STABILITY AND CHANGE OF KILLER WHALE *(ORCINUS ORCA)* DIALECTS

by

VOLKER BERNT DEECKE

B.Sc. (Honours), The University of British Columbia, 1994

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR
THE DEGREE OF

MASTER OF SCIENCE
in
THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
June 1998

ABSTRACT

Vocal dialects have been described in many species, but most studies so far have focused on territorial species such as songbirds and humans. This study investigates patterns of structural variation in the stereotyped calls of 9 matrilineal units of killer whales (*Orcinus orca*) with congruent home ranges.

In Chapter I, I describe an index of acoustic similarity based on neural network analysis of frequency contours. I test this index on simulated signals, and compare it to similarity ratings from three human subjects. The index could discriminate along global differences in contour frequency, as well as localized differences in frequency and shape. It rated similarity comparably to humans, since differences between ratings among subjects exceeded differences between subject ratings and the neural network index.

In the second Chapter, I analyse 2 call types used by 2 groups over a 12 year period to identify mechanisms of vocal differentiation. A test for structural modification detected significant changes in one call type in both groups, but not in the other. The rate of differentiation between both groups was significantly lower for the modified call type than the rate of modification in one group showing that modifications are transmitted between groups. Results of an analysis of structural parameters are consistent with a theory of structural drift.

In Chapter III, I quantify patterns of structural variation for 4 call types shared by 9 matrilineal units. Patterns are consistent across some call types, and similarity ratings for two call types are correlated with the frequency of association among groups. This presents additional evidence for the role of cultural transmission in maintaining structural similarity of shared calls.

This study shows that discrete calls of killer whales are modifiable behavioural traits and transmitted through learning. Since multiple vocal traditions persist in spite of frequent acoustic contact between their members, this study presents evidence for selective copying in resident killer whales. If association patterns reflect kinship among matrilineal units as they do among individuals and among communities, similarity of shared call types indicates the degree of maternal relatedness, and may function in kin recognition or mate choice.

TABLE OF CONTENTS

CHAPTER I: Quantifying Complex Patterns of Acoustic Variation: Use of a Neural Network to Compare Killer Whale Calls

CHAPTER II: Mechanisms and Rates of Vocal Differentiation in Resident Killer Whales

CHAPTER III: Patterns of Acoustic Variation Within a Killer Whale Vocal Tradition

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would like to thank John Ford for his support and expertise during this second instar of my academic career. This study draws immensely from his work on the dialects of resident killer whales, and I am very grateful for the knowledge and the skills he passed on to me. I am equally indebted to the other members of my thesis committee: to John Gosline for his enthusiasm and his comments, and for unreservedly agreeing to act as my co-supervisor. His suggestions helped solve key problems in the methodology. Thanks to Jamie Smith for keeping me grounded throughout this study and for his comments and his criticism which was always well taken and constructive. His contribution greatly improved the quality of this work.

This thesis would not have been possible without tremendous support from the northern resident community of whale researchers. Virtually anyone who has recorded a sound from northern resident killer whales has made their recordings available to me, and I hope this spirit of cooperation will continue into the future. In particular I would like to thank Dave Bain, Dave Briggs, Jim Borrowman, Graeme Ellis, Brian Falconer, John Ford, Bill and Donna Mackay, Alex Morton, Erin Nyhan, Rod Palm, Paul Spong, Helena Symonds, Frank Thomsen, and Steve Wischniowski for their contributions. Paul Spong and Helena Symonds, I owe additional thanks for their frequent hospitality on Hanson Island, the fresh-baked bread and the many discussions, and for providing charismatic encounters with my study animal. Jim Borrowman, Graeme Ellis, Bill and Donna Mackay, Alex Morton, and Dave and Maureen Towers also provided invaluable logistic help, useful comments, and hospitality. Thanks to Graeme Ellis also for coordinating the photo-identification work, and for sharing his expertise and enthusiasm about BC’s killer whales. His contribution to killer whale research on this coast cannot be overrated.

The Department of Zoology and the Marine Mammal Research Unit have been a second home for me during the last four years. I want to thank Andrew Trites for his help, his encouragement, the parties, and for his passion for science. Thanks to Lance Barrett-

Lennard, Kathy Heise, and Harald Jurk for the stimulating discussions, the invaluable comments on countless drafts and proposals, and for helping me keep the big picture in mind. Ed Gregr, Durrell Kapan, Dave Rosen, Rob Williams, and Arliss Winship gave helpful tips and comments over beers or during frequent trips for coffee. Many thanks to Pamela Rosenbaum for her help and support, for keeping a check on things, and for editing drafts of this thesis. Thanks also for everyone in the UBC Biomaterials lab for the comments, the parties, and for showing me that there is a world outside of bioacoustics.

