviour of interacting individual pilot whales has yet to be explored.

#### **4.5 Summary**

I examined the similarity of pilot whale complex whistles and pulsed calls across social, behavioural and group composition contexts from different perspectives, and patterns in the data identified by multiple methods were considered to be the most robust. As such, pulsed call structure appears to be governed by the social unit or group producing the calls and by the behaviour or arousal state of the group during recording. Pulsed calls may thus reflect unit membership, facilitate group cohesion during behaviour in which the members of a group are moving quickly or are spread out, and transmit multiple pieces of information necessary during social interactions. Mixed groups of social units produced similar pulsed calls, and may indicate the presence of broader vocal clans of units that share aspects of their vocal repertoires. Complex whistle structure, conversely, appears to be most influenced by the average group size present during recording, may be modified over time and likely facilitates group coordination during active behaviour.

## CHAPTER 5 – CONCLUSION

### 5.1 General Conclusions and Implications

Previous to this study, there had been little investigation or description of the vocalizations of long-finned pilot whales (*Globicephala melas*). Preliminary descriptions of their vocal repertoire were offered by Busnel and Dziedzic (1966) and Busnel et al. (1971). Detailed and large-scale studies of their whistles undertaken by Taruski (1979) and, more recently, by Weilgart and Whitehead (1990), provided a more in-depth study of whistle usage in various contexts. Pilot whale whistle structure, in the context of species specificity, has also been examined by several authors, including Steiner (1981) and Rendell et al. (1999). However, little work had been done recently, and a complete description of pilot whale pulsed calls had never been attempted. In light of exciting developments in the field of animal bioacoustics, including myriad studies on the multi-functional qualities of complex vocal signals (e.g. Heberts and Papaj 2005), group-specific dialects (Ford 1991, Weilgart and Whitehead 1997), vocal learning (e.g. McCowan and Reiss 1997, Janik and Slater 2000, Tyack 2000, Deecke et al. 2000, Crockford et al. 2004), and the fitness consequences of vocal clans (Whitehead and Rendell 2004, Marcoux et al. 2007), it was clearly time to take a second look at the diverse and complex vocalizations of pilot whales.

Quantifying the pulsed calls produced by pilot whales was a fundamental first step in the investigation of their functionality and social relevance. In Chapter 2, I made multiple measures of pulsed call spectrograms, extracted from four years of recordings spanning eight years overall. The results offered a detailed, quantitative description of pulsed call structure that can be used to facilitate identification of pilot whale calls from recordings, and allowed subsequent research on the usage patterns and possible functions of these complex calls. The independent modulation of multiple components within each signal, along with the presence of an upper frequency component in many of the calls, suggests that pulsed calls transmit multiple pieces of information within each signal (Bradbury and Vehrencamp 1998, Heberts and Papaj 2005). Such calls may be difficult for eavesdroppers to imitate, and thus may act as honest signals between related individuals (Maynard Smith 1991). Pilot whale and resident killer whale (*Orcinus orca*)

pulsed calls are aurally and structurally very similar, despite their relative distance on the phylogenetic tree. Such convergence in design suggests that call function may have played an important role in the evolution of the complex pulsed call produced by both species, perhaps enabling them to solve similar communication challenges. The vocalizations and social organization of resident killer whales have been studied extensively for decades (see Ford and Fisher 1978, Bigg et al. 1990b), and the course and findings of killer whale acoustic research may suggest how to proceed for pilot whales. Pilot whale pulsed calls also appear to be highly variable, and no apparently discrete call type categories were identified in this study. The graded nature of pilot whale whistles was previously described by Taruski (1979). As such, similarity matrices were produced for both complex whistles and pulsed calls in Chapter 3, to permit subsequent analyses of both classes of sounds across social and behavioural contexts. Both statistical measures of similarity from measured pulsed call and whistle parameters and perceptual measures of similarity from human observer ratings were used to explore the similarity between calls. The statistical measures were clearly the most logistically efficient, although did not offer any indication of how the structure of calls are perceived. The perceptual measures produced very sparse matrices, as it was impossible to recruit a large enough number of participants and/or ask them to rate sufficient pairs of calls, to rate every possible pair of calls. However, participants were highly consistent with each other, supporting use of the method. The two different methods produced results that were not very well correlated, indicating that the methods examine call similarity from different perspectives. Support for each method is abundant in the literature (e.g. perceptual: Janik 1999, Deecke et al. 2000; statistical: Rendell and Whitehead 2003b, Brown et al. 2006), and the results of both were used when examining pulsed call and complex whistle similarity across contexts in Chapter 4.

In Chapter 4, I attempted to broadly deduce the communicative functions of pilot whale complex whistles and pulsed calls from the context in which the calls were made. I examined the similarity of calls within and between social units and groups, behavioural states, group sizes, the number of calves present, the year and the encounter during which recordings were made. Pulsed call structure appears to be dependent on the social units producing them, and may thus reflect unit membership. There was also a strong

suggestion of clusters of social units producing similarly structured calls that were different than those produced by other clusters of units, which may indicate the presence of broader vocal clans of units that share aspects of their call structure. There is also a strong relationship between pulsed call structure and behaviour, suggesting that pulsed calls also function in maintaining group cohesion and transmitting information during social interactions. Pilot whale complex whistles, on the other hand, appear to differ little between social units or behavioural state but are more similar when produced by groups with the same average number of whales. They may function in group coordination, and play more of a population-wide communicative role than a unit-specific one.

Because communication forms the foundation of most inter and intraspecific interactions, interference in the transfer and receipt of signals due to external factors (such as anthropogenic ocean noise) can have a significant impact on the health and status of a species. For highly mobile marine animals, the acoustic channel is often the primary method of communication between individuals, and an understanding of the structure and function of their vocalizations is thus essential if the impact of such interference is to be determined. Pilot whales have been shown to be sensitive to anthropogenic noise and disturbance, reducing their vocalizations in the presence of killer whales and during a Newfoundland drive (Schevill 1964), ceasing to vocalize at all during broadcasts of low-frequency sounds off Heard Island (Bowles et al. 1994), and altering their whistle type usage patterns during and after sonar output in the Ligurian Sea (Rendell and Gordon 1999). The importance of pilot whale vocal behaviour in the social and behavioural interactions within and between groups suggests that such disturbances may have substantial impacts on pilot whale populations.

## **5.2 Limitations of the Current Study and Suggestions for Future Work**

### **5.2.1 Recording Calls, Measuring Spectrograms and Describing Call Similarity**

The calls analyzed in this study are first limited by the equipment used during recordings. While there is no evidence in the literature that pilot whale whistles or pulsed calls contain energy above the 20 kHz limit of our recording equipment, numerous studies on other cetacean species have found significant energy above 20 kHz (e.g. Dawson 1991, Lammers et al. 2003, Oswald et al. 2004), and killer whales have been shown to reliably

respond to tones above 100 kHz (Szymanski et al. 1999). The presence of aliasing distortion in several of my recordings suggests that extremely high frequency components exist in pilot whale calls as well (Pohlmann 2005). Researchers should consider incorporating higher frequency equipment during future recordings, as this may reveal interesting new facets of pilot whale vocalizations.

Another basic limitation of this study is the subjectivity inherent in describing any acoustic signal, as the choice of which spectrographic parameters to measure can drastically alter results. In order to reduce this effect, I attempted to measure variables that best reflected the contour of the calls, but that were also consistent with previous studies. However, the resolution of measurements can alternatively conceal possible variation between calls if too coarse, or overemphasize differences between them if too fine. Because of the highly variable nature of pilot whale pulsed calls, I used a fairly fine-scale set of measurements to describe them. However, it is possible that some pilot whale pulsed calls are actually categorizable into discrete types, once variable or “aberrant” versions have been set aside (e.g. Ford 1984). Future work should focus on exploring pulsed calls at different levels of resolution, as working with call types as opposed to graded calls is certainly easier for humans, considering our aptitude for categorization (Tomasello 1999) and may more accurately reflect how the whales themselves interpret the acoustic signals (Richards et al. 1984, Ralston and Herman 1995).

Regardless, accurately and consistently representing the frequency contour of a whistle or the pulse repetition rates of a pulsed call remains a challenging task. Recent developments in unsupervised artificial neural networks offer an interesting solution to this problem. Neural networks model biological systems of information processing and classify unknown data based on information obtained from a known training set (see Hinton 1992). They have been successfully used in the automated classification of acoustic signals in several species (Neumann et al. 1992, Ramani et al. 1993, Murray et al. 1998, Deecke et al. 1999). The main advantage of this method is that its bio-mimetic nature allows for a measure of call similarity that assesses acoustic variation in a biologically meaningful way, while still being objective and repeatable (Deecke et al. 1999). The development of such automated procedures for extracting both whistle and pulsed call contours and rating call similarity would be a valuable tool for future analyses

of pilot whale acoustics, and more easily allow comparison of results across studies, species, and time (Deecke et al. 1999).

### **5.2.2 Contextual Information and Pilot Whale Social Structure off Cape Breton**

Ascribing contextual information to pilot whale calls, such as the social unit producing them or the behavioural state during which they were produced, is often difficult to do in a way that mimics how such attributes may be perceived by the whales. Attributing calls to specific social units is confounded by the presence of unidentified individuals within a group being recorded, mixed groups and the presence of unobserved distant groups. This is further complicated by the fact that marine mammals spend most of their time underwater and out of view, rendering group sampling difficult as not all individuals can be observed at all times (Mann 1999). In terms of behaviour, I cannot rule out the possibility that submerged animals behaved differently from the rest of the group. Moreover, all of the whales within a group did not often exhibit the same behaviour, even at the surface. Instead, the noted behavioural state reflects the modal behaviour observed. As such, our behavioural estimations may be confounded by highly vocal individuals exhibiting a different behaviour than the modal state. Future studies should attempt underwater behavioural recordings in conjunction with hydrophone recordings and focal follows.

Relating call structure to contextual factors is further complicated by confounding factors such as environmental conditions, maturational effects, and genetic differences, none of which were included in this study. Our current understanding of pilot whale social structure in the North Atlantic comes mainly from genetic studies using samples from Cape Cod, West Greenland, the Faeroe Islands, and the U.K. (Amos et al. 1993a, Fullard et al. 2000). No genetic studies have been successfully undertaken on the population of pilot whales along the northwest coast of Cape Breton. What we do know about their population substructure comes from behavioural studies using photographic identification of individuals and estimations of association based on presence in the same group during an encounter (Ottensmeyer and Whitehead 2003, Jankowski 2005, Lusseau unpublished). One of the main limitations of this study, then, is the basic assumption that pilot whales in the Northwest Atlantic live in kin-based social units, as suggested by

studies of other pilot whale populations in the North Atlantic (e.g. Amos et al. 1993a). Genetic sampling and kinship analysis of the Cape Breton population is an important next step in pilot whale research. In addition to learning more about the social structure of the population, including gender information to investigate bisexual natal group philopatry, it would be interesting to know how parental (or at least maternal) genes influence similarities between siblings in vocal learning abilities, if at all, and if they contribute to the fine-scale structural differences between calls.

An important methodological limitation is our current inability to ascribe particular sounds to the individuals within a group that produced them, thereby restricting the questions that we can answer. Are calves producing calls that are structurally different than other members of their unit? Is there a significant effect of sex or body size on the structure of calls? Is call matching occurring within a unit or group? Accurate descriptions of such call production patterns require recordings that allow accurate location and identification of sound sources. Recent advances in the use of passive acoustic localization have provided useful tools for studying the communication patterns of vocalizing marine mammals (e.g. Miller and Tyack 1998, Schulz et al. 2006). Such hydrophone arrays, which can be deployed and recovered manually from small research vessels, facilitate the discrimination of vocalizations made by marine cetaceans in relatively close proximity to each other. Overhead video recording of whale orientation relative to the array can then increase the precision of visual and acoustic data and facilitate detailed analysis after data collection in the field (Miller and Tyack 1998). The development of towed (Miller and Tyack 1998) or remotely-piloted hydrophone arrays (Schulz et al. 2006) and focal behavioural observations may contribute substantially to our understanding of call production and usage patterns within and between social units of pilot whales off Cape Breton.

## APPENDIX I – php script used for online comparison of calls

This script generated the first ten specified comparisons (identical for everyone) and the following random 70 comparisons for each participant. After the first ten, calls were pulled from four different folders: half the time from the dissimilar folder that contained all calls, and the rest of the time divided equally between similar1, similar2 and similar3, which contained broadly similar calls.

```
<?php
    $pictures = array();
    $soundfiles = array();
    $i = -1;
    function checkDir($c)
    {
        global $pictures, $soundfiles, $i;
        $i = -1;
        $d = opendir($c);
        while( $f = readdir($d) ) //recurse over directories
        {
            if( strpos($f, '.') === 0 ) continue;
            $ff = $c . '/' . $f;
            if(is_dir($ff)) checkDir($ff);
        }
        $d = opendir($c);
        while( $f = readdir($d) ) //add pictures to array
        {
            if( strpos($f, '.') === 0 ) continue;
            $ff = $c . "/" . $f;
            if( preg_match('/.jpg/', $ff, $test) )
            {
                $pictures[] = $ff;
                $soundfiles[] = str_replace( '.jpg', '.mp3', $ff);
                ++$i;
            }
        }
    }
    if ( empty($_REQUEST['set']) ) {
        $num = 1;
    } else {
        $num = $_REQUEST['set'];
        $num = $num <= 0 || $num > 80 ? 1 : $num ;
    }
    if( $num <= 10 && $_REQUEST['type'] == 'Pulsed Calls' ) {
    $pictures[0] = "./comparisons/pulsed_calls/pc_dissimilar/BS2129_pc_5.jpg" ;
```

## Appendix I, continued

```
$pictures[1] = "/comparisons/pulsed_calls/pc_dissimilar/BS0095_pc_9.jpg";
$pictures[2] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_27.jpg";
$pictures[3] = "/comparisons/pulsed_calls/pc_dissimilar/BS2129_pc_31.jpg";
$pictures[4] = "/comparisons/pulsed_calls/pc_dissimilar/BS1155_pc_15.jpg";
$pictures[5] = "/comparisons/pulsed_calls/pc_dissimilar/BS1022_pc_12.jpg";
$pictures[6] = "/comparisons/pulsed_calls/pc_dissimilar/BS0204_pc_9.jpg";
$pictures[7] = "/comparisons/pulsed_calls/pc_dissimilar/BS0207_pc_13.jpg";
$pictures[8] = "/comparisons/pulsed_calls/pc_dissimilar/BS1144_pc_4.jpg";
$pictures[9] = "/comparisons/pulsed_calls/pc_dissimilar/BS0115_pc_12.jpg";
$pictures[10] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_9.jpg";
$pictures[11] = "/comparisons/pulsed_calls/pc_dissimilar/BS0166_pc_1.jpg";
$pictures[12] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_23.jpg";
$pictures[13] = "/comparisons/pulsed_calls/pc_dissimilar/BS1005_pc_1.jpg";
$pictures[14] = "/comparisons/pulsed_calls/pc_dissimilar/BS0095_pc_8.jpg";
$pictures[15] = "/comparisons/pulsed_calls/pc_dissimilar/BS1005_pc_27.jpg";
$pictures[16] = "/comparisons/pulsed_calls/pc_dissimilar/BS0166_pc_11.jpg";
$pictures[17] = "/comparisons/pulsed_calls/pc_dissimilar/BS0207_pc_14.jpg";
$pictures[18] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_19.jpg";
$pictures[19] = "/comparisons/pulsed_calls/pc_dissimilar/PB3162_pc_4.jpg";
$soundfiles[0] = "/comparisons/pulsed_calls/pc_dissimilar/BS2129_pc_5.mp3";
$soundfiles[1] = "/comparisons/pulsed_calls/pc_dissimilar/BS0095_pc_9.mp3";
$soundfiles[2] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_27.mp3";
$soundfiles[3] = "/comparisons/pulsed_calls/pc_dissimilar/BS2129_pc_31.mp3";
$soundfiles[4] = "/comparisons/pulsed_calls/pc_dissimilar/BS1155_pc_15.mp3";
$soundfiles[5] = "/comparisons/pulsed_calls/pc_dissimilar/BS1022_pc_12.mp3";
$soundfiles[6] = "/comparisons/pulsed_calls/pc_dissimilar/BS0204_pc_9.mp3";
$soundfiles[7] = "/comparisons/pulsed_calls/pc_dissimilar/BS0207_pc_13.mp3";
$soundfiles[8] = "/comparisons/pulsed_calls/pc_dissimilar/BS1144_pc_4.mp3";
$soundfiles[9] = "/comparisons/pulsed_calls/pc_dissimilar/BS0115_pc_12.mp3";
$soundfiles[10] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_9.mp3";
$soundfiles[11] = "/comparisons/pulsed_calls/pc_dissimilar/BS0166_pc_1.mp3";
$soundfiles[12] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_23.mp3";
$soundfiles[13] = "/comparisons/pulsed_calls/pc_dissimilar/BS1005_pc_1.mp3";
$soundfiles[14] = "/comparisons/pulsed_calls/pc_dissimilar/BS0095_pc_8.mp3";
$soundfiles[15] = "/comparisons/pulsed_calls/pc_dissimilar/BS1005_pc_27.mp3";
$soundfiles[16] = "/comparisons/pulsed_calls/pc_dissimilar/BS0166_pc_11.mp3";
$soundfiles[17] = "/comparisons/pulsed_calls/pc_dissimilar/BS0207_pc_14.mp3";
$soundfiles[18] = "/comparisons/pulsed_calls/pc_dissimilar/BS1153_pc_19.mp3";
$soundfiles[19] = "/comparisons/pulsed_calls/pc_dissimilar/PB3162_pc_4.mp3";
$pic1 = $pictures[$num - 1];
$snd1 = $soundfiles[$num - 1];
$pic2 = $pictures[$num + 9];
$snd2 = $soundfiles[$num + 9];
} else if( $num <= 10 && $_REQUEST['type'] == 'Whistles' ) {
```

## Appendix I, continued

```
$pictures[0] = "/comparisons/whistles/w_dissimilar/BS0095_w_13.jpg";
$pictures[1] = "/comparisons/whistles/w_dissimilar/BS2127_w_4.jpg" ;
$pictures[2] = "/comparisons/whistles/w_dissimilar/BS0166_w_1.jpg" ;
$pictures[3] = "/comparisons/whistles/w_dissimilar/BS2157_w_4.jpg" ;
$pictures[4] = "/comparisons/whistles/w_dissimilar/BS1159_w_13.jpg";
$pictures[5] = "/comparisons/whistles/w_dissimilar/PB3223_w_1.jpg" ;
$pictures[6] = "/comparisons/whistles/w_dissimilar/BS0095_w_142.jpg";
$pictures[7] = "/comparisons/whistles/w_dissimilar/BS0166_w_5.jpg" ;
$pictures[8] = "/comparisons/whistles/w_dissimilar/BS2085_w_12.jpg";
$pictures[9] = "/comparisons/whistles/w_dissimilar/PB3024_w_1.jpg" ;
$pictures[10] = "/comparisons/whistles/w_dissimilar/BS1012_w_8.jpg" ;
$pictures[11] = "/comparisons/whistles/w_dissimilar/PB3021_w_5.jpg" ;
$pictures[12] = "/comparisons/whistles/w_dissimilar/BS0166_w_13.jpg";
$pictures[13] = "/comparisons/whistles/w_dissimilar/BS2150_w_6.jpg" ;
$pictures[14] = "/comparisons/whistles/w_dissimilar/BS2110_w_19.jpg";
$pictures[15] = "/comparisons/whistles/w_dissimilar/PB3225_w_6.jpg" ;
$pictures[16] = "/comparisons/whistles/w_dissimilar/BS1155_w_12.jpg";
$pictures[17] = "/comparisons/whistles/w_dissimilar/BS0144_w_16.jpg";
$pictures[18] = "/comparisons/whistles/w_dissimilar/PB3022_w_9.jpg";
$pictures[19] = "/comparisons/whistles/w_dissimilar/BS2091_w_11.jpg";
$soundfiles[0] = "/comparisons/whistles/w_dissimilar/BS0095_w_13.mp3";
$soundfiles[1] = "/comparisons/whistles/w_dissimilar/BS2127_w_4.mp3" ;
$soundfiles[2] = "/comparisons/whistles/w_dissimilar/BS0166_w_1.mp3" ;
$soundfiles[3] = "/comparisons/whistles/w_dissimilar/BS2157_w_4.mp3" ;
$soundfiles[4] = "/comparisons/whistles/w_dissimilar/BS1159_w_13.mp3";
$soundfiles[5] = "/comparisons/whistles/w_dissimilar/PB3223_w_1.mp3" ;
$soundfiles[6] = "/comparisons/whistles/w_dissimilar/BS0095_w_142.mp3";
$soundfiles[7] = "/comparisons/whistles/w_dissimilar/BS0166_w_5.mp3" ;
$soundfiles[8] = "/comparisons/whistles/w_dissimilar/BS2085_w_12.mp3";
$soundfiles[9] = "/comparisons/whistles/w_dissimilar/PB3024_w_1.mp3" ;
$soundfiles[10] = "/comparisons/whistles/w_dissimilar/BS1012_w_8.mp3" ;
$soundfiles[11] = "/comparisons/whistles/w_dissimilar/PB3021_w_5.mp3" ;
$soundfiles[12] = "/comparisons/whistles/w_dissimilar/BS0166_w_13.mp3";
$soundfiles[13] = "/comparisons/whistles/w_dissimilar/BS2150_w_6.mp3" ;
$soundfiles[14] = "/comparisons/whistles/w_dissimilar/BS2110_w_19.mp3";
$soundfiles[15] = "/comparisons/whistles/w_dissimilar/PB3225_w_6.mp3" ;
$soundfiles[16] = "/comparisons/whistles/w_dissimilar/BS1155_w_12.mp3";
$soundfiles[17] = "/comparisons/whistles/w_dissimilar/BS0144_w_16.mp3";
$soundfiles[18] = "/comparisons/whistles/w_dissimilar/PB3022_w_9.mp3";
$soundfiles[19] = "/comparisons/whistles/w_dissimilar/BS2091_w_11.mp3";
$pic1 = $pictures[$num - 1];
$snd1 = $soundfiles[$num - 1];
$pic2 = $pictures[$num + 9];
$snd2 = $soundfiles[$num + 9];
```

## Appendix I, continued

```
    } else {
        srand((double) microtime() * 1000000);
        $rootdirectory = "./comparisons";
        if($_REQUEST['type'] == 'Pulsed Calls' )
            $rootdirectory = $rootdirectory . '/pulsed_calls/pc_';
        if($_REQUEST['type'] == 'Whistles' )
            $rootdirectory = $rootdirectory . '/whistles/w_';
        $rand = (int) rand(0, 5);
        if( $rand == 0 )    $rootdirectory = $rootdirectory . 'similar1';
        else if( $rand == 1 ) $rootdirectory = $rootdirectory . 'similar2';
        else if( $rand == 2 ) $rootdirectory = $rootdirectory . 'similar3';
        else                $rootdirectory = $rootdirectory . 'dissimilar';
        checkDir($rootdirectory);
        $rand = (int) rand(0, $i - 1);
        $pic1 = $pictures[$rand];
        $snd1 = $soundfiles[$rand];
        $rand = (int) rand(0, $i - 1);
        $pic2 = $pictures[$rand];
        $snd2 = $soundfiles[$rand];
    }
    $file1 = $pic1;
    $file2 = $pic2;
?>
```

## **APPENDIX II – Instructions for online call comparisons**

Before a session, participants were asked to read the following instructions carefully:

1. To begin the session, click on "Do the Research!"
2. You will be brought to a Background Information page. Please fill this out honestly. Note that NO experience is required, and that all your information will be kept strictly confidential and will be used for data analysis purposes only.
3. Once your background information is submitted, you will be offered a choice between comparing Pulsed Calls or Whistles. Make your choice and press "Submit". If you choose pulsed calls, all the spectrograms and audio files you will be given will be pulsed calls (and vice-versa with whistles).
4. Now you are on the comparisons page. This is where the research begins. You will be shown two pictures with two associated audio files for each comparison, pulled randomly from a large pool of calls. A total of 80 comparisons will be made if you complete the entire session. The first 10 pairs are for training purposes, to help you feel more comfortable with your choices and increase consistency.
5. Take your time and examine each picture. The pictures are called spectrograms, and they show what the contour of the sound you will be listening to looks like, using time on the horizontal axis and frequency (Hz) on the vertical axis. Note: the call of interest will be centered within the spectrogram, and should be easy to pick out. When there is a lot of background noise, the call of interest will be circled in red. For calls with several bands (harmonics for whistles or sidebands if pulsed calls), the fundamental frequency (the main band) is the darkest of all the bands. NOTE: vertical lines on the spectrograms are echolocation clicks (they sound like someone tapping the microphone). Do not consider them when deciding on your similarity rating.
6. **When comparing the spectrograms, get a good idea of the following for each call, shown in order of importance:**
  1. General contour (the shape of the call)
  2. Number and location of inflection points (when the call changes frequency abruptly, e.g. turns upwards)
  3. General frequency range (start & end, max & min frequencies)

## Appendix II, continued

4. Duration (length of the call)
5. For pulsed calls only: the number of elements (sections of the call separated by abrupt shifts in the side band interval -- i.e. the space between the bands – see below for an example). This is very important when comparing pulsed calls
6. See below for examples.
7. **When comparing the audio files, take note of how the calls sound.** Does one oscillate more than the other? Is one higher pitched? Disregard how loud the calls are, since that is likely just a consequence of how close the whale was to the hydrophone. See below for some audio examples.
8. When you are done examining the spectrograms and listening to the audio files, select a similarity rating from the drop-down bar. **The rating that you choose should be based on what percentage of the calls you think are the same:**
  1. Identical: more than 90% of the two calls are the same
  2. High Similarity: between 60-90% of the two calls are the same
  3. Medium Similarity: between 40-60% of the two calls are the same
  4. Low Similarity: between 10-40% of the two calls are the same
  5. Totally Different: less than 10% of the two calls are the same
9. Once your rating has been chosen, click "Submit Answer". You will then be shown the next pair of calls for you to compare. Once you have done all 80 calls, you will be brought automatically to a Thank You screen and your answers will be submitted to the database. If you want to stop before you have finished all 80 pairs, click on the "I Quit" button on the bottom-right corner of the page. This will ensure that your answers up to that point will be submitted.
10. That's all! Thanks very much for taking the time to participate in this research.

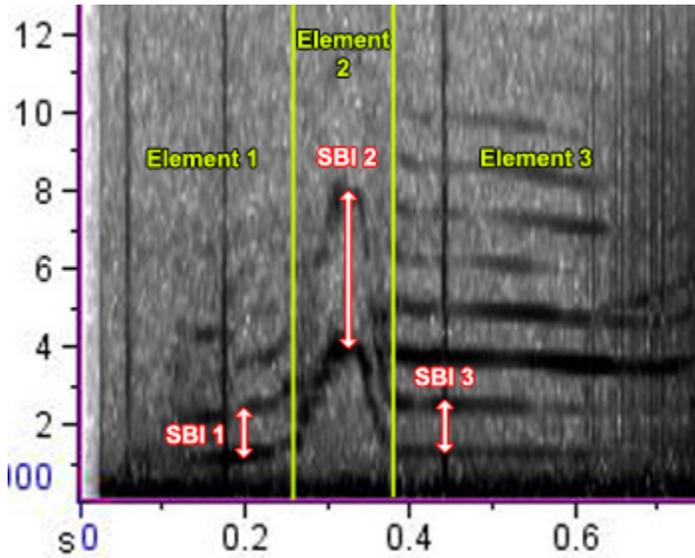
### EXAMPLES

Below are three diagrams. The first is a pulsed call clearly showing shifts in the sideband intervals, creating three elements. The second is a pulse call and the third is

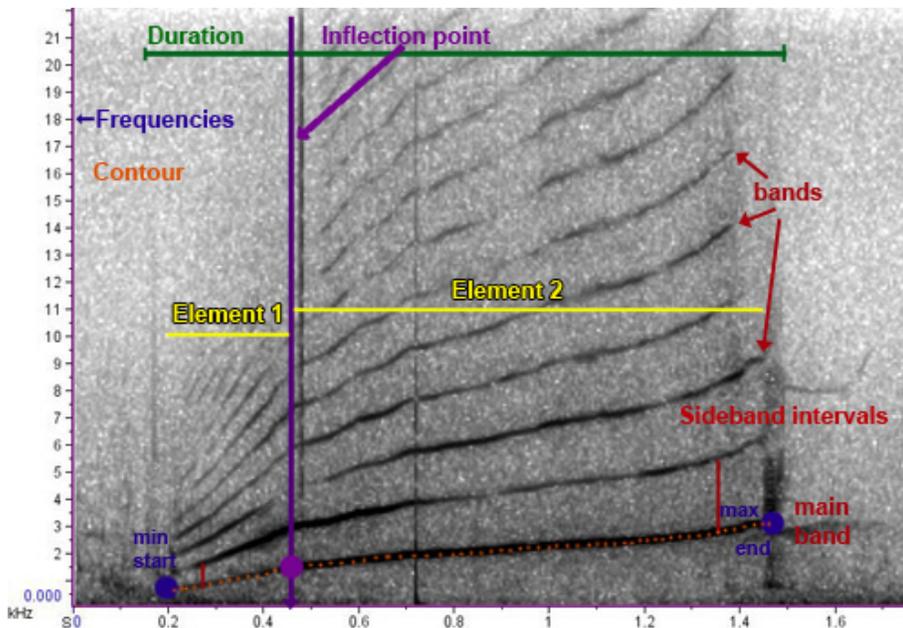
## Appendix II, continued

a whistle. The last two are labeled with general variables that you can use as a guide when comparing the pairs of calls presented to you. Remember, you don't have to write down actual measurements! You can press the red play button to listen to the associated audio files. (Note: use your computer's volume settings to increase or decrease volume.)

Elements:

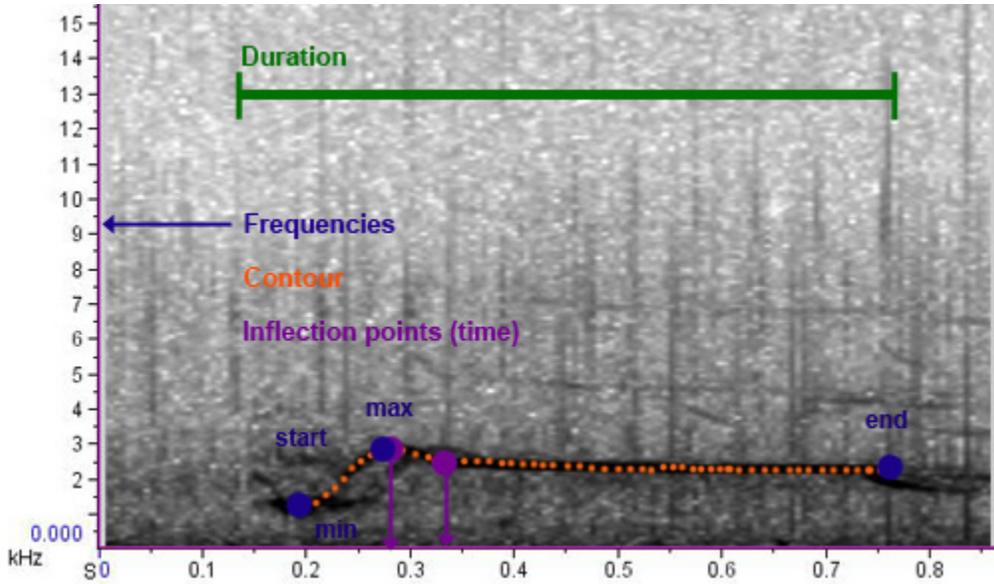


Pulsed Call:



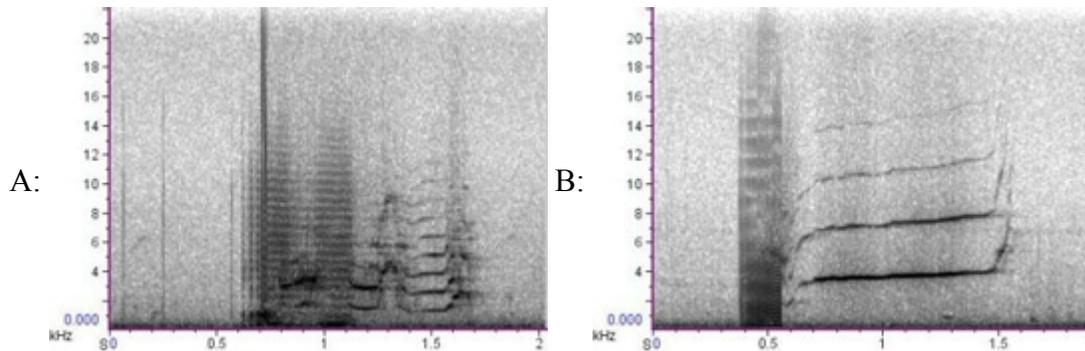
## Appendix II, continued

Whistle:



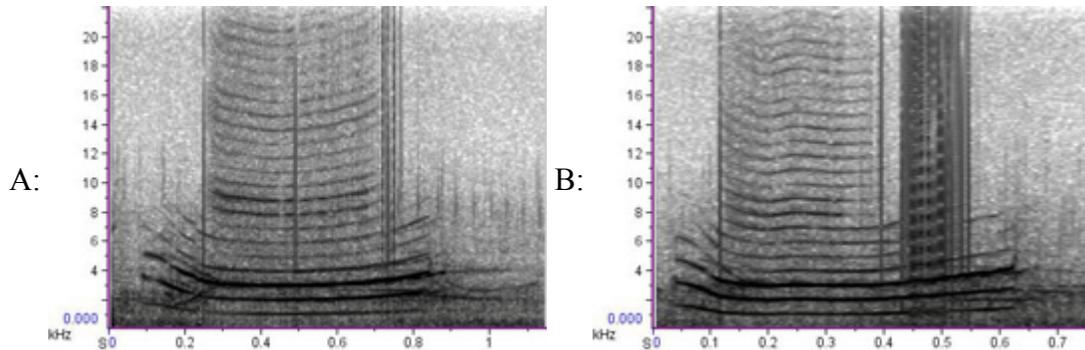
Below are two pairs of pulsed calls, with both audio files and spectrograms to compare. Note down your similarity rating for each pair, and then check the answers and reasoning! Press the red play button to listen to the associated audio files. (Note: use your computer's volume settings to increase or decrease volume.)

**First pair:**



## Appendix II, continued

### Second pair:



The answers to the two comparisons are below, including a breakdown of the reasoning behind each answer:

### First pair

*Answer:* Totally different (less than 10% of the two calls are the same).

*Reasoning:* The sounds are clearly very different when the audio is listened to. When the spectrograms are looked at, we can see that call A has a very different contour than call B, it has many more inflection points, as well as > 5 elements (while call B only has 2).

The frequency ranges of the two calls are also different. Call A has a lower main band frequency (around 3.5kHz), while call B's main band is almost 4kHz. The maximum frequency of call B is higher (reaching over 7kHz while call A only reaches around 5kHz), though both do have similar minimum frequencies. Both are approximately one second long, but duration is not the most important factor (# 4 on the list).

### Second pair

*Answer:* Identical (more than 90% of the two calls are the same).

*Reasoning:* The two sounds are extremely similar when the audio is listened to. This similarity is also seen in the spectrograms. Both contours are almost identical, although call B does have a bit of a waver near the beginning of the call. The frequencies are likewise similar. Call B is about 0.2 seconds shorter than call A, but not significantly.

## APPENDIX III – Participant deviation from the modal ratings for the first ten comparisons of pulsed calls and whistles

Values for individual deviations from the modal rating: +1 if one higher rating, -1 if one lower rating (+2 if two higher than modal rating, -2, etc.), 0 = no deviation. A blank indicates that the participant skipped that particular comparison. Also shown is the sum of the absolute values and the mean deviations.

Participant	Experience (Y/N)	Pulsed calls			Whistles		
		Deviation from mode	Sum abs values	Means	Deviation from mode	Sum abs values	Means
1	N	[ 0 1 0 0 0 0 1 0 0 -1 ]	3	0.3	[ 0 0 0 0 -2 0 3 0 0 1 ]	6	0.6
2	N	[ 2 1 -1 1 1 0 1 -1 1 -1 ]	10	1.0	[ 2 0 -1 0 -1 0 0 0 -2 -1 ]	7	0.7
3	Y	[ 0 -1 -1 1 0 0 1 0 1 0 ]	5	0.5	[ 1 0 -1 -1 0 0 1 0 0 -1 ]	5	0.5
4	N	[ 0 0 0 1 2 1 2 0 0 0 ]	6	0.6	[ 2 1 0 1 0 0 2 0 0 0 ]	6	0.6
5	N	[ 0 -1 0 0 0 0 0 0 0 0 ]	1	0.1	[ 0 0 0 -1 -1 0 0 0 0 -1 ]	3	0.3
6	N	[ 0 1 0 1 0 2 2 0 2 1 ]	9	0.9	[ 2 2 0 1 1 0 1 0 0 0 ]	7	0.7
7	N	[ 0 3 0 -1 0 1 2 0 2 0 ]	9	0.9	[ 0 0 0 0 0 1 0 0 1 1 ]	3	0.3
8	Y	[ 0 2 0 2 1 1 0 0 2 0 ]	8	0.8	[ 1 1 0 2 1 2 2 0 0 0 ]	9	0.9
9	N	[ 1 2 0 1 0 0 2 0 1 -1 ]	8	0.8	[ 1 0 0 0 1 0 1 0 0 0 ]	3	0.3
10	Y	[ 1 1 0 2 1 1 1 0 0 1 ]	8	0.8	[ 2 1 0 0 0 0 1 0 -1 0 ]	5	0.5
11	N	[ 0 -1 0 -1 0 2 2 0 0 0 ]	6	0.6	[ 0 0 0 0 0 0 2 0 -3 1 ]	6	0.6
12	N	[ 0 -1 0 -1 0 1 2 0 0 -1 ]	6	0.6	[ 1 0 0 1 0 1 -1 0 0 1 ]	5	0.5
13	Y	[ 0 -1 -1 -1 0 0 0 0 -1 ]	4	0.4	[ 1 0 -1 -1 -2 0 0 0 -2 0 ]	7	0.7
14	N	[ 2 0 0 1 1 2 0 0 1 -1 ]	8	0.8	[ 0 0 0 2 1 2 1 1 -2 -2 ]	11	1.1
15	N	[ 1 -1 0 -1 1 0 0 0 0 1 ]	5	0.5	[ 0 0 -1 -1 0 0 0 1 1 0 ]	4	0.4
16	Y	[ 0 -1 0 -1 0 0 -1 0 0 0 ]	3	0.3	[ 0 0 0 -1 0 0 0 0 -3 -1 ]	5	0.5
17	N	[ 1 1 -1 1 1 2 1 0 0 -1 ]	9	0.9	[ 2 1 0 2 0 2 2 3 0 -1 ]	13	1.3
18	N	[ 0 -1 0 -1 0 0 0 0 0 -1 ]	3	0.3	[ 0 0 0 -1 -2 0 -1 0 1 0 ]	5	0.5
19	N	[ 1 1 0 0 0 1 -1 0 0 ]	4	0.4	[ 2 0 0 -1 1 0 1 0 -1 0 ]	6	0.6
20	Y	[ 0 -1 0 0 0 0 0 0 0 0 ]	1	0.1	[ 1 0 0 -1 -1 0 -1 0 0 0 ]	4	0.4
21	N	[ 0 -1 0 1 1 0 0 0 0 0 ]	3	0.3	[ 1 0 -1 0 0 2 -1 0 0 -1 ]	6	0.6
22	N	[ 0 -1 0 2 1 2 1 0 1 0 ]	8	0.8	[ 1 0 0 0 0 1 0 0 -2 0 ]	4	0.4
23	N	[ 0 -1 0 0 1 0 1 0 0 0 ]	3	0.3	[ 1 0 0 2 0 0 0 0 -1 0 ]	4	0.4
24	N	[ 0 -1 0 0 0 0 2 0 0 ]	3	0.3	[ 0 0 -1 0 0 0 1 0 -3 0 ]	5	0.5
25	Y	[ 0 0 0 -1 0 0 1 0 0 0 ]	2	0.2	[ 0 0 0 -1 -1 0 -1 0 -1 0 ]	4	0.4
26	N	[ 0 0 0 -1 0 0 1 0 0 0 ]	2	0.2	[ 1 0 0 0 1 0 1 0 -3 0 ]	6	0.6
27	N	[ 0 0 -1 -1 0 0 1 0 0 0 ]	3	0.3	[ 3 1 0 1 0 2 2 1 1 1 ]	12	1.2
28	Y	[ 0 1 0 0 0 0 0 0 0 -1 ]	2	0.2	[ 0 0 0 -1 -1 0 0 0 0 0 ]	2	0.2
29	Y	[ 1 -1 0 1 1 0 1 0 0 0 ]	5	0.5	[ 1 1 -1 1 0 0 -1 0 0 0 ]	5	0.5
30	N	[ 0 -1 -2 -1 0 0 -1 0 0 -1 ]	6	0.6	[ 0 0 -1 0 0 0 -1 0 -3 -3 ]	8	0.8
31	N	[ 1 0 0 1 0 0 0 0 0 0 ]	2	0.2	[ 2 1 -1 0 -1 0 0 0 -1 -1 ]	7	0.7
32	Y	[ 0 0 0 2 0 0 0 0 0 -1 ]	3	0.3	[ 1 0 0 0 0 1 1 0 -1 0 ]	4	0.4
33	N	[ 0 -1 0 0 1 0 0 0 0 0 ]	2	0.2	[ 2 1 0 0 -1 0 0 0 -1 -1 ]	6	0.6
34	N	[ 0 1 0 -1 0 0 0 0 0 -1 ]	3	0.3	[ 0 0 0 0 -1 3 2 0 1 0 ]	7	0.7
35	N	[ 0 -1 0 2 1 0 -1 0 0 -1 ]	6	0.6	[ 0 0 0 2 1 1 1 0 -3 -1 ]	9	0.9
36	N	[ 0 0 0 -1 0 0 0 0 0 -1 ]	2	0.2	[ 2 0 0 1 0 0 0 0 -1 -2 ]	6	0.6
37	Y	[ 2 0 -1 0 1 1 0 0 0 0 ]	5	0.5	[ 1 1 -1 0 -1 1 0 0 -1 0 ]	6	0.6
38	Y	[ 0 -1 0 -1 0 0 0 0 0 0 ]	2	0.2	[ 1 0 0 -1 -1 0 0 0 -2 -2 ]	7	0.7
39	N	[ 0 0 0 1 1 0 0 0 0 0 ]	2	0.2	[ 0 0 0 1 -1 0 1 0 -1 -2 ]	6	0.6
40	Y	[ 0 0 0 1 0 0 1 0 2 1 ]	5	0.5	[ 1 0 0 -1 -1 1 1 0 -1 0 ]	6	0.6
41	N	[ 0 -1 -1 0 1 1 0 0 0 0 ]	4	0.4	[ 1 1 0 0 -1 0 0 0 -1 -1 ]	5	0.5
42	N	[ 0 0 0 -1 0 0 1 0 1 -1 ]	4	0.4	[ 1 0 0 2 1 2 2 1 0 1 ]	10	1.0
43	N	[ 0 -1 0 2 0 1 0 0 0 ]	4	0.4	[ 2 1 0 0 -1 0 1 0 -1 0 ]	6	0.6
44	N	[ 0 0 -2 -1 0 0 1 0 1 -1 ]	6	0.6	[ 0 0 0 1 -1 0 1 0 0 -1 ]	4	0.4
45	N	[ 0 0 0 -1 0 0 0 0 0 0 ]	1	0.1	[ 0 0 -1 -1 -2 0 0 0 -2 -2 ]	8	0.8