Many people contributed in the making of this thesis. Conversations with Dave Bain helped me immensely in getting my concepts straightened out. Jarek Harezlak, Durrell Kapan, and Harald Siedentop gave invaluable statistical advice. Alistair Blachford provided great assistance with my computing needs. Lisa Farroway, Sharon Midwinter and Catharine Shankel acted as subjects for the classification tasks. Hal Weinberg, Bill Gaetz, and K-J Jantzen of the Brain Behaviour Lab at Simon Fraser University got me started on neural networks, and I am grateful for all the support received from them. I also want to thank Hal and Linda Weinberg for the productive writing retreats at their cabin in Fanny Bay where much of this thesis materialized. Earlier drafts benefited from comments from my committee, as well as from Lance Barrett-Lennard, Lüder Deecke, Denise Herzing, Vincent Janik, Harald Jurk, Durrell Kapan, Peter Slater, and Rob Williams.

I want to thank the members of the BC Wild Killer Whale Adoption Program for their financial support and its administrator Meg Pocklington for her logistic help and cheerfulness. I am grateful to the MathWorks Inc. for generously donating a copy of MATLAB for the signal processing and neural network analysis.

Last, but by no means least, thanks to all my friends, family and housemates for keeping me going during the last four years. Special thanks to Janet Wieser for her love and support, to my parents Lüder and Gertraud Deecke, my brothers Ulf and Arved, and to Ivan Alves, Erin Baines, Alistair Blachford, Manfred Enstipp, Harald Jurk, Mikis Manolis, Goshka Szczodrak, Monique Trépanier, Gunna Weingartner, and Barbara Zupančič.

DEDICATION

I dedicate this thesis to my parents, Lüder and Gertraud Deecke, in appreciation for the cultural behaviour complex I inherited from them. Among the many traits they have transmitted to me are their respect for nature and their love for wild places, an appreciation for people and for scientific thought, a great curiosity about the world around us, as well as a tendency to lisp when stressed out. I realize and appreciate that in spite of my dispersal, this cultural transmission still continues strong.

Resident killer whales spyhopping (photo courtesy Graeme Ellis)

GENERAL INTRODUCTION

True vocal dialects in the communicative signals of a species are best defined as variations in the vocalizations of social groups of animals which are in acoustic contact (Conner, 1982). This definition distinguishes vocal dialects from geographic variation in the vocal behaviour of a species, defined in turn as differences in the vocalizations of groups or populations caused and maintained by acoustic isolation. Since the first definition implies that the vocal distinctiveness of individuals or groups is maintained in spite of the potential for exchange with neighbouring individuals or groups, it infers that the dialects serve a social function, and are not merely by-products of genetic, or cultural drift.

Mundinger (1982) studying bird song defines vocal dialects as variant acoustic traditions shared by local populations and separated by other acoustic traditions through dialect boundaries. This definition is similar to that of Conner (1982) in that it postulates the presence of vocal differences among neighbouring animals (dialect boundaries). Mundinger’s definition, however, is strictly geographic and therefore only useful for territorial species, such as birds or humans, where dialects can be delineated by spatial boundaries. It cannot be easily applied to those species where dialects distinguish social groups or populations with congruent or overlapping home ranges.

True dialects have been documented in a variety of taxa, but are probably most prevalent among birds (e.g., Mundinger, 1982; Catchpole and Slater, 1995). The presence of group specific or regional dialects appears to be the rule rather than the exception among most families of songbirds (*Oscines* ; Mundinger, 1982), and vocal dialects have also been documented among parrots (*Psittaciformes* ; Nottebohm, 1976; Wright, 1996) and hummingbirds (*Trochilidae* ; Snow, 1968; Wiley, 1971).

Among mammals, individual variation in vocal signals has been documented for many species. Examples are the signature whistles of bottlenose dolphins (*Tursiops truncatus* ; Caldwell and Caldwell, 1965; Sayigh et al., 1990; Sayigh et al., 1995), the individual-specific isolation calls of newborn big brown bats (*Eptesicus fuscus* ; Rasmuson and Barclay, 1992), and the mother-pup recognition calls of many species of pinnipeds (e.g., Insley, 1992, but see Job et al., 1995). In contrast, group-specific vocal dialects in the sense of Conner (1982) so far have only been established in killer whales (*Orcinus orca* ; Ford, 1989, 1991; Strager, 1995), sperm whales (*Physeter macrocephalus* ; Weilgart and Whitehead, 1997), greater spear-nosed bats (*Phyllostomus hastatus* ; Wenrick Boughman, 1997), and pigtail macaques (*Macaca nemestrina* ; Gouzules and Gouzules, 1990). Many other reports of dialects in non-human primates (e.g., Mitani et al., 1992) describe geographic variation of acoustically isolated groups rather than true dialects in the sense of Conner (1982).