### Appendix III, continued

Participant	Experience (Y/N)	Pulsed calls			Whistles		
		Deviation from mode	Sum abs values	Means	Deviation from mode	Sum abs values	Means
46	Y	[ 0 0 0 0 1 2 0 -1 1 2 ]	7	0.7	[ 3 1 0 1 0 0 0 0 0 0 ]	5	0.5
47	Y	[ 0 0 0 0 1 2 0 -1 0 1 ]	5	0.5	[ 2 1 -1 1 0 0 1 0 0 0 ]	6	0.6
48	Y	[ 0 1 0 0 1 0 0 0 0 1 ]	3	0.3	[ 2 0 0 1 1 0 1 0 0 -1 ]	6	0.6
49	Y	[ 1 -1 0 -1 0 0 2 0 0 1 ]	6	0.6	[ 0 0 0 -1 0 0 1 0 -2 1 ]	5	0.5
50	Y	[ 0 -1 0 0 0 0 -1 0 0 0 ]	2	0.2	[ 0 0 0 -1 -1 0 -1 0 -3 -1 ]	7	0.7
51	Y	[ 0 2 0 -1 0 0 1 0 3 0 ]	7	0.7	[ 1 0 -1 0 -1 0 0 0 0 -1 ]	4	0.4
52	Y	[ 0 0 0 1 0 0 -1 0 1 0 ]	3	0.3	[ 1 0 -1 -1 -1 0 1 0 0 -1 ]	6	0.6
53	Y	[ 0 0 -1 0 0 1 1 0 2 2 ]	7	0.7	[ 1 1 0 1 1 2 0 0 0 0 ]	6	0.6
54	N	[ 0 0 0 -1 0 0 1 0 1 0 ]	3	0.3	[ 1 0 -1 0 -1 0 0 0 0 -1 ]	4	0.4
55	Y	[ 0 1 0 0 0 0 0 0 0 0 ]	1	0.1	[ 0 0 0 -1 1 0 0 0 0 -2 ]	4	0.4
56	N	[ 0 1 -1 -1 0 0 1 0 3 2 ]	9	0.9	[ 1 0 0 2 1 2 1 0 1 0 ]	8	0.8
57	N	[ 1 -1 -1 0 0 0 0 1 -1 ]	5	0.6	[ 0 0 -1 -2 0 -1 0 -1 -2 ]	8	0.8
58	Y	[ 0 0 0 1 0 1 0 0 1 1 ]	4	0.4	[ 2 1 -1 0 0 0 2 0 0 ]	6	0.7
59	Y	[ 0 -1 -1 0 0 0 0 0 0 1 ]	3	0.3	[ 1 0 -1 -1 -2 0 -1 0 -2 -2 ]	10	1.0
60	Y	[ 0 -1 -1 0 2 0 -1 0 0 -1 ]	6	0.6	[ 2 0 0 1 1 0 0 0 0 -1 ]	5	0.5
61	N	[ 1 -1 -1 1 1 2 2 0 1 0 ]	10	1.0	[ 1 0 0 1 -1 1 2 1 0 1 ]	8	0.8
62	N	[ 0 2 0 1 1 1 3 0 2 2 ]	12	1.2	[ 0 0 0 1 0 2 2 0 1 1 ]	7	0.7
63	Y	[ 0 -1 0 0 0 0 -1 0 1 0 ]	3	0.3	[ 2 0 -1 1 0 0 -1 0 -2 0 ]	7	0.7
64	N	[ 0 0 -1 0 1 0 -1 0 0 0 ]	3	0.3	[ ]		
65	Y	[ 0 0 0 0 0 0 0 0 1 0 ]	1	0.1	[ ]		
66	N	[ 0 1 -1 0 0 2 0 0 0 0 ]	4	0.4	[ ]		
67	Y	[ 0 -1 -1 1 0 0 2 0 1 0 ]	6	0.6	[ ]		
68	Y	[ 1 0 0 1 0 0 0 0 0 -1 ]	3	0.3	[ ]		
69	Y	[ 1 -1 0 -1 2 1 1 0 1 1 ]	9	0.9	[ ]		
70	Y	[ 1 0 -1 0 0 1 0 -1 0 0 ]	4	0.4	[ ]		
71	N	[ 0 -1 -1 -1 0 0 0 0 0 -1 ]	4	0.4	[ ]		
72	N	[ 0 1 0 0 1 2 1 0 1 -1 ]	7	0.7	[ ]		
73	N	[ 0 -1 -1 -1 0 0 -1 0 0 -1 ]	5	0.5	[ ]		
74	Y	[ 2 -1 0 0 1 1 0 0 0 0 ]	5	0.5	[ ]		
75	N	[ 0 1 -1 0 1 1 1 0 0 -1 ]	6	0.6	[ ]		
76	N	[ 0 0 0 1 0 1 0 0 0 0 ]	2	0.2	[ ]		
77	N	[ 0 -1 -1 0 0 0 1 -1 0 -1 ]	5	0.5	[ ]		
78	N	[ 0 0 0 0 0 0 0 0 0 1 ]	1	0.1	[ ]		
79	Y	[ 0 0 -1 1 0 2 2 0 3 1 ]	10	1.0	[ ]		
80	N	[ 0 -1 -1 0 0 0 -1 0 0 0 ]	3	0.3	[ ]		
81	N	[ 0 0 -1 0 0 0 3 0 0 -1 ]	5	0.5	[ ]		
82	Y	[ 0 0 0 0 0 0 1 0 0 0 ]	1	0.1	[ ]		
83	N	[ 0 2 0 0 0 0 2 0 2 0 ]	6	0.6	[ ]		
84	N	[ 0 -1 0 1 0 0 2 0 1 1 ]	6	0.6	[ ]		
85	N	[ 2 2 3 2 2 0 0 1 1 ]	13	1.4	[ ]		
86	N	[ 1 1 0 1 1 3 2 0 1 0 ]	10	1.0	[ ]		
87	N	[ 0 3 -1 0 0 2 2 0 2 1 ]	11	1.1	[ ]		
88	N	[ 0 0 -1 -1 0 0 1 0 0 -1 ]	4	0.4	[ ]		
89	N	[ 0 1 -1 0 0 0 0 -1 0 0 ]	3	0.3	[ ]		
90	N	[ 0 0 -1 1 0 0 1 0 0 -1 ]	4	0.4	[ ]		
91	N	[ 0 -1 -1 1 0 0 0 1 -1 ]	5	0.6	[ ]		
92	N	[ 0 1 -1 0 0 0 2 0 1 0 ]	5	0.5	[ ]		
93	N	[ 0 -1 0 1 0 0 0 0 1 1 ]	4	0.4	[ ]		
94	N	[ 1 0 -1 -1 0 2 1 0 0 0 ]	6	0.6	[ ]		
95	Y	[ 0 1 -1 0 0 0 -1 0 0 0 ]	3	0.3	[ ]		
96	Y	[ 0 1 0 1 1 0 1 0 1 2 ]	7	0.7	[ ]		
97	N	[ 0 0 -1 0 1 1 1 0 0 -1 ]	5	0.5	[ ]		
98	N	[ 0 0 -1 -1 0 0 1 0 1 1 ]	5	0.5	[ ]		
99	Y	[ 1 1 0 1 1 0 1 0 0 1 ]	6	0.6	[ ]		
100	N	[ 0 -1 -2 -1 0 1 0 -1 0 0 ]	6	0.6	[ ]		

### Appendix III, continued

Participant	Experience (Y/N)	Pulsed calls			Whistles		
		Deviation from mode	Sum abs values	Means	Deviation from mode	Sum abs values	Means
101	N	[ 0 0 0 0 1 0 0 0 0 -1 ]	2	0.2	[		
102	Y	[ 1 -1 0 0 1 0 1 0 0 0 ]	4	0.4	[		
103	N	[ 0 -1 -1 1 1 0 0 0 0 0 ]	4	0.4	[		
104	N	[ 0 -1 0 -1 0 0 -1 0 0 -1 ]	4	0.4	[		
105	N	[ 0 -1 -2 -1 0 0 0 0 0 -1 ]	5	0.5	[		
106	N	[ 0 1 0 0 1 0 2 0 2 0 ]	6	0.6	[		
107	N	[ 0 2 0 -1 0 0 1 0 1 -1 ]	6	0.6	[		
108	N	[ 0 -1 -1 -1 0 0 0 0 0 -1 ]	4	0.4	[		
109	N	[ 0 -1 -2 0 1 1 1 0 0 0 ]	6	0.6	[		
110	N	[ 0 0 -1 -1 0 0 0 0 0 0 ]	2	0.2	[		
111	Y	[ 1 -1 0 0 0 0 -1 0 1 1 ]	5	0.5	[		
112	Y	[ 0 0 0 0 1 0 0 0 0 1 ]	2	0.2	[		
113	Y	[ 0 0 0 0 1 2 0 0 0 2 ]	5	0.5	[		
114	N	[ 2 -1 -1 1 1 1 3 0 0 0 ]	10	1.0	[		
115	Y	[ 0 0 0 1 1 1 2 0 2 0 ]	7	0.7	[		
116	N	[ 0 0 -1 -1 0 1 1 0 2 1 ]	7	0.7	[		
117	N	[ 1 0 -1 0 1 2 1 0 1 0 ]	7	0.7	[		
118	N	[ 1 0 -1 0 0 2 1 0 1 0 ]	6	0.6	[		
119	Y	[ 0 -1 0 0 1 0 0 0 0 -1 ]	3	0.3	[		
120	Y	[ 1 0 0 0 0 0 0 0 1 0 ]	2	0.2	[		
121	N	[ 0 1 -1 1 1 1 1 0 0 -1 ]	7	0.7	[		
122	N	[ 0 -1 0 1 0 0 0 0 1 0 ]	3	0.3	[		
123	Y	[ 0 0 0 1 0 0 -1 0 2 0 ]	4	0.4	[		
124	N	[ 0 2 0 0 1 2 1 0 0 0 ]	6	0.6	[		
125	Y	[ 1 1 0 -1 1 0 0 1 0 ]	5	0.6	[		
126	N	[ 0 1 -1 0 0 0 0 0 0 0 ]	2	0.2	[		
127	N	[ 0 0 0 0 1 1 0 0 1 -1 ]	4	0.4	[		
128	Y	[ 0 -1 -1 0 0 -1 0 0 -1 ]	4	0.4	[		
129	Y	[ 0 2 0 -1 0 0 1 0 0 1 ]	5	0.5	[		
130	N	[ 1 1 0 1 2 2 0 0 0 -1 ]	8	0.8	[		
131	N	[ 1 1 0 1 2 2 0 0 0 -1 ]	8	0.8	[		
132	N	[ 0 0 -1 1 0 0 0 -1 0 -1 ]	4	0.4	[		
133	Y	[ 0 0 0 0 1 1 1 0 1 1 ]	5	0.5	[		
134	N	[ 0 1 0 2 2 1 1 0 0 1 ]	8	0.8	[		
135	Y	[ 0 0 -1 0 0 0 0 -1 0 -1 ]	3	0.3	[		
136	N	[ 0 -1 0 -1 0 0 0 0 0 -1 ]	3	0.3	[		
137	N	[ 0 -1 -1 -1 0 1 -1 0 0 -1 ]	6	0.6	[		
138	N	[ 0 0 -1 0 0 1 0 0 1 0 ]	3	0.3	[		
139	Y	[ 0 0 0 -1 0 1 0 0 0 1 ]	3	0.3	[		
140	N	[ 0 0 0 0 0 0 0 0 0 0 ]	0	0.0	[		
141	N	[ 0 0 0 -1 0 0 0 0 0 -1 ]	2	0.2	[		
142	N	[ 0 -1 -1 -1 0 1 -1 0 0 -1 ]	6	0.6	[		
143	N	[ 0 2 0 -1 1 3 2 0 1 2 ]	12	1.2	[		
144	Y	[ 0 0 -1 0 0 0 0 0 0 -1 ]	2	0.2	[		
145	N	[ 0 -1 -1 1 1 0 -1 0 0 -1 ]	6	0.6	[		
146	N	[ 0 0 -1 0 1 0 1 -1 0 -1 ]	5	0.5	[		
147	N	[ 0 -1 -1 0 0 0 0 0 0 0 ]	2	0.2	[		
148	N	[ 0 -1 -1 -1 1 0 -1 -1 0 -1 ]	7	0.7	[		
149	Y	[ 0 0 0 -1 0 0 0 0 0 -1 ]	2	0.2	[		
150	N	[ 0 1 0 0 0 1 2 0 0 -1 ]	5	0.5	[		
151	Y	[ 0 0 0 0 0 0 0 0 0 1 ]	1	0.1	[		
152	N	[			[ 2 2 -1 2 1 3 3 1 -2 -1 ]	18	1.8
153	N	[			[ 3 0 0 1 1 2 3 0 0 0 ]	10	1
154	N	[			[ 0 0 0 1 1 2 1 0 -3 -2 ]	10	1
155	N	[			[ 0 0 -1 0 -1 0 0 0 -1 0 ]	3	0.3
156	N	[			[ 0 0 0 1 -1 0 0 0 -3 0 ]	5	0.5
157	N	[			[ 0 0 -1 0 0 1 0 1 -1 0 ]	4	0.4
158	Y	[			[ 1 1 -1 0 -1 0 0 0 -2 -1 ]	7	0.7
159	Y	[			[ 1 1 -1 0 0 1 1 2 -1 0 ]	8	0.8
160	N	[			[ 1 0 1 0 0 0 0 -3 -1 ]	6	0.7

## Appendix III, continued

Participant	Experience (Y/N)	Pulsed calls			Whistles		
		Deviation from mode	Sum abs values	Means	Deviation from mode	Sum abs values	Means
161	N	[	]		[ 0 1 0 0 -2 0 0 0 -2 -2 ]	7	0.7
162	N	[	]		[ 0 0 -2 -1 -2 0 0 0 -2 -3 ]	10	1
163	N	[	]		[ 0 0 0 0 -1 0 1 0 -3 -2 ]	7	0.7
164	N	[	]		[ 1 1 -1 0 0 0 1 0 0 -1 ]	5	0.5
165	N	[	]		[ 2 1 0 0 -1 1 1 0 0 -1 ]	7	0.7
166	N	[	]		[ 2 1 0 0 -1 1 1 0 0 -1 ]	7	0.7
167	Y	[	]		[ 1 0 -1 0 0 0 0 1 -2 0 ]	5	0.5
168	N	[	]		[ 1 0 -1 0 -2 0 0 0 -1 -1 ]	6	0.6
169	N	[	]		[ 1 0 0 1 1 1 2 1 0 0 ]	7	0.7
170	N	[	]		[ 0 0 0 1 -1 0 0 0 -1 0 ]	3	0.3
171	N	[	]		[ 1 0 -1 0 0 0 0 0 -3 -1 ]	6	0.6
172	N	[	]		[ 1 0 -1 1 2 1 0 0 0 ]	6	0.7
173	N	[	]		[ 1 0 0 0 0 1 3 0 -2 0 ]	7	0.7
174	N	[	]		[ 1 1 0 0 -1 0 0 0 -2 -2 ]	7	0.7
175	Y	[	]		[ 1 0 -1 -1 -2 0 -1 0 0 -1 ]	7	0.7
176	N	[	]		[ 0 0 -1 0 -2 0 -1 0 -2 -2 ]	8	0.8
177	N	[	]		[ 1 0 0 0 0 1 2 0 -1 0 ]	5	0.5
178	N	[	]		[ 1 0 -1 0 0 0 0 0 0 -1 ]	3	0.3
179	N	[	]		[ 0 0 -1 0 0 0 2 0 -2 0 ]	5	0.5
180	N	[	]		[ 0 0 0 -1 -2 0 0 -1 0 ]	4	0.4
181	Y	[	]		[ 1 0 0 0 -2 0 1 0 0 0 ]	4	0.4
182	N	[	]		[ 0 1 -1 1 -1 2 -1 0 -1 0 ]	8	0.8
183	Y	[	]		[ 0 0 0 -1 0 0 0 0 -1 -2 ]	4	0.4
184	N	[	]		[ 0 1 -1 0 0 0 0 0 1 1 ]	4	0.4
185	Y	[	]		[ 2 1 -1 1 0 0 2 1 0 0 ]	8	0.8
186	N	[	]		[ 0 0 -1 0 -2 0 0 0 -2 -2 ]	7	0.7
187	N	[	]		[ 0 0 -1 -1 -1 0 0 0 -2 -1 ]	6	0.6
188	Y	[	]		[ 1 0 0 0 -1 0 -1 0 0 -1 ]	4	0.4
189	N	[	]		[ 1 1 -1 0 -1 0 0 0 0 -1 ]	5	0.5
190	N	[	]		[ 2 1 0 0 1 1 1 1 -1 0 ]	8	0.8
191	N	[	]		[ 0 0 0 -1 -2 1 0 0 -1 -2 ]	7	0.7
192	Y	[	]		[ 0 0 -1 0 -2 0 1 1 -3 -1 ]	9	0.9
193	N	[	]		[ 0 1 0 0 2 0 1 0 0 1 ]	5	0.5
194	N	[	]		[ 0 0 0 1 0 0 1 0 -3 -3 ]	8	0.8
195	N	[	]		[ 0 0 -1 0 1 0 2 0 -1 -2 ]	7	0.7
196	Y	[	]		[ 0 0 0 0 1 0 -1 0 0 -1 ]	3	0.3
197	N	[	]		[ 2 2 0 0 -1 0 2 1 0 1 ]	9	0.9
198	Y	[	]		[ 2 1 0 0 -1 0 1 1 -1 -1 ]	8	0.8
199	N	[	]		[ 2 1 0 1 1 0 2 0 0 0 ]	7	0.7
200	Y	[	]		[ 0 0 0 -1 0 0 2 0 0 -2 ]	5	0.5
201	N	[	]		[ 0 0 -1 0 0 1 1 0 0 -1 ]	4	0.4
202	N	[	]		[ 0 0 -1 0 -1 0 -1 0 -2 -1 ]	6	0.6
203	Y	[	]		[ 2 0 -1 1 0 0 0 0 0 -1 ]	5	0.5
204	Y	[	]		[ 0 0 0 0 0 0 -1 0 -1 0 ]	2	0.2
205	N	[	]		[ 0 0 0 0 -2 0 -1 0 -1 0 ]	4	0.4
206	Y	[	]		[ 0 0 0 0 1 2 1 1 0 0 ]	5	0.5
207	N	[	]		[ 0 0 0 -1 -1 0 0 0 -3 -3 ]	8	0.8
208	N	[	]		[ 0 0 -1 1 -1 1 -1 0 -3 0 ]	8	0.8
209	N	[	]		[ 0 0 0 1 -1 0 1 0 -1 -1 ]	5	0.5
210	N	[	]		[ 1 0 0 0 1 2 1 0 -1 0 ]	6	0.6
211	N	[	]		[ 1 0 0 0 -2 0 0 0 -1 -1 ]	5	0.5
212	Y	[	]		[ 0 0 0 0 -1 0 -1 0 0 -1 ]	3	0.3
213	N	[	]		[ 1 1 0 2 2 0 1 0 0 0 ]	7	0.7
214	N	[	]		[ 0 0 -1 -1 -2 0 0 0 -3 -2 ]	9	0.9
215	N	[	]		[ 0 0 -1 1 -1 0 1 0 0 0 ]	4	0.4

### Appendix III, continued

Participant	Experience (Y/N)	<i>Pulsed calls</i>			<i>Whistles</i>		
		Deviation from mode	Sum abs values	Means	Deviation from mode	Sum abs values	Means
216	N	[	]		[ 0 0 -1 0 -1 0 -1 0 -1 0 ]	4	0.4
217	N	[	]		[ 1 0 -1 -1 -2 0 -1 0 -3 -2 ]	11	1.1
218	Y	[	]		[ 2 0 0 1 1 0 0 0 0 -1 ]	5	0.5
219	N	[	]		[ 0 0 -1 -1 -1 1 0 0 -1 -2 ]	7	0.7
220	Y	[	]		[ 1 0 0 0 -1 1 1 0 -1 0 ]	5	0.5
221	Y	[	]		[ 1 0 0 0 -1 1 0 0 0 1 ]	4	0.4
222	N	[	]		[ 0 0 0 1 0 2 2 0 -2 0 ]	7	0.7
223	Y	[	]		[ 1 0 0 0 0 0 0 0 0 0 ]	1	0.1
224	N	[	]		[ 0 0 -1 -1 2 0 1 0 0 0 ]	5	0.5
225	Y	[	]		[ 1 0 -1 0 0 0 -1 0 1 -1 ]	5	0.5
226	Y	[	]		[ 1 0 0 -1 -1 0 0 1 -3 -2 ]	9	0.9
227	N	[	]		[ 0 0 0 0 1 0 0 0 -1 1 ]	3	0.3
228	Y	[	]		[ 1 0 -1 1 -2 0 1 0 0 -1 ]	7	0.7
229	N	[	]		[ 0 1 -1 1 0 0 0 0 -2 -1 ]	6	0.6
230	Y	[	]		[ 1 0 0 0 0 1 0 0 -2 -2 ]	6	0.6

## **APPENDIX IV – Unit membership based on key individuals and constant companions, Bayesian hierarchical mixture modeling and aggregative network modularity**

- (a) Key individuals and constant companion method  
(adapted from Ottensmeyer and Whitehead 2003)

<b>KIN unit ID</b>	<b>IDs of unit members</b>
A	59, 60, 80
B	139, 140, 142, 248, 254
C	120, 123, 243
D	28, 62, 65, 66
E	152, 263
F	261, 262
G	302

- (b) Bayesian hierarchical mixture model method  
(adapted from Jankowski 2005)

<b>BAY unit ID</b>	<b>IDs of unit members</b>
A	59, 60, 80
B	139, 140, 142, 248, 254
C	123, 243
F	260, 261, 262, 264, 265, 433, 507
H	330, 331
I	311, 312, 314, 407
J	400, 401
K	274, 480
L	76, 463
M	374, 508, 518, 570
N	82, 280, 510
O	234, 237, 346
P	270, 466, 473, 513, 543, 569, 600, 617
Q	540, 559
R	370, 372
S	324, 379, 380, 514
T	202, 537
U	489, 490, 495, 550

**Appendix IV, continued**

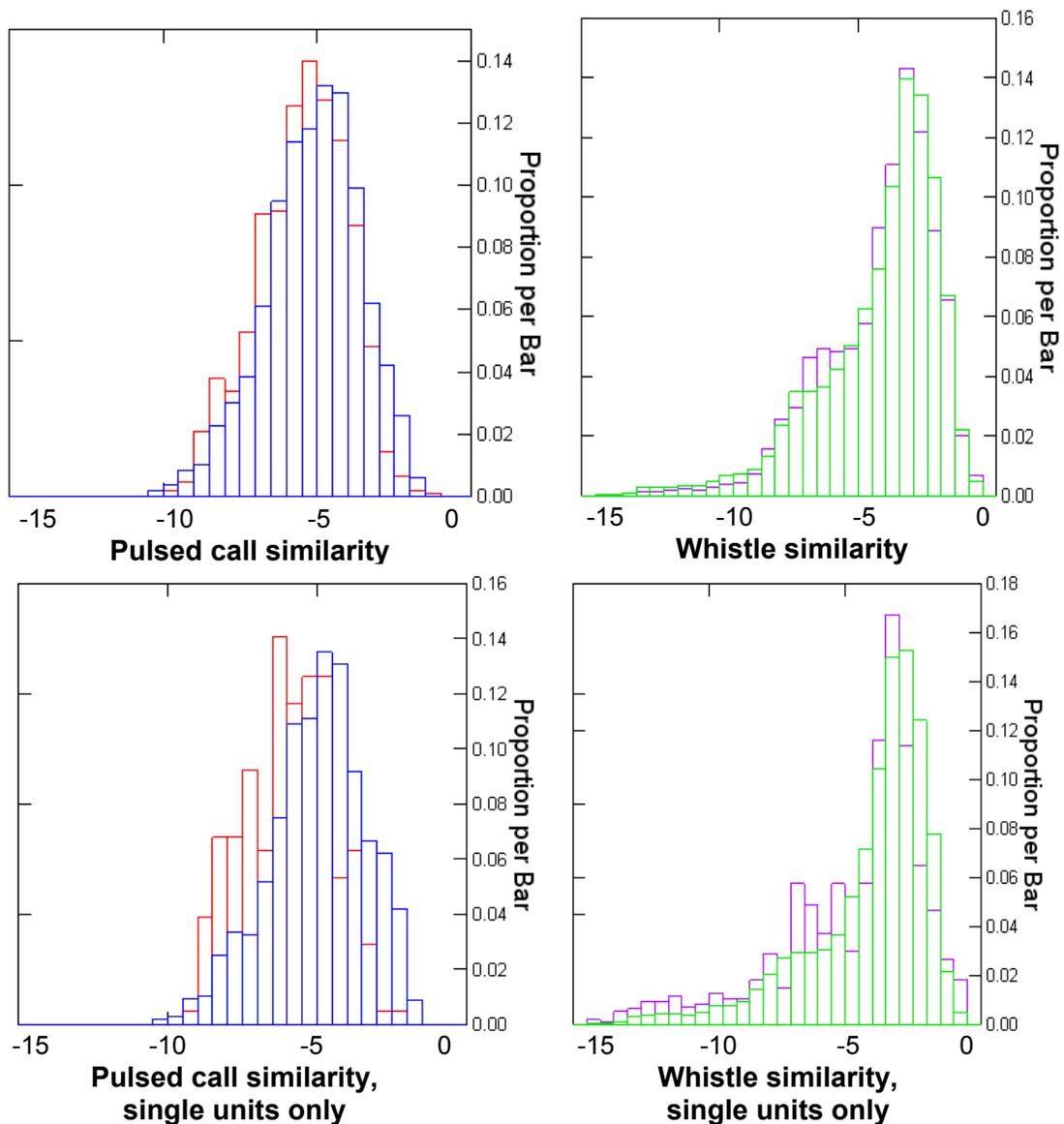
(c) Network modularity method (adapted from Lusseau, unpublished)

<b>unit ID</b>	<b>IDs of unit members</b>
A	205, 348, 362, 363, 451, 479, 482, 496, 530, 531, 555, 588, 660, 661, 662, 663, 677, 699, 701, 726, 781, 785, 804, 808, 903, 960, 1088, 1134
B	324, 367, 378, 379, 380, 415, 416, 514, 594, 615, 692, 769, 777, 783, 786, 789, 821
C	57, 59, 60, 80, 230, 252, 304, 317
D	300, 491, 493, 710, 827, 887, 889
E	160, 226, 260, 261, 273, 274, 276, 315, 339, 409, 429, 431, 475, 480, 488, 507, 545, 587, 610, 632, 633, 636, 638, 667, 678, 852, 861, 862, 896, 906, 1235
F	2, 28, 62, 64, 66, 74, 76, 111, 119, 120, 122, 123, 139, 142, 212, 233, 243, 254, 264, 277
G	449, 558, 619, 697, 871, 922, 923
H	281, 298, 358, 879, 881, 1064
I	251, 307, 374, 414, 455, 508, 510, 515, 516, 517, 518, 570, 595, 637, 698, 704, 733, 754, 766, 787, 795, 829, 1089
J	262, 279, 294, 296, 302, 310, 3100, 312, 314, 365, 407, 408, 424, 478, 497, 498, 500, 549, 580, 598, 599, 643, 700, 716, 717, 803, 831, 832, 1048, 1071
K	301, 308, 333, 334, 375, 673
L	329, 330, 331, 345, 494
M	288, 376, 377, 601, 602, 674, 863
N	228, 270, 383, 463, 466, 473, 483, 485, 486, 513, 543, 569, 600, 614, 617, 675, 679, 680, 752, 910, 1073, 1074
O	227, 645, 932, 944, 945, 999
P	35, 202, 204, 347, 461, 489, 490, 495, 533, 537, 550, 551, 575, 690, 703, 705, 707, 708, 718, 760, 788, 848, 886, 905, 1118
Q	65, 418, 538, 578, 934
R	1, 140, 203, 246, 248, 293, 368, 370, 372, 412, 476, 492, 505, 511, 527, 631, 737, 755, 756, 779, 833, 870, 1059, 1144
S	152, 263, 400, 401, 432, 433, 683, 684, 728, 740, 874, 992
T	44, 82, 216, 217, 239, 280, 521, 528, 666, 691, 719, 744, 745, 746, 860, 876, 885, 912, 918, 927, 1075
U	234, 237, 346, 520, 540, 541, 559, 720, 725, 893, 894, 998
V	26, 40, 711
W	52, 133, 240, 265, 291, 295, 316, 352, 357, 384, 402, 420, 506, 609, 668, 669, 670, 671, 672, 682, 857, 858, 1022, 1053

## APPENDIX V – Histograms illustrating the statistical similarity of calls from different encounters between and within social groups (as defined by the KIN and BAY methods)

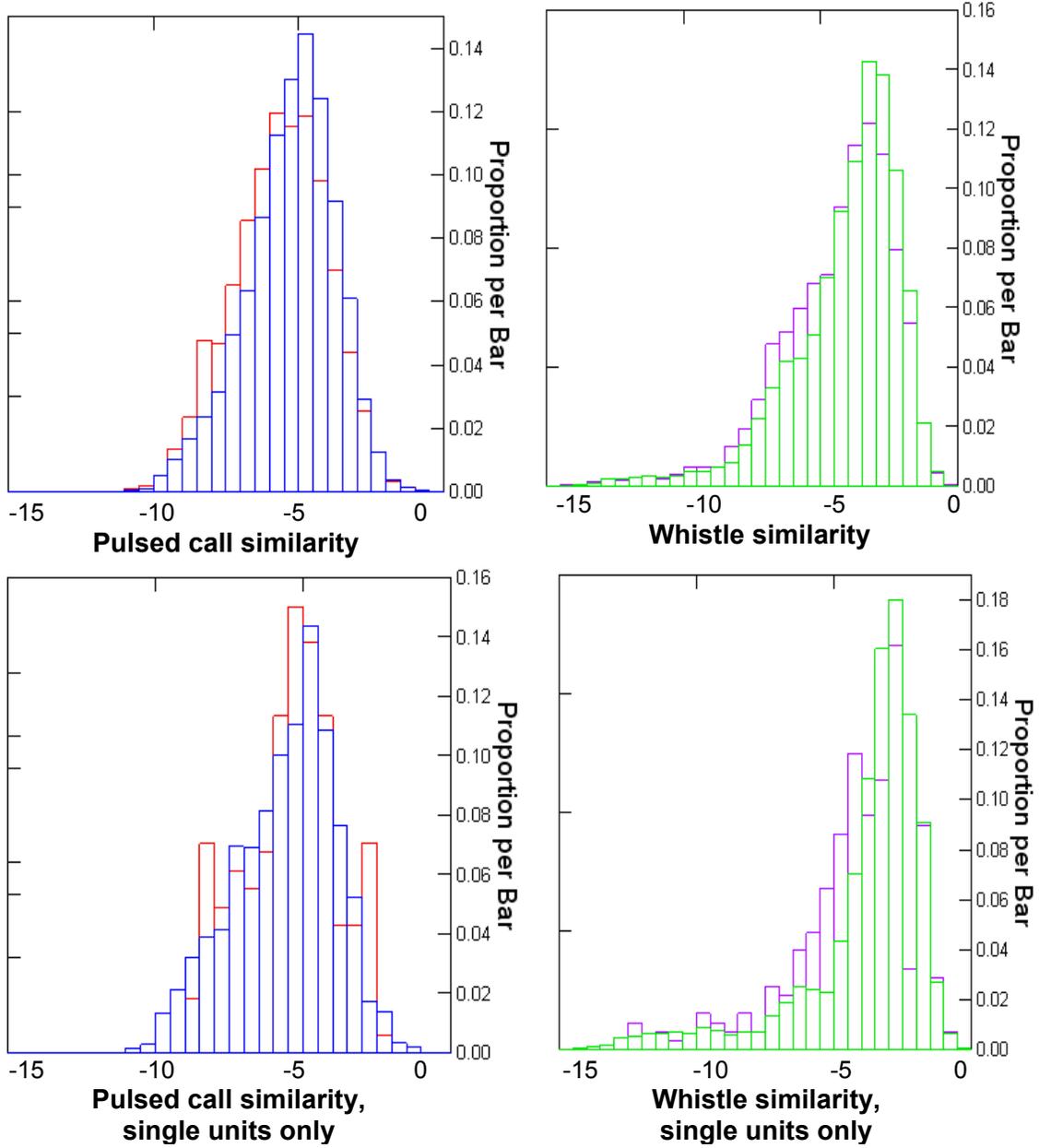
Corresponding histograms for the NET method are in Figure 4.2. Note that blue and green bars indicate the statistical measure of call similarity *between* groups, while red and purple bars indicate call similarity *within* groups.

*Key individuals and constant companions method (KIN):*



**Appendix V, continued**

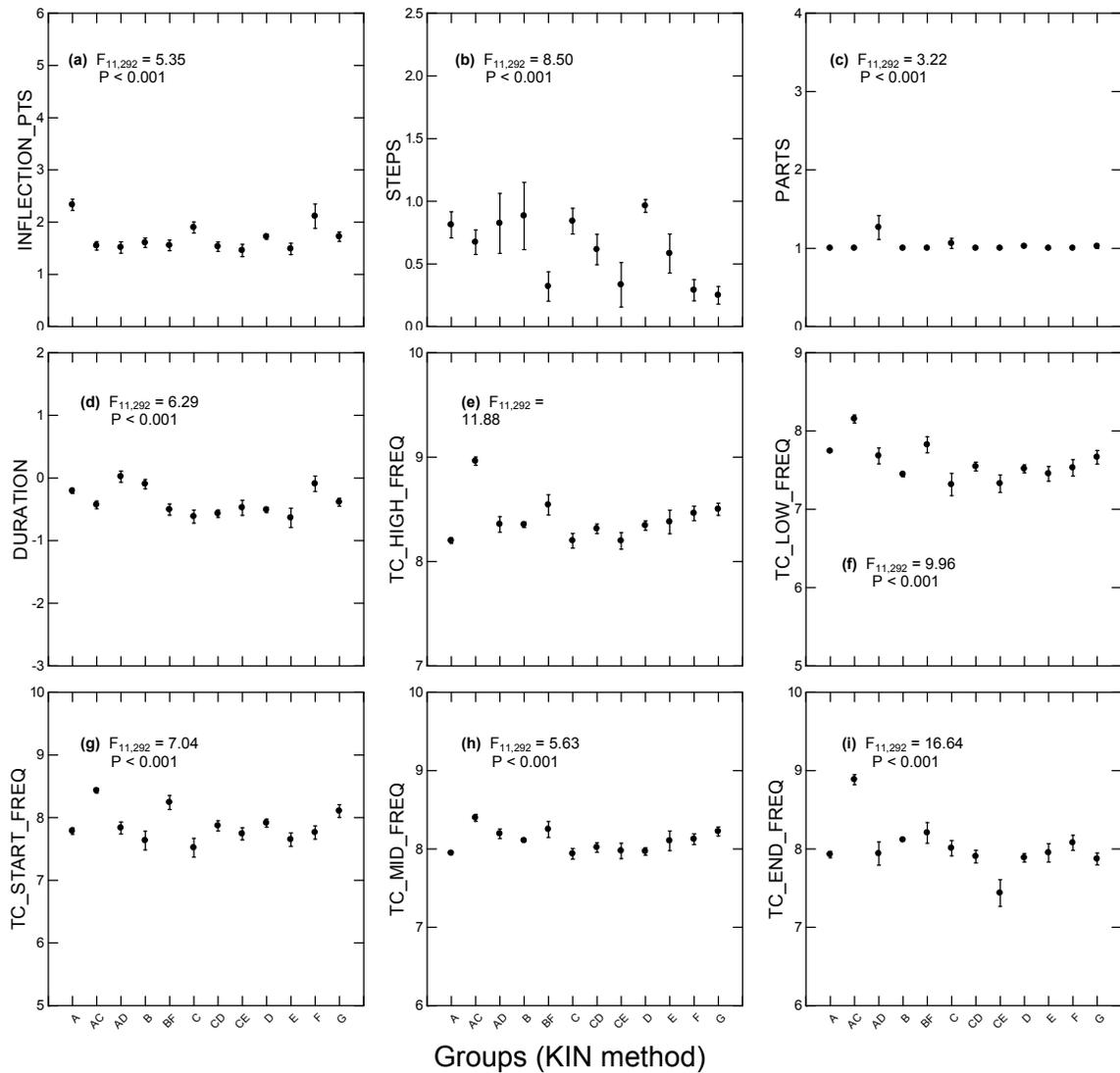
Bayesian hierarchical mixture model method (BAY):



**APPENDIX VI – Means of each whistle and pulsed call measurement variable ( $\pm 1$ SE) for mixed groups and single social units (from the KIN and BAY methods), with associated ANOVA  $F$ -statistics and significance values.**

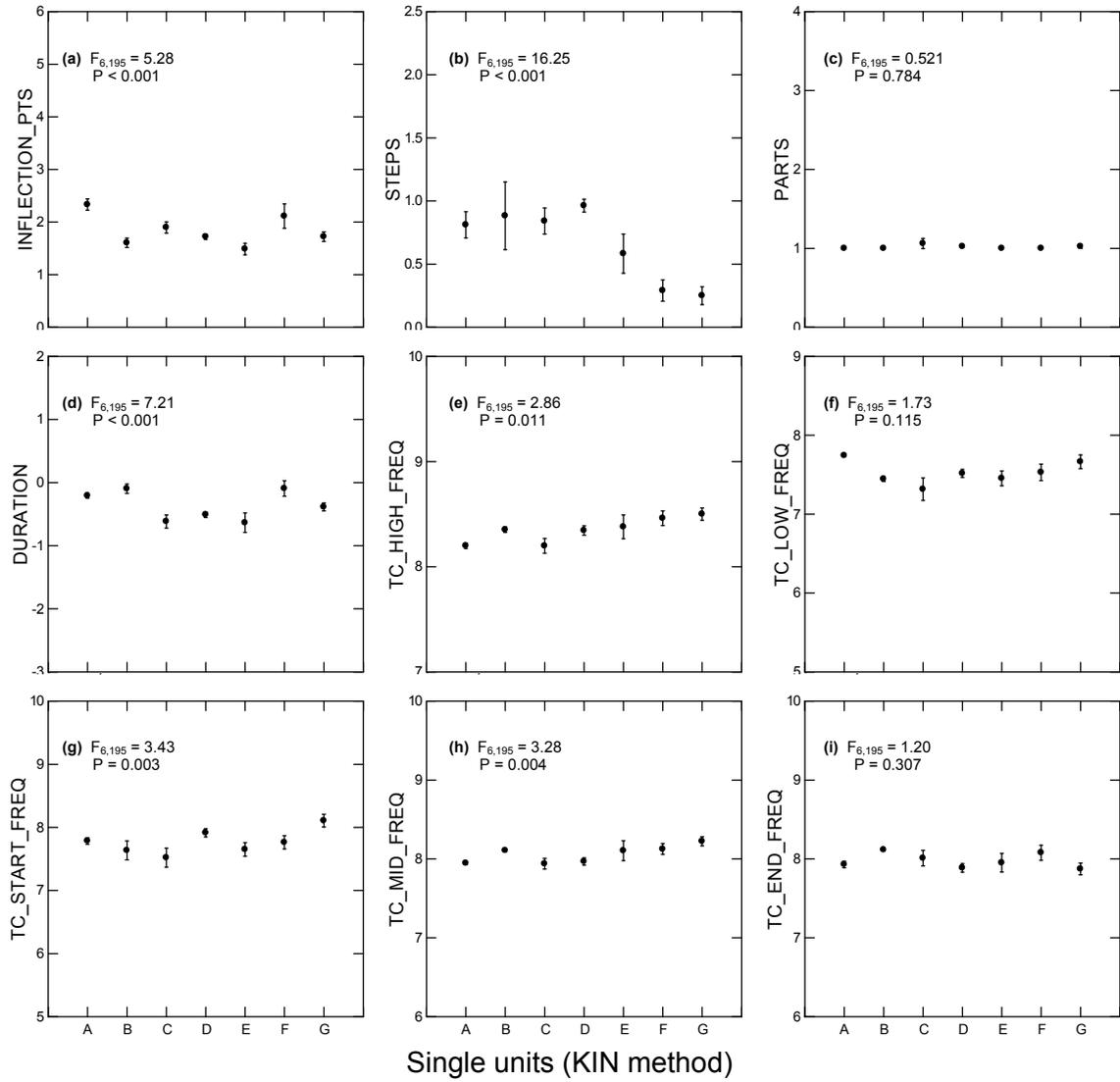
Corresponding graphs for the NET method are in Figures 4.3-4.6.

*Whistles*



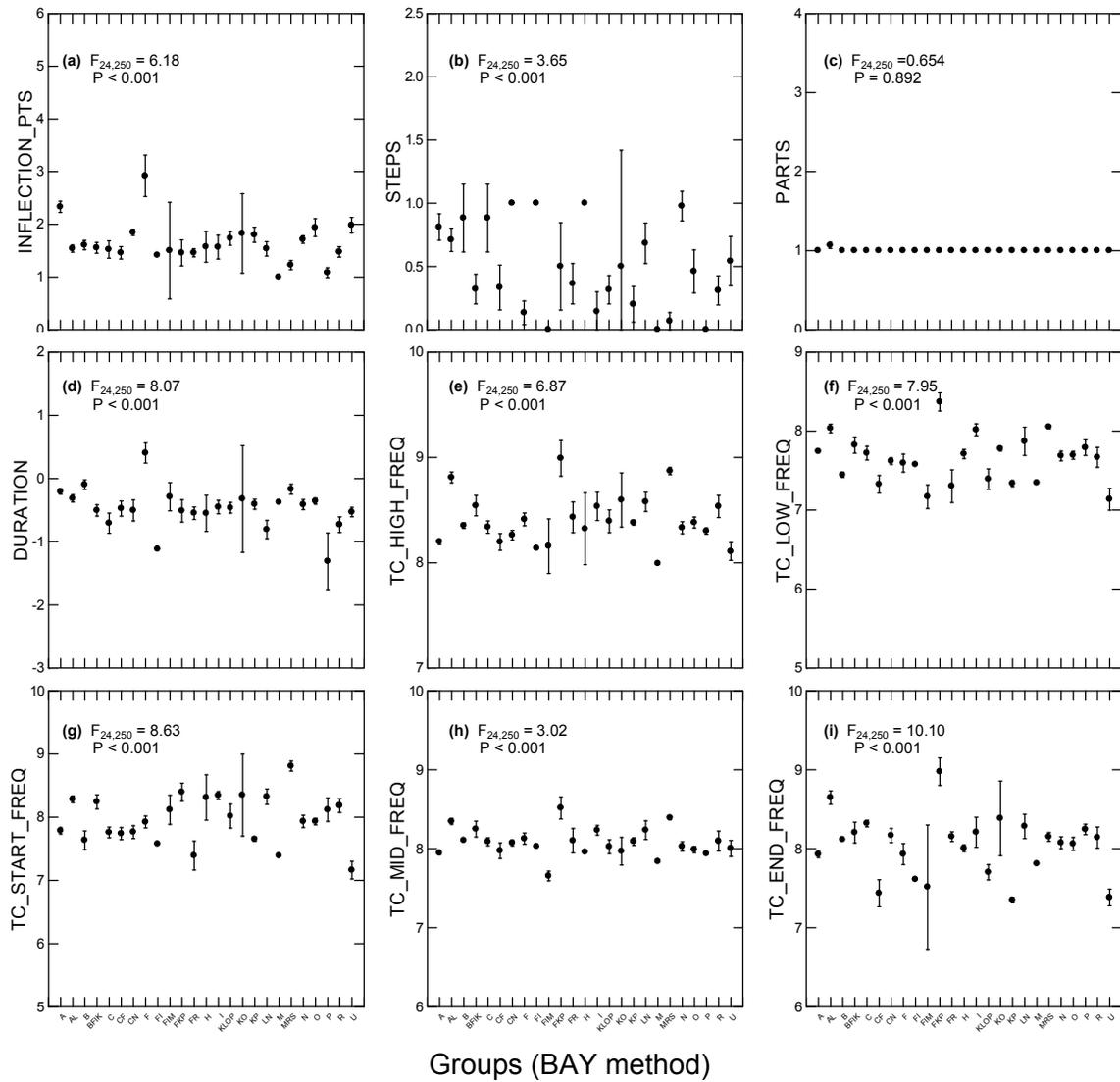
Appendix VI, continued

Whistles, continued



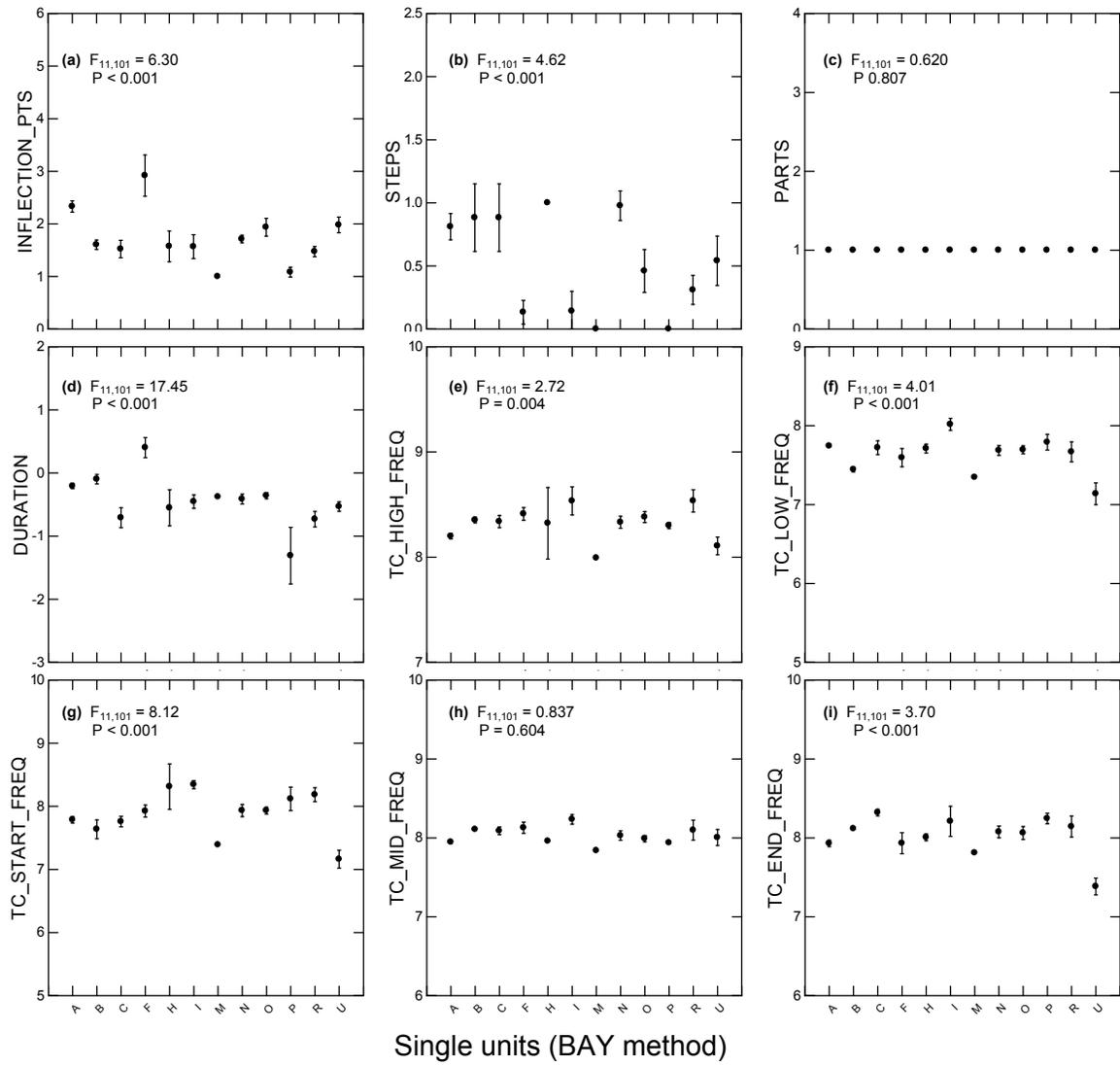
## Appendix VI, continued

### Whistles, continued



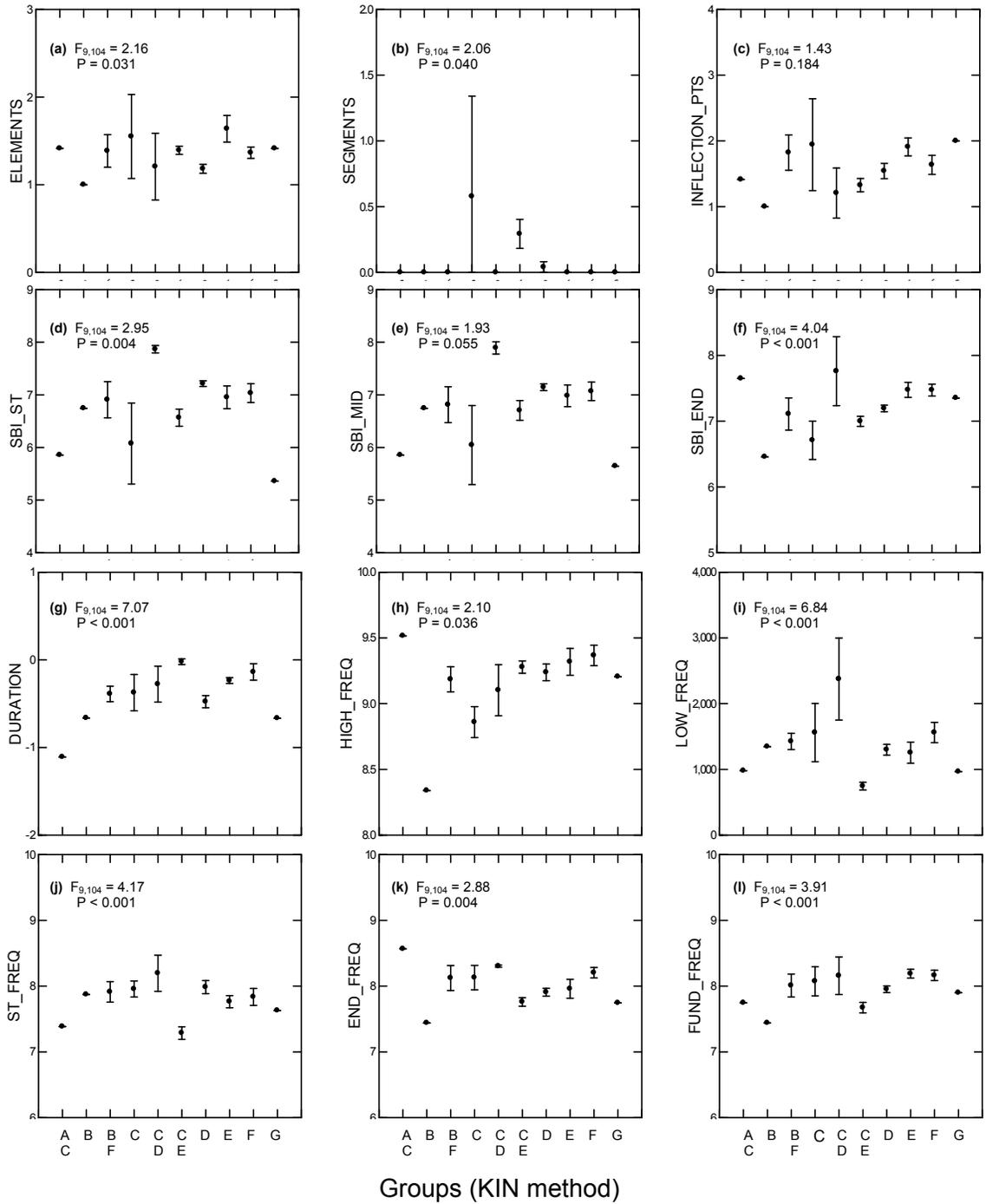
Appendix VI, continued

Whistles, continued



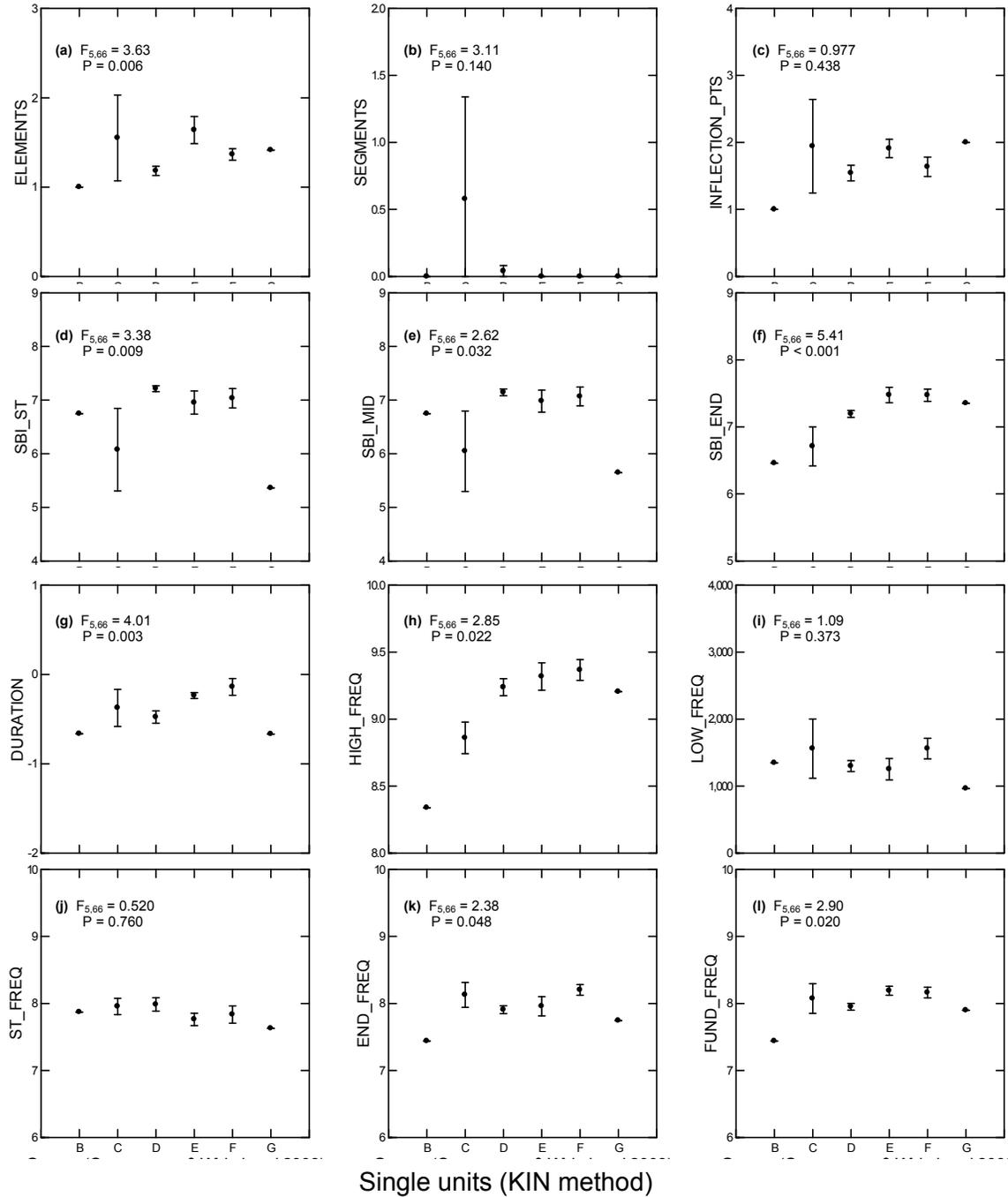
Appendix VI, continued

Pulsed calls



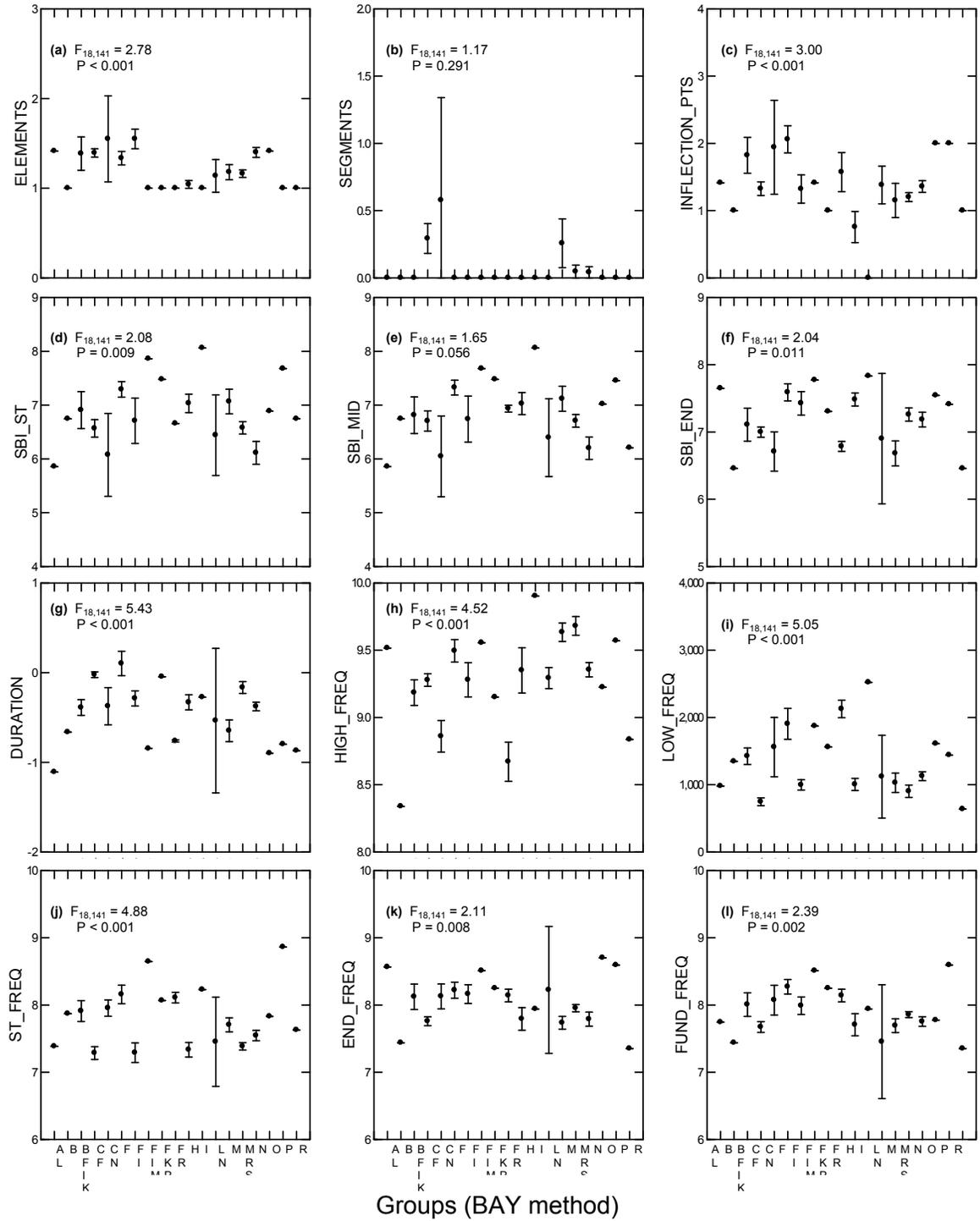
Appendix VI, continued

Pulsed calls, continued



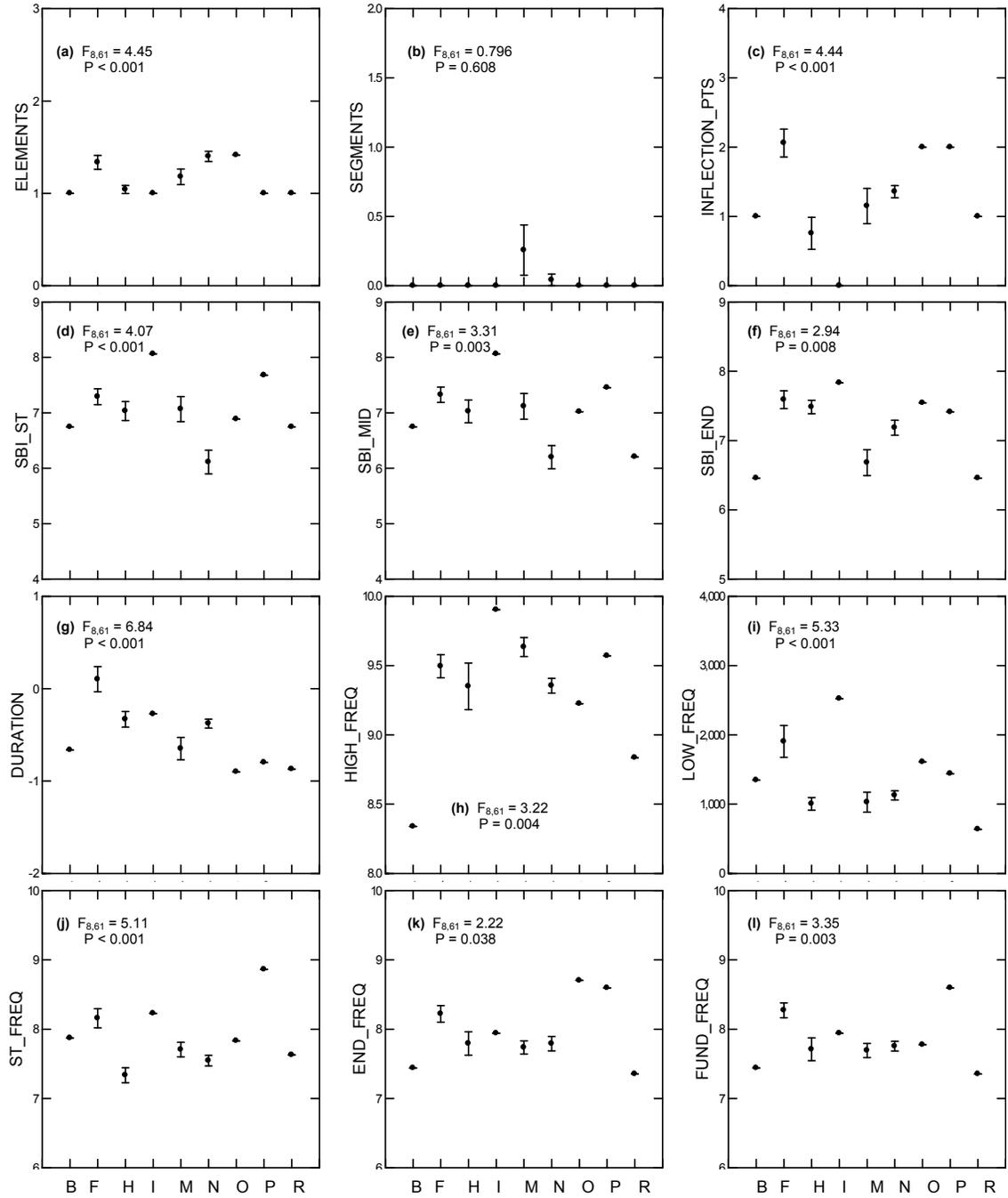
Appendix VI, continued

Pulsed calls, continued



Appendix VI, continued

Pulsed calls, continued

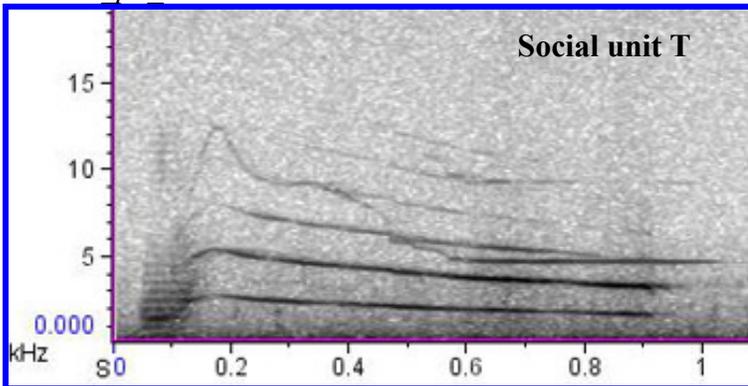


Single units (BAY method)

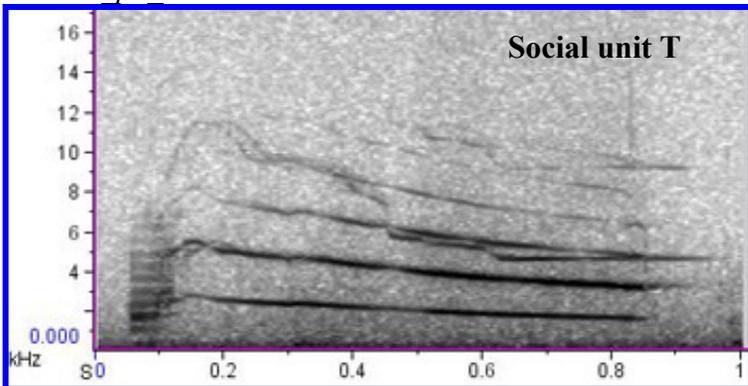
## APPENDIX VII – Spectrograms of every pulsed call included in the network depiction of pulsed call similarity (Figure 4.17)

Calls are from social unit T, social unit F, and social group FT (as defined by the NET method). The first 6 digits of each pulsed call name represent the encounter during which the call was recorded.

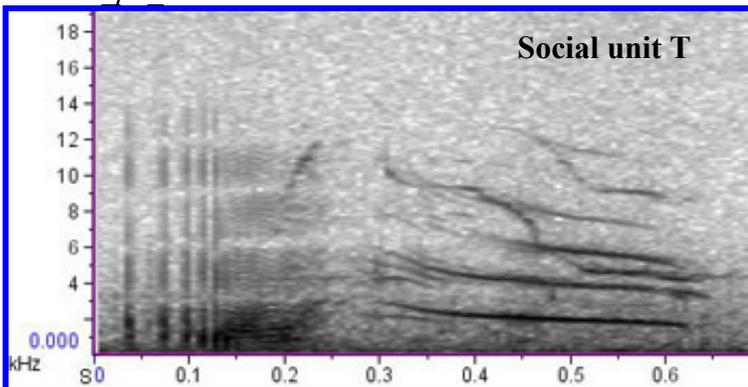
*BS0207 pc 1*



*BS0207 pc 2*

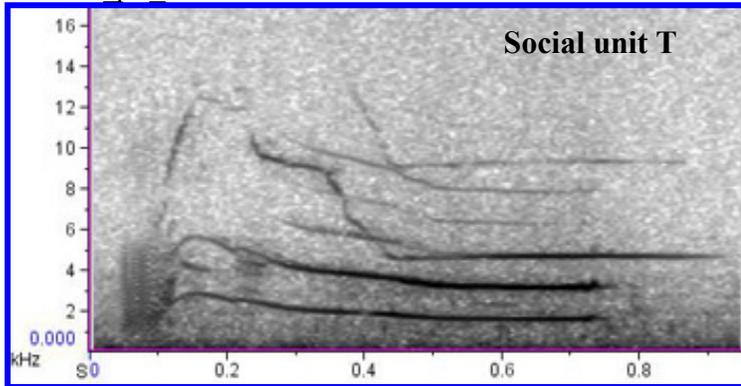


*BS0207 pc 3*

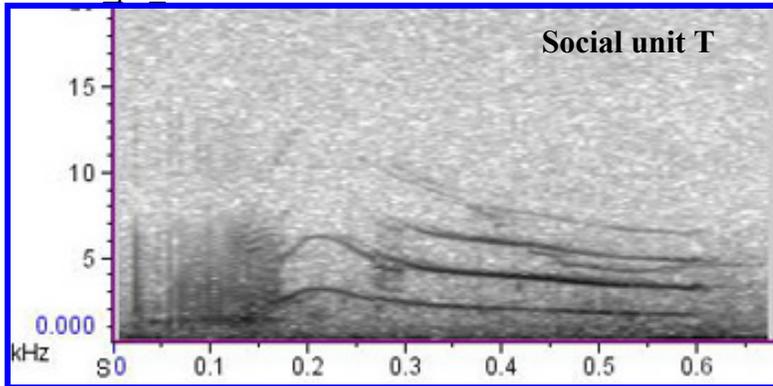


Appendix VII, continued

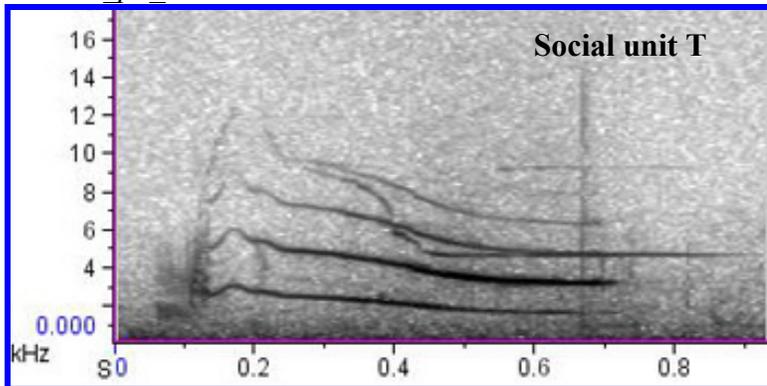
*BS0207 pc 5*



*BS0207 pc 10*

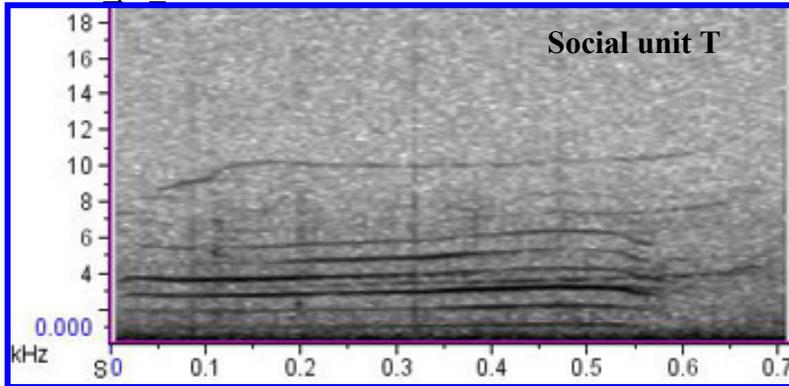


*BS0207 pc 13*

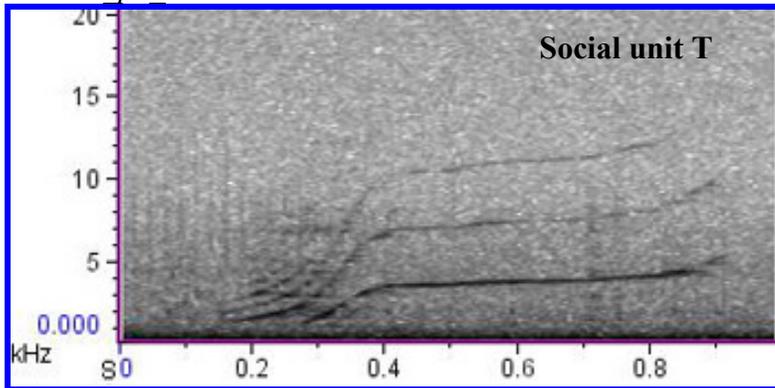


Appendix VII, continued

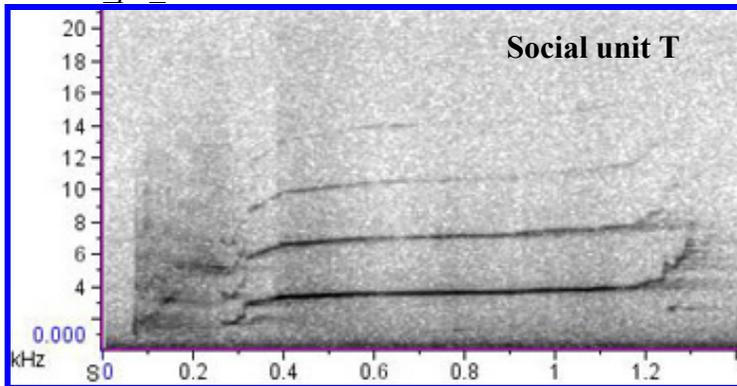
*BSI022 pc 7*



*BSI022 pc 9*

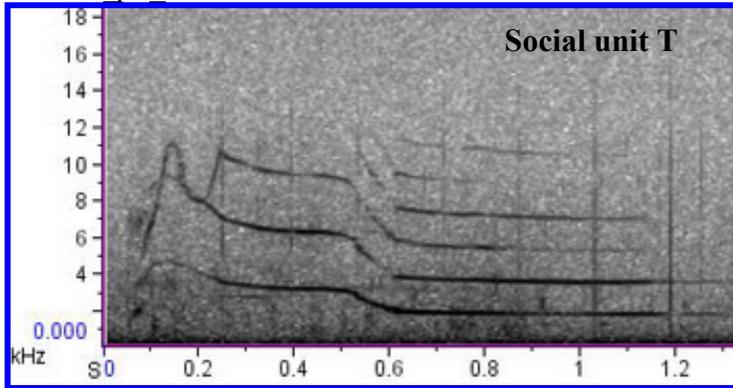


*BSI022 pc 14*

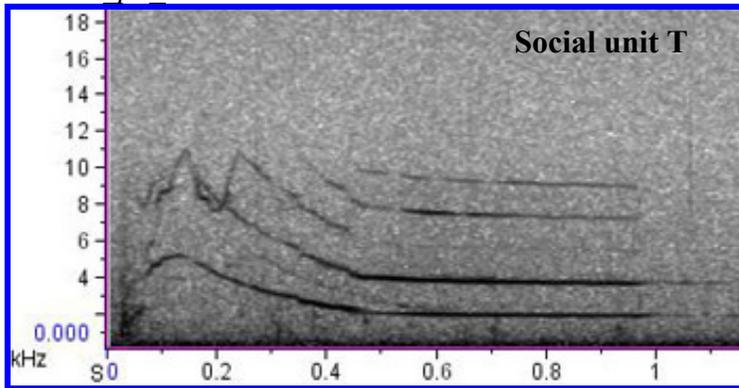


Appendix VII, continued

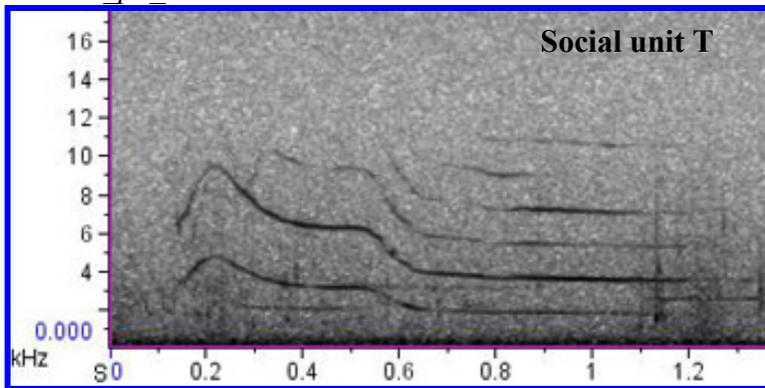
*BS2091 pc 18*



*BS2091 pc 22*

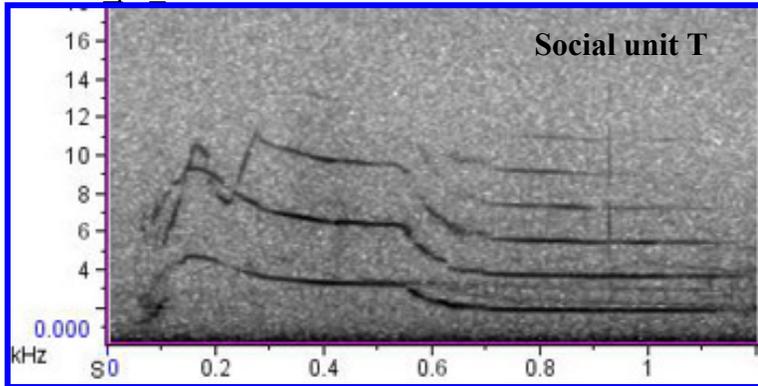


*BS2091 pc 27*

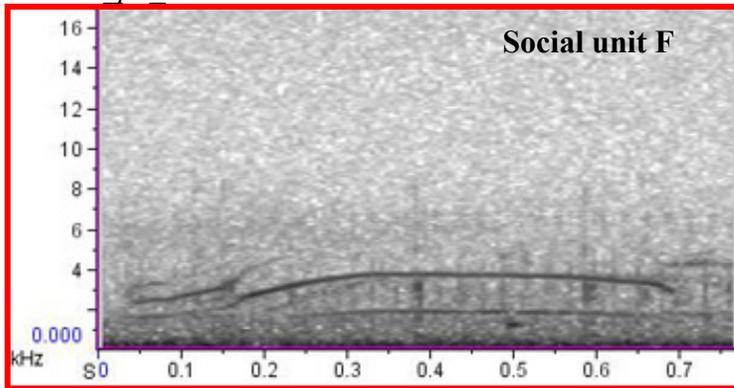


Appendix VII, continued

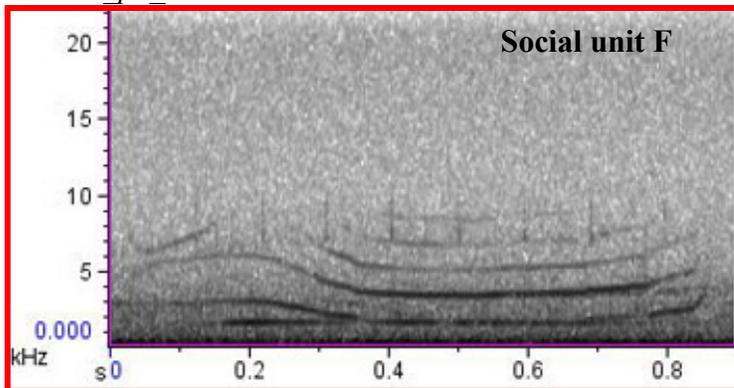
*BS2091 pc 170*



*BS0089 pc 1*

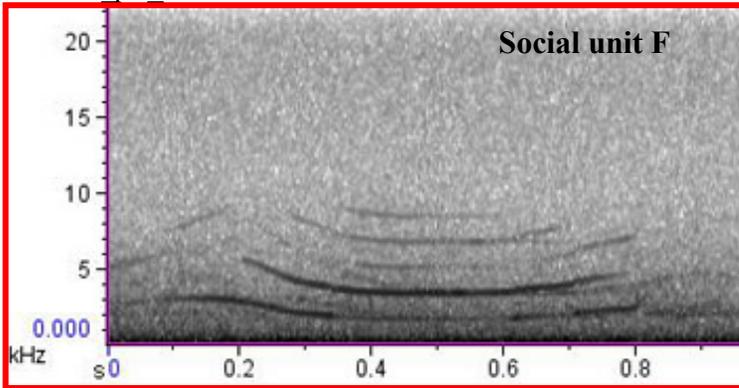


*BS0089 pc 32*

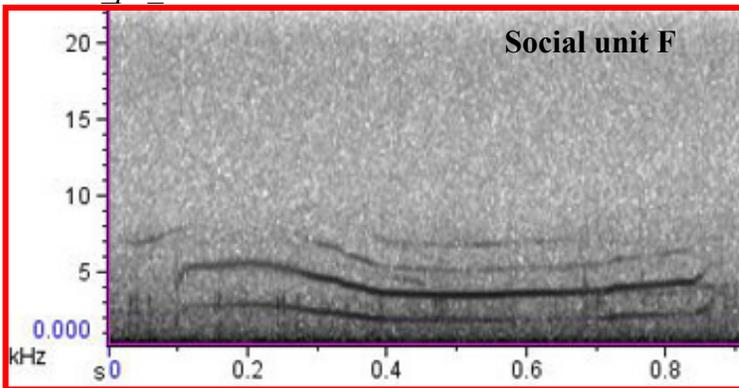


Appendix VII, continued

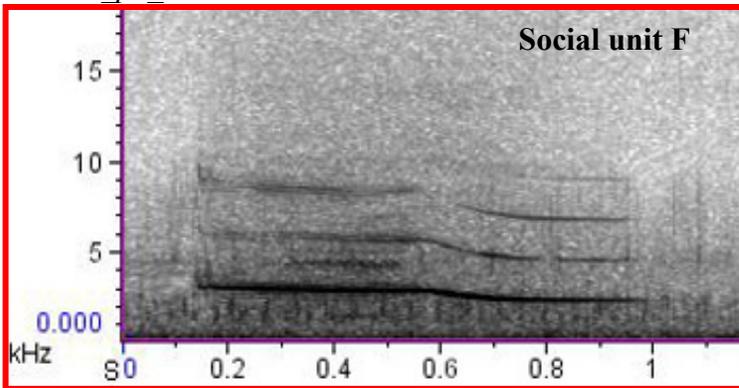
*BS0089 pc 39*



*BS0089 pc 310*

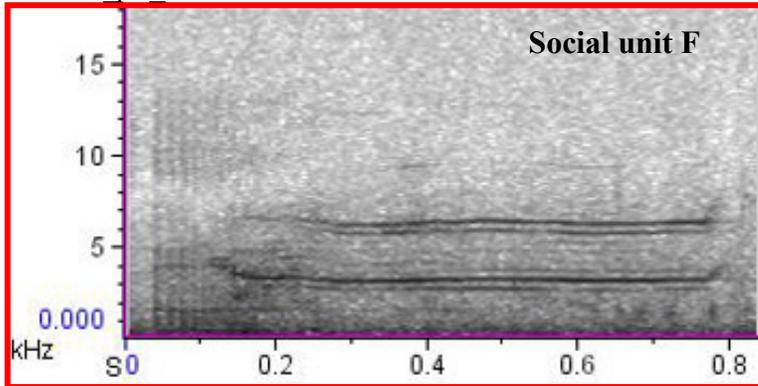


*BS1159 pc 1*

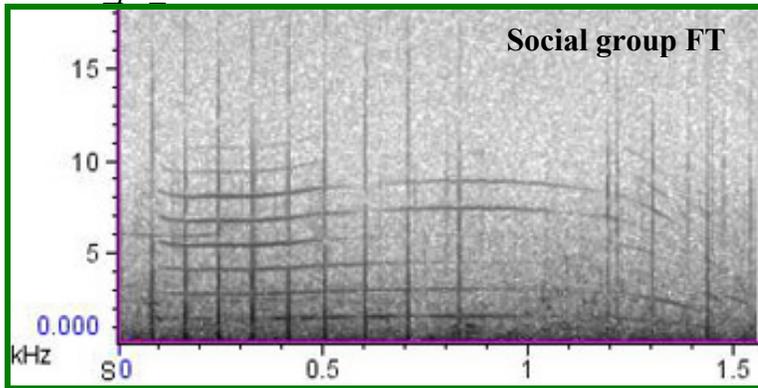


Appendix VII, continued

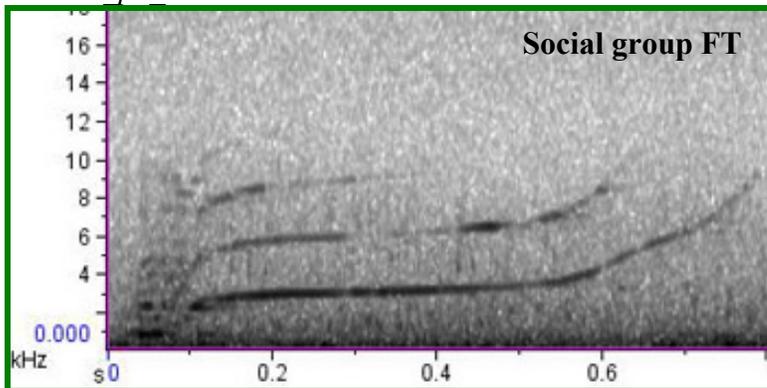
*BS1159 pc 2*



*BS0115 pc 12*



*BS0115 pc 30*



## LITERATURE CITED

- Abend, A. G. and Smith, T.D. (1997). Differences in stable isotope ratios of carbon and nitrogen between long-finned pilot whales (*Globicephala melas*) and their primary prey in the western north Atlantic. *ICES Journal of Marine Science*, 54: 500-503.
- Amos, B., Barrett, J. and Dover, G.A. (1991). Breeding behaviour of pilot whales revealed by DNA fingerprinting. *Heredity*, 67: 49-55.
- Amos, B., Bloch, D., Desportes, G., Majerus, T.M.O., Bancroft, D.R., Barrett, J.A. and Dover, G.A. (1993a). A review of molecular evidence relating to social organization and breeding system in the long-finned pilot whale. Report of the International Whaling Commission. Special Issue 14: 209-217.
- Amos, B., Schlotterer, C. and Tautz, D. (1993b). Social structure of pilot whales revealed by analytical DNA profiling. *Science*, 260 (5108): 670-672.
- Andersen, L.W. and Siegismund, H.R. (1994). Genetic evidence for migration of males between schools of the long-finned pilot whale *Globicephala melas*. *Marine Ecology Progress Series*, 105: 1-7.
- Araabi, B.N., Kehtarnavaz, N., McKinney, T., Hillman, G. and Würsig, B. (2000). A string matching computer-assisted system for dolphin photoidentification. *Annals of Biomedical Engineering*, 28: 1269-1279.
- Atchley, W.R. and Bryant, E.H. (1975). *Multivariate statistical methods, among-groups covariation*. California: Dowden, Hutchinson & Ross, 464pgs.
- Au, W.W.L. (2000). Hearing by whales and dolphins: an overview. In: *Hearing by Whales and Dolphins*. Edited by: Au, W.W.L., Popper, A.N. and Fay, R.R., New York: Springer-Verlag.
- Au, W.W.L., Carder, D.A., Penner, R.H. and Scronce, B.L. (1985). Demonstration of adaptation in beluga whale (*D. leucas*) echolocation signals. *Journal of the Acoustical Society of America*, 77: 726-730.
- Au, W.W.L., Ford, J.K.B., Horne, J.K. and Allman, K.A.N. (2003). Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*). *Journal of the Acoustical Society of America*, 115 (2): 901-909.
- Auger-Méthé, M. and Whitehead, H. (2007). The use of natural markings in the studies of long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science*, 23(1): 77-93.

- Bain, D.E. (1986). Acoustic behavior of *Orcinus*: sequences, periodicity, behavioral correlates and an automated technique for call classification. In: *Behavioral Biology of Killer Whales*. Edited by Kirkeveld, B.C. & Lockard, J.S., New York: Alan R. Liss, Inc., 335-371.
- Baker, M.C., Baker, E.M. and Baker, M.S.A. (2001). Island and island-like effects on vocal repertoire of singing honeyeaters. *Animal Behaviour*, 62: 767-774.
- Barrett-Lennard, L.G. (2000). Population structure and mating patterns of killer whales, *Orcinus orca*, as revealed by DNA analysis. Ph.D. thesis, Zoology, University of British Columbia.
- Bigg, M.A., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. (1990a). Feeding habits of the resident and transient forms of killer whale in British Columbia and Washington State. In: *Abstracts of the Third International Orca Symposium*, Victoria, BC.
- Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B. and Balcomb, K.C. (1990b). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission, Special Issue 12: 383-405.
- Bloch, D., Zachariassen, M., and Zachariassen, P. (1993a). Some external characters of the long-finned pilot whale off the Faroe Islands and a comparison with the short-finned pilot whale. Report of the International Whaling Commission. Special Issue 14: 117-135.
- Bloch, D., Lockyer, C., and Zachariassen, M. (1993b). Age and growth parameters of the long-finned pilot whale off the Faroe Islands. Report of the International Whaling Commission. Special Issue 14: 163-207.
- Bloch, D., Desportes, G., Mouritsen, R., Skaaning, S. and Stefansson, E. (1993c). An introduction to studies of the ecology and status of the long-finned pilot whale (*Globicephala melas*) off the Faroe Islands, 1986-1988. Report of the International Whaling Commission. Special Issue 14: 1-32.
- Boinski, S. and Mitchell, C.L. (1992). The ecological and social factors affecting adult female squirrel monkey vocal behavior. *Ethology*, 92: 316-330.
- Boinski, S. and Mitchell, C.L. (1997). Chuck vocalizations of wild female squirrel monkeys (*Saimiri sciureus*) contain information on caller identity and foraging activity. *International Journal of Primatology*, 18(6): 975-993.
- Borgatti, S.P. (2002). *Netdraw Network Visualization*. Harvard, Massachusetts: Analytic Technologies.

- Boughman, J.W. (1997). Greater spear-nosed bats give group-distinctive calls. *Behavioral Ecology and Sociobiology*, 40(1): 61-70.
- Bowles, A.E., Smoltea, M., Würsig, B., Demaster, D.P. and Palka, D. (1994). Relative abundance and behavior of marine mammals exposed to transmission from the Heard Island feasibility test. *Journal of the Acoustical Society of America*, 96: 2469-2480.
- Bradbury, J.W. and Vehrencamp, S.L. (1998). *Principles of Animal Communication*. Massachusetts: Sinauer Associates Inc.
- Bridge, P.D. (1993). Classification. In: *Biological Data Analysis*. (Edited by: Fry, J.C.), Oxford: Oxford University Press, 219-242.
- Brown, C.H. (1982). Auditory localization and primate vocal behavior. In: *Primate Communication*. Edited by Snowdon, C.T., Brown, C.H., Petersen, M.R. Cambridge University Press: Cambridge, 144-163.
- Brown, C.H. and Cannito, M.P. (1995). Modes of vocal variation in sykes's monkey (*Cercopithecus albogularis*) squeals. *Journal of the Optical Society of America A*, 109: 398-415.
- Brown, J.C., Hodgins-Davis, A. and Miller, P.J.O. (2006). Classification of vocalizations of killer whales using dynamic time warping. *Journal of the Acoustical Society of America*, 119(3): 34-40.
- Buckland, S.T., Bloch, D., Cattanach, K.L., Gunnlaugsson, Th., Hoydal, K., Lens, S. and Sigurjónsson, J. (1993). Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Report of the International Whaling Commission. Special Issue 14: 33-49.
- Busnel, R.H. and Dziedzic, A. (1966). Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoise *delphinus delphis* and *Phocoena phocoena*. In: *Whales, Dolphins and Porpoises*. Edited by: Norris, K.S., Berkeley: University of California Press, 608-648.
- Busnel, R.G., Escudie, B., Dziedzic, A., and Hellion, A. (1971). Structure des clics doubles d'écholocation du *globicephale* (Cetace odontocete). *Comptes rendus de l'Académie des sciences*. 272: 2459-2461.
- Caldwell, M.C, Caldwell, D.K. and Tyack, P.L. (1990). Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin. In: *The Bottlenose Dolphin*. Edited by: Letherwood, S. and Reeves, R.R., San Diego: Academic.
- Cetacean Specialist Group (1996). *Globicephala melas*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species: [www.iucnredlist.org](http://www.iucnredlist.org). Accessed on August 28, 2008.

- Clark, C.W., Marler, P. and Beeman, B. (1987). Qualitative analysis of animal vocal phonology and application to swamp sparrow song. *Ethology*, 76: 101-115.
- Compton, L.A., Clarke, J.A., Seidensticker, K. and Ingrisano, D.R. (2001). Acoustic characteristics of white-nosed coati vocalizations: a test of motivation-structural rules. *Journal of Mammology*, 92(4): 1054-1058
- Connor, R.C., Mann, J., Tyack, P.L., and Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology and Evolution*, 13 (6): 228-232.
- Corkeron, P.J. and Van Parijs, S.M. (2000). Vocalizations of eastern Australian Risso's dolphins, *Grampus griseus*. *Canadian Journal of Zoology*, 79: 160-164.
- COSEWIC (2008). Long-finned pilot whale status. In: *Committee on the Status of Endangered Wildlife in Canada*: <http://www.cosewic.gc.ca>. Accessed on August 28, 2008.
- Cranford, T.W. (2000). In search of impulse sound sources in odontocetes. In: *Hearing by Whales and Dolphins*. Edited by: Au, W.W.L., Popper, A.N. and Fay, R.R., New York: Springer-Verlag, 109-155.
- Cranford, T.W., Amundin, M., and Norris, K.S. (1996). Functional morphology and homology in the Odontocete nasal complex: implications for sound generation. *Journal of Morphology*, 228:223-285.
- Cranford, T.W., Elsberry, W.R., van Bonn, W.G., Carr, J.A., Blackwood, D.J., Carder, D.A., Kamolnick, T., Todd, M., Decker, E.C., Bozliniski, D.M. and Ridgway, S.H. (2001). Two independent sonar signal generators in the bottlenose dolphin: Implications of morphologic and physiologic evidence. *Journal of Morphology*, 248: 219-220.
- Crockford, C., Herbinger, I., Vigilant, L. and Boesch, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, 110: 221-243.
- Dawson, S.M. (1991). Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology*, 88: 265-276.
- de Stephanis, R., García-Tiscar, S., Verborgh, P., Esteban-Pavo, R., Pérez, S., Minvielle-Sebastia, L., and Guinet, C. (2008). Diet of the social groups of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Marine Biology*, 154(4): 603-612.
- Deecke, V.B., Ford, J.K.B. and Spong, P. (1999). Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *Journal of the Acoustical Society of America*, 105: 2499-2507.

- Deecke, V.B., Ford, J.K.B. and Spong, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour*, 60: 629-638.
- Desportes, G. and Mouritsen, R. (1993). Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission. Special Issue 14: 305-324.
- Desportes, G., Saboureau, M., and Lacroix, A. (1993). Reproductive maturity and seasonality of male long-finned pilot whales, off the Faroe Islands. Report of the International Whaling Commission. Special Issue 14: 233-262.
- Ding, W., Würsig, B. and Evans, W.E. (1995). Comparisons of whistles among seven odontocete species. In *Sensory Systems of Aquatic Mammals*. Edited by: Kastelein, R.A. and Thomas, J.A., De Spil Publishers: Woerden, Netherlands.
- Dormer, K.J. (1979). Mechanism of sound production and air recycling in delphinids: Cineradiographic evidence. *The Journal of the Acoustical Society of America*, 65(1): 229-239.
- Dunbar, R. (1999). Culture, honesty and the freerider problem. In: *The Evolution of Culture*. Rutgers University Press: New Brunswick, NJ.
- Durbin, J. and Watson, G.S. (1951). Testing for serial correlation in least squares regression. II. *Biometrika*, 38: 159-177.
- Dusenbery, D.B. (1992). *Sensory Ecology*. W.H. Freeman: New York.
- Eberhardt, L. S. (1994). Oxygen consumption during singing by male Carolina wrens (*Thyrothorus ludovicianus*). *Auk*, 111: 124-130.
- Evans, P.G.H. (1998). Biology of cetaceans of the north-east Atlantic. In: *Relation to seismic energy*. The Proceedings of the Seismic and Marine Mammals Workshop, Edited by Tasker, M.L. and Weir, C., London, 23-25 June 1998.
- Everitt, B. S., Landau, S., and Leese, M. (2001). *Cluster Analysis*, Oxford University Press: London.
- Filatova, O.A., Fedutin, I.D., Burdin, A.M. and Hoyt, E. (2007). The structure of the discrete call repertoire of killer whales *Orcinus orca* from southeast Kamchatka. *Bioacoustics*, 16: 261-280.
- Fitch, W.T. (2004). Evolving Honest Communication Systems: Kin Selection and “Mother Tongues” In: *The Evolution of Communication Systems: A Comparative Approach*. Edited by Oller, D.K. and Griebel, U., MIT Press: Cambridge.

- Fitch, W.T. and Hauser, M.D. (2003). Unpacking “Honesty”: Vertebrate Vocal Production and the Evolution of Acoustic Signals. In: *Acoustic Communication*. Edited by: Simmons, A.M., Fay, R. and Popper, A.N., Springer: New York, 65-137.
- Fletcher, N.H. (1992). *Acoustic Systems in Biology*. Oxford University Press: Oxford, UK.
- Ford, J.K.B. (1984). Call traditions and dialects of killer whales (*Orcinus orca*) in British Columbia. Ph.D. thesis, Zoology, University of British Columbia.
- Ford, J.K.B. (1987). A catalogue of underwater calls produced by killer whales (*Orcinus orca*) in British Columbia. Canadian Data Report of Fisheries and Aquatic Sciences, 633: 165pgs.
- Ford, J.K.B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology, 67: 727-745.
- Ford, J.K.B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology, 69: 1454-1483.
- Ford, J.K.B. and Fisher, H.D. (1978). Underwater acoustic signals of the narwhal (*Monodon monoceros*). Canadian Journal of Zoology, 56: 552-560.
- Ford, J.K.B. and Fisher, H.D. (1983). Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In: *Communication and Behavior of Whales*. Edited by Payne, R., Westview Press: Boulder, Colorado, 129-161.
- Fullard, K.J. (2000). Microsatellite analysis of long-finned pilot whales. Ph.D. thesis, Department of Zoology, Cambridge University, Cambridge, UK.
- Fullard K.J., Early, G., Heide-Jorgensen, M.P., Bloch, D., Rosing-Asvid, A. and Amos, W. (2000). Population structure of long-finned pilot whales in the North Atlantic: A correlation with sea surface temperature? *Molecular Ecology*, 9(7): 949-958.
- Gelman, A., Carling, J.B., Stern, H.S. and Rubin, D.B. (2004). *Bayesian Data Analysis*. Chapman and Hall: New York.
- Gerhardt, H.C. (1994). The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics*, 25: 293-324.
- Gupta, R.D. and Richards, D.S.P. (1997). Multivariate Liouville distributions, V. In: *Advances in the theory & practice of statistics: a volume in honor of Samuel Kotz*. Edited by: Johnson, N.L. and Balakrishnan, K., John Wiley and Sons Inc: New York, 377-396.

- Hay, K. (1982). Aerial line-transect estimates of abundance of humpback, fin, and long-finned pilot whales in the Newfoundland-Labrador area. Report of the International Whaling Commission, 32: 475-486.
- Hebets, E.A. and Papaj, D.R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, 57: 197-214.
- Hillman, G.R., Würsig, B., Gailey, G.A., Kehtarnavaz, N., Drobyshevsky, A., Araabi, B.N., Tagare, H.D. and Weller, D.W. (2003). Computer-assisted photo-identification of individual marine vertebrates: a multi-species system. *Aquatic Mammals*, 29: 117-123.
- Hinton, G.E. (1992). How neural networks learn from experience. *Scientific American*, 268: 145-151.
- Hoelzel, A.R. and Osborne, R.W. (1986). Killer whale call characteristics: Implications for cooperative foraging strategies. In: *Behavioral Biology of Killer Whales*. Edited by Lockard, J.S., Alan R. Liss, Inc.: New York, 373-403.
- Hooker, S.K., Baird, R.W. and Showell, M.A. (1997). Cetacean strandings and bycatches in Nova Scotia, Eastern Canada, 1991-1996. IWC Document SC/49/05, 9 pgs.
- Horn, A.G. and Falls, J.B. (1996). Categorization and the design of signals: The case of song repertoires. In: *Ecology and Evolution of Acoustic Communication in Birds*. Edited by Kroodsma, D.E. and Miller, E.H., Cornell University Press: Ithaca and London, 121-135.
- Horn, A.G., Leonard, M.L. and Weary, D.M. (1995). Oxygen consumption during crowing by roosters: talk is cheap. *Animal Behavior*, 50: 1171-1175.
- Janik, V. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behaviour*, 57: 133-143.
- Janik, V. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*, 289: 1355-1357.
- Janik, V.M. and Slater, P.J.B. (1997). Vocal learning in mammals. *Advances in the Study of Behavior*, 26: 59-99.
- Janik, V.M. and Slater, P.J.B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behavior*, 56: 829-838.
- Janik, V.M. and Slater, P.J.B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, 60: 1-11.

- Jankowski, M. (2005). Long-finned pilot whale movement and social structure: residency, population mixing and identification of social units. M.Sc. thesis, Biology, Dalhousie University, 124 pgs.
- Johnson, S.C. (1967). Hierarchical clustering schemes. *Psychometrika*, 32(3): 241-254.
- Johnstone, R.A. (1995). Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Review*, 70: 1-65.
- Jolliffe, I.T. (2002). *Principal Component Analysis*. Springer: New York.
- Jones, A.E., Ten Cate, C. and Bijleveld, C.J.H. (2001). The interobserver reliability of scoring sonagrams by eye: a study on methods, illustrated on zebra finch songs. *Animal Behaviour*, 62: 791-801.
- Jürgens, U. (1988). Central control of monkey calls. In: *Primate Vocal Communication*. Edited by Todt, D., Goedeke, P. and Symmes, D., Springer-Verlag: Berlin, 50-62.
- Karlsen, J.D., Bisther, A., Lydersen, C., Haug, T., and Kovacs, K.M. (2002). Summer vocalizations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Polar Biology*, 25: 808-817.
- Katz, D. (1950). *Gestalt Psychology, its Nature and Significance*. Ronald Press: New York.
- Kellogg, W.N., Kohler, R. and Morris, H.N. (1953). Porpoise sounds as sonar signals. *Science*, 117: 239-243.
- Ketten, D.R. (2000). Cetacean ears. In: *Hearing by Whales and Dolphins*. Edited by: Au, W.W.L., Popper, A.N. and Fay, R.R., Springer-Verlag: New York, 43-108.
- King, B.J. and Shanker, S.G. (2003). How can we know the dancer from the dance? The dynamic nature of African great ape social communication, *Anthropological Theory*, 3: 5-26.
- Kingsley, M.C.S. and Reeves, R.R. (1998). Aerial surveys of cetaceans in the Gulf of St. Lawrence in 1995 and 1996. *Canadian Journal of Zoology*, 76: 1529-1550.
- Klinowska, M. (1991). Dolphins, porpoises and whales of the world. In: *The IUCN Red Data Book*. International Union for Conservation of Nature and Natural Resources: Gland, Switzerland, and Cambridge, U.K.
- Kritzler, H. (1952). Observations on the pilot whale in captivity. *Journal of Mammology*, 33 (3): 321-334.

- Lammers, M.O., Au, W.W.L. and Herzing, H.L. (2003). The broadband social acoustic signaling behavior of spinner and spotted dolphins. *Journal of the Acoustical Society of America*, 114: 1629-1639.
- LeDuc, R.G., Perrin, W.F. and Dizon, A.E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Marine Mammal Science*, 15(2): 619-648.
- Lesage, V., Barrette, C., Kingsley, M.C.S. and Sjare, B. (1999). The effect of vessel noise on the vocal behaviour of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*, 15: 65-84.
- Lindström, L. and Kotiaho, J.S. (2002). *Signalling and Reception*. Encyclopedia of Life Sciences. Macmillan Publishers Ltd, Nature Publishing Group, 1-6.
- Lusseau, D., Whitehead, H. and Gero, S. (2008). Incorporating uncertainty into the study of animal social networks. *Animal Behaviour*, 75: 1809-1815.
- Lynch, A. (1996). Population memetics of bird song. In: *Ecology and Evolution of Acoustic Communication in Birds*. Edited by: Kroodsma, D.E. and Miller, E.H., Comstock Publishing Associates: Ithaca.
- Mackenzie, K.V. (1981). Discussion of sea-water sound-speed determinations. *Journal of the Acoustical Society of America*, 70(3): 801-806.
- Manly, B.F.J. (1994). *Multivariate Statistical Methods: A Primer*. Chapman and Hall: London.
- Mann, J. (1999). Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science*, 15(1): 102-122.
- Marcoux, M., Rendell, L. and Whitehead, J. (2007). Indications of fitness differences among vocal clans of sperm whales. *Behavioral Ecology and Sociobiology*, 61: 1093-1098.
- Marino, L., Connor, R.C., Fordyce, R.E., Herman, L.M., Hof, P.R., Lefebvre, L., Lusseau, D., McCowan, B., Nimchinsky, E.A., Pack, A.A., Rendell, L., Reidenberg, J.S., Reiss, D., Uhen, M.D., Van der Gucht, E. and Whitehead, H. (2007). Cetaceans have complex brains for complex cognition. *PLoS Biology*, 5(5): 966-972.
- Marler, P. and Peters, S. (1982). Subsong and plastic song: their role in the vocal learning process. In: *Acoustic Communication in Birds*. Edited by: Kroodsma, D.E. and Miller, E.H., Vol. 2, Academic Press: New York.

- Mathews, J.N., Rendall, L.E., Gordon, J.C.D. and Macdonald, D.W. (1999). A review of frequency and time parameters of cetacean tonal calls. *Bioacoustics*, 10(1): 47-71.
- May-Collado, L.J. and Agnarsson, I. (2006). Cytochrome b and Bayesian inference of whale phylogeny. *Molecular Phylogenetics and Evolution*, 38: 344-354.
- May-Collado, L.J. and Wartzok, D. (2008). A comparison of bottlenose dolphin whistles in the Atlantic ocean: factors promoting whistle variation. *Journal of Mammalogy*, 89(5): 1229-1240.
- Maynard Smith, J. (1991). Honest signaling: the Philip Sydney game. *Animal Behaviour*, 42: 1034-1035.
- McCowan, B. (1995). A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (*Delphinidae: Tursiops truncatus*). *Ethology*, 100: 177-193.
- McCowan, B. and Hooper, S.L. (2002). Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. *The Journal of the Acoustical Society of America*, 111(3): 1157-1160.
- McCowan, B. and Reiss, D. (1995). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (*Delphinidae, Tursiops truncatus*): a re-evaluation of the signature whistle hypothesis. *Ethology*, 100: 194-209.
- McCowan, B. and Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: a comparison with humans and nonhuman animals. In: *Social Influences on Vocal Development*. Edited by: Snowdon, C.T. and Hausberger, M., Cambridge University Press: Cambridge, 178-207.
- McCowan, B. and Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour*, 62: 1151-1162.
- McCowan, B., Reiss, D. and Gubbins, C.M. (1998). Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, 24: 21-40.
- McGregor, P.K. (2005). *Animal Communication Networks*. Cambridge University Press: Cambridge.
- Medrano, L., Salinas, M., Salas, I., Ladron de Guevara, P.L., Aguayo, A., Jacobsen, J., and Baker, C.S. (1994). Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering ground of the Mexican Pacific. *Canadian Journal of Zoology*, 72: 1771-1774.

- Meijer, P.B.L. (1992). An experimental system for auditory image representations. *Biomedical Engineering*, 39(2): 112-121.
- Mercado, E. III, Herman, L.M., and Pack, A.A. (2005). Song copying by humpback whales: themes and variations. *Animal Cognition*, 8(2): 93-102.
- Mercer, M.C. (1975). Modified Leslie-DeLury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. *Journal of the Fisheries Research Board of Canada*, vol 32 (7): 1145-1155.
- Milinski, M. (1997). How to avoid seven deadly sins in the study of behavior. *Advances in the Study of Behavior*, 26: 159-180.
- Miller, P.J.O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, 192: 449-459.
- Miller, P.J.O. and Bain, D.E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, 60: 617-628.
- Miller, P.J.O. and Tyack, P.L. (1998). A small towed beamforming array to identify vocalizing resident killer whales (*Orcinus orca*) concurrent with focal behavioral observations. *Deep-sea Research II*, 45: 1389-1405.
- Miller, P.J.O., Shapiro, A.D., Tyack, P.L. and Solow, A.R. (2004). Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. *Animal Behaviour*, 67: 1099-1107.
- Miller, R.G., Jr, (1986). *Beyond ANOVA, Basics of Applied Statistics*. John Wiley and Sons: New York.
- Mundinger, P.C. (1995). Behaviour-genetic analysis of canary song inter-strain differences in sensory learning, and epigenetic rules. *Animal Behaviour*, 50: 1491-1511.
- Murray, S.O., Mercado, E., and Roitblat, H.L. (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *Journal of the Acoustical Society of America*, 104(3): 1679-1688.
- Myrberg, A.A. Jr. (1981). Sound communication and interception in fishes. In: *Hearing and Sound communication in Fishes*. Edited by: Tavolga, W.N., Popper, A.N., Fay, R.R., Springer: New York.
- Naguib M. and Wiley, R.H. (2001). Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour*, 62: 825-837.

- Naguib, M., Mundry, R., Hultsch, H. and Todt, Dietmas (2002). Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance. *Behavioral Ecology and Sociobiology*, 52: 216-223.
- Neumann, E.K., Wheeler, D.A., Bernstein, A.S., Burnside, J.W. and Hall, J.C. (1992). Artificial neural network classification of *Drosophila* song mutants, *Biological Cybernetics*, 66: 485-469.
- Newman, M.E.J. (2004). Analysis of weighted networks. *Physical Review E*, 70: 056131.
- Newman, M.E.J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, 103: 8577-8582.
- Newman, M.E.J. and Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E*, 69: 026113.
- Oswald, J.N., Rankin, S. and Barlow, J. (2004). The effect of recording and analysis bandwidth on acoustic identification of delphinid species. *Journal of the Acoustical Society of America*, 116(5): 3178-3185.
- Ottensmeyer, A. and Whitehead, H. (2003). Behavioural evidence for social units in long-finned pilot whales. *Canadian Journal of Zoology*. 81: 1327-1338.
- Partan, S., Jerger, K., Xitco, M., Roitblat, H., Herman, L., Williams, H., Hoffhines, M., Gory, J. and Ralston, J. (1988). Behavior specific vocalizations of two Atlantic bottlenose dolphins (*Tursiops truncatus*). (Abstract). *Journal of the Acoustical Society of America* (Suppl 1), 84:S77.
- Payne, P.M. and Heinemann, D.W. (1993). The distribution of pilot whales (*Globicephala* spp.) in shelf/shelf-edge and slope waters of the northeastern United States, 1978-1988. Report of the International Whaling Commission. Special Issue 14: 51-68.
- Payne, P.M. and McVay, S. (1971). Songs of humpback whales. *Science*, 173: 585-597.
- Payne, P.M., Selzer, L.A. and Knowlton, A.T. (1984). Distribution and density of cetaceans, marine turtles, and seabirds in the shelf waters of the northeastern United States, June 1980-December 1983, from shipboard observations. Final Report, National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA, Contract No. NA-81-FA-C-00023. 246pp.
- Pitman, R.L., Balance, L.T., Mesnick, S.L. and Chivers, S.J. (2001). Killer whale predation on sperm whales: observations and implications. *Marine Mammal Science*, 17: 494-507.
- Podos, J., Peters, S., Rudnicki, T., Marler, P. and Nowicki, S. (1992). The organization of song repertoires in song sparrows: Themes and variations. *Ethology*, 90: 89-106.

- Pohlmann, K.C. (2005). *Principles of Digital Audio*. Knowledge Industrie Publications: New York, London.
- Price, J.J. (1998). Family- and sex-specific vocal traditions in a cooperatively breeding songbird. *Proceedings of the Royal Society of London, series B*, 265: 497-502.
- Price, J.J. (1999). Recognition of family-specific calls in stripe-backed wrens. *Animal Behaviour*, 57(2): 483-492.
- R Development Core Team (2005). *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing. Available at <http://www.R-project.org>.
- Ralston, J.V. and Herman, L.M. (1995). Perception and generalization of frequency contours by a bottlenosed dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology*, 109: 268-277.
- Ramani, N., Hanson, W.G., Patrick, P.H. and Sheehan, R.W. (1993). An automated environmental monitoring system-phase 1: amphibian species identification from calls. *Proceedings of the World Conference on Neural Networks*, 1: 304-307.
- Reeves, R.R., B.S. Stewart, P.J. Clapham and Powell, J.A. (2002). *National Audubon Society Guide to Marine Mammals of the World*. Alfred A. Knopf: New York.
- Reeves, R.R., Smith, B.D., Crespo, R.A. and di Sciara, N. (2003). *Dolphins, Whales and Porpoises: 2002–2010 Conservation Action Plan for the World's Cetaceans*. Cetacean Specialist Group. IUCN: Gland, Switzerland and Cambridge, UK.
- Rendell, L.E. (2003). Cultural variation and usage of coda vocalizations by sperm whales, *Physeter macrocephalus*. Ph.D. thesis, Biology, Dalhousie University.
- Rendell, L.E. and Gordon, J.C.D. (1999). Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. *Marine Mammal Science*, 15(1): 198-204.
- Rendell, L.E. and Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, 24: 309-382.
- Rendell, L.E. and Whitehead, H. (2003a). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society: Series B*, 270: 225-231.
- Rendell, L.E. and Whitehead, H. (2003b). Comparing repertoires of sperm whale codas: a multiple methods approach. *Bioacoustics* 14(1): 61-81

- Rendell, L.E., Matthews, J.N., Gill, A., Gordon, J.C.D., and Macdonald, D.W. (1999). Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *Journal of Zoology, London*, 249: 403-410.
- Richards, D.G., Wolz, J.P. and Herman, L.M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenose dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology*, 98: 10-28.
- Richardson, W.J., Greene, Jr., C.R., Malme, C.I. and Thomson, D.H. (1995). *Marine Mammals and Noise*. Academic: San Diego.
- Richerson, P.J. and Boyd, R. (2005). *Not by Genes Alone*. Chicago University Press: Chicago.
- Riesch, R., Ford, J.K.B. and Thomsen, F. (2006). Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, 71: 79-91.
- Ryan, M.J. (1988). Energy, calling, and selection. *American Zoologist*, 28:885-898.
- Saayman, G.S., Taylor, C.K. and Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins *Tursiops Ad Uncus Ehrenburg*. *Behaviour*, 44: 212-233.
- Sayigh, L.S., Esch, H.C., Wells, R.S. and Janik, V.M. (2007). Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 74: 1631-1642.
- Sayigh, L.S., Tyack, P.L., Wells, R.S. and Scott, M.D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26: 247-260.
- Schevill, W.E. (1964). Underwater sounds of cetaceans, vol 1. In: *Marine Bio-Acoustics*. Edited by: Tavolga, W.N., Pergammon Press: New York, 307-316.
- Schevill, W.E. and Watkins, W.A. (1966). Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, 51: 70-76.
- Schulz, T.M. (2007). The production and exchange of sperm whale coda vocalizations. Ph.D. thesis, Department of Biology, Dalhousie University.
- Schulz, T.M., Whitehead, H. and Rendell, L. (2006). A remotely-piloted acoustic array for studying sperm whale vocal behaviour. *Journal of the Canadian Acoustical Association*, 34: 54-55.

- Schulz, T., Whitehead, H., Gero, S. and Rendell, L. (2008). Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. *Animal Behaviour*, 76: 1977-1988.
- Sergeant, D.E. (1962). On the external characteristics of the blackfish or pilot whales (genus *Globicephala*). *Journal of Mammology*, 43(3): 395-413.
- Similä, T. and Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71: 1494-1499.
- Slater, P.B.J., Ince, S.A. and Colgan, P.W. (1980). Chaffinch song types, their frequencies in the population and distribution between the repertoires of different individuals. *Behaviour*, 75: 207-218.
- Smith, E., Lusseau, D. and Whitehead, H. (2008). The Effects of whale watching in Pleasant Bay, Cape Breton, Nova Scotia: balancing long-term benefits to whale watchers and immediate behavioral changes in long-finned pilot whales (*Globicephala melas*). Document SC/59-ForInformation21 presented to the IWC Scientific Committee (unpublished).
- Sokal, R.R. and Rohlf, F.J. (1995). *Biometry: The principles and practice of statistics in biological research*. W.H. Freeman and Company: New York.
- Speakman, R. and Racey, P.A. (1991). No cost of echolocation for bats in flight. *Nature*, 350: 421-422.
- Steiner, W.W. (1981). Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. *Behavioral Ecology and Sociobiology*, 9: 241-246.
- Szymanski, M.D., Bain, D.E., Kiehl, K., Pennigton, S., Wong, S. and Henry, K.R. (1999). Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. *Journal of the Acoustical Society of America*, 106(2): 1134-1141.
- Taruski, A.G. (1979). The whistle repertoire of the north Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: *Behavior of Marine Animals, Vol. 3: Cetaceans*. Edited by: Winn, H.E. and Olla, B.C., Plenum Press: New York, 345-368.
- Thomas, J.A., Moss, C., and Vater, M. (2004). *Echolocation in Bats and Dolphins*. University of Chicago Press: Chicago.

- Thomson, R.K.R. and Herman, L.M. (1975). Underwater frequency discrimination in the bottlenose dolphin (1-140kHz) and the human (1-8kHz). *Journal of the Acoustical Society of America*, 57: 943-948.
- Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Harvard University Press: Cambridge, Massachusetts.
- Trites, A.W. and Pauly, D. (1998). Estimating mean body masses of marine mammals from maximum body lengths. *Canadian Journal of Zoology*, 76: 886-896.
- Tyack, P.L. (1986). Population biology, social behavior, and communication in whales and dolphins. *Trends in Ecology and Evolution*, 1:144-150.
- Tyack, P.L. (1997). Development and social functions of signature whistles in bottlenose dolphins, *Tursiops truncatus*. *Bioacoustics*, 8: 21-46.
- Tyack, P.L. (2000). Functional aspects of cetacean communication. In: *Cetacean Societies*. Edited by: Mann, J., Connor, R.C., Tyack, P.L., and Whitehead, H., University of Chicago Press: Chicago, 270-307.
- Van Parijs, S.M., Parra, G.J. and Corkeron, P.J. (2000). Sounds produced by Australina Irrawaddy dolphins, *Orcaella brevirostris*. *Journal of the Acoustical Society of America*, 108(4): 1938-1940.
- Vehrencamp, S.L., Bradbury, J.W. and Gibson, R.M. (1989). The energetic cost of display in male sage grouse. *Animal Behaviour*, 38: 885-896.
- Warton, D.I. and Hudson, H.M. (2004). A manova statistic is just as powerful as distance-based statistics, for multivariate abundances. *Ecological Society of America*, 85(3), 858-874.
- Watkins, W.A. (1967). The harmonic interval: fact or artifact in spectral analysis of pulse trains. In: *Marine Bioacoustics*. Vol 2. Edited by: Tavolga, W.N., Pergamon Press: New York, 15-43.
- Watkins, W.A., Daher, M.A., Samuels, A. and Gannon, D.P. (1997). Observations of *Peponocephala electra*, the melon-headed whale, in the Southeastern Caribbean. *Caribbean Journal of Science*, 33: 34-40.
- Weilgart, L.S. and Whitehead, H. (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioral Ecology and Sociobiology*, 26: 399-402.
- Weilgart, L.S. and Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, 40: 277-285.

- Wells, R.S., Boness, D.J. and Rathbun, G.B. (1999). Behavior. In: *Biology of Marine Mammals*. Edited by Reynolds, J.E. and Rommel, S.A., Smithsonian Institution Press: Washington.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, 38: 237-244.
- Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour*, 53: 1053-1067.
- Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. The University of Chicago Press: Chicago and London.
- Whitehead, H. and Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior*, 28: 33-74.
- Whitehead, H. and Rendell, L. (2004). Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, 73: 190-196.
- Wiley, R.H. and Richards, D.G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds*, vol 2. Edited by: Kroodsma, D.E. and Miller, E.H., Academic Press: New York.
- Wilkinson, L., Blank, G. and Gruber, C. (1996). *Desktop Data Analysis with SYSTAT*. Prentice-Hall: New Jersey.
- Williams, J.M. and Slater, P.J.B. (1991). Computer analysis of bird sounds: a guide to current methods. *Bioacoustics*, 3: 121-128.
- Wimmer, T. (2000). Distribution of cetaceans in St. Lawrence Bay, Nova Scotia from 1992-1999. Honours thesis, Dept. of Biology, Dalhousie University, Halifax, Nova Scotia.
- Wrangham, R.W. (1983). Ultimate factors determining social structure. In: *Primate Social Relationships: an integrated approach*. Edited by Hinde, R.A., Sinauer Associates Inc: Sunderland, Massachusetts.
- Yurk, H. (2005). Vocal culture and social stability in resident killer whales (*Orcinus orca*). Ph.D. thesis, Zoology, University of British Columbia.
- Yurk, H., Barrett-Lennard, L., Ford, J.K.B., and Matkin, C.O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behavior*, 63: 1103-1119.