The function of individual vocal variation is often obvious. Both bats and pinnipeds rear their young in communal roosts or rookeries, and vocal signatures allow females to identify their offspring after returning from foraging trips. The role of individual signatures in bottlenose dolphins, on the other hand, is somewhat more debated, although kin recognition probably also plays an important role. Sayigh (1992) showed that female bottlenose dolphins are more likely to turn towards the signature whistle of an offspring (including independent offspring). Furthermore, bottlenose dolphins hunt cooperatively (Hoese, 1971; Bel'kovich et al., 1991), which creates a need for individual recognition (Crowley et al., 1996). Sayigh et al. (1995) found that male bottlenose dolphins, which is the dispersing sex in this species, develop a signature whistle similar to that of their mother. This vertical transmission between generations of the signature whistles of bottlenose dolphins may serve to prevent inbreeding, since in subsequent encounters males would be recognized as kin by their mothers as well as their sisters (since they are familiar with the maternal signature whistle). The same function has been postulated for dialects in the song and distance call of zebra finches (*Taeniopygia guttata* ; Zann, 1990), where juvenile males preferentially copy their father's song (Zann, 1990; Mann and Slater, 1995). Familiarity with their father's vocalizations may allow female birds to avoid mating with their brothers.

Several hypotheses have attempted to explain the function of group dialects in birds (see Payne, 1981a; Mundinger, 1982 for summaries). Marler and Tamura (1962), as well as Treisman (1977, 1978) suggest that vocal dialects indicate the genetic constitution of a population, and promote philopatry or prevent inbreeding. Payne and Payne (1977) studying village indigo-birds (*Vidua chalybeata*) concluded that dialects in this species act as a secondary sexual characteristic and function in sexual selection. Finally, Nottebohm (1975, 1985) argues that vocal dialects in birds are products of vocal adaptation to local differences in the acoustic environment since juvenile birds may preferentially learn those song elements which are best transmitted in the local sound scape.

As behavioural traits which exhibit variation across a wide range of scales, vocal dialects have received a great deal of attention from researchers interested in the ontogeny of behaviours (e.g., Mundinger, 1995). Whether the ability to actively acquire and modify vocal patterns is a prerequisite for vocal dialects is still the subject of much debate. Mundinger (1982) postulates that all dialects are the product of vocal learning, and all studies which tested for vocal learning in bird species with vocal dialects support his claim (Kroodsma and Baylis, 1982; Slater, 1989). Other researchers, however, argue that differences in the vocalizations of individuals could be genetic (Janik and Slater, 1997), or could be the product of differential selection of certain vocal patterns from a common, genetically coded repertoire (Nelson and Marler, 1994).

In species where dialects are the product of vocal learning, they represent complex, culturally transmitted behavioural traits. Cultural transmission is defined as the acquisition and modification of behaviours through learning and copying as opposed to genetic inheritance (Mundinger, 1980). The main functional differences between these forms of behavioural ontogeny are that cultural transmission allows for horizontal transmission of behaviours between members of the same generation, and for oblique transmission between unrelated members of different generations (Lynch, 1996). Because learned vocal dialects represent a highly variable behavioural trait that is often easy to quantify, they have played an important part in generating and testing theories on gene-culture co-evolution (humans: Cavalli-Sforza and Feldman, 1981; Barbujani, 1991; Cavalli-Sforza, 1997; songbirds: Gibbs, 1990; Lougheed and Handford, 1992).

In killer whales, vocal dialects were first described by Ford and Fisher (1982) from the coastal waters of British Columbia. Here, so-called *resident* killer whales live in extremely stable matrilineally organized social groups. The nuclear unit of resident killer whale society is the *matrilineal unit* which consists of a female and her offspring. Juvenile dispersal appears to be completely absent in the resident populations, since even after 19 years of study, members of the same matrilineal unit have never been observed out of acoustic range of each other (Bigg et al., 1990). Because killer whales are long-lived (mean life expectancy for females: 50.2 years; for males 29.2 years; Olesiuk et al., 1990), matrilineal units often contain three, sometimes four generations. Only after the oldest female dies, do her daughters who by then usually have offspring of their own, start travelling apart. This break-up, however, is very gradual, and sisters whose mother has died, may still spend the majority of time associated.

Bigg et al. (1990) grouped matrilineal units that travelled together more than 95% of the time into *subpods.* Subpods which were seen the majority (>50%) of the time together were grouped into larger social groups called *pods.* All pods that have been seen travelling together make up a *community.* The resident killer whales of British Columbia, Washington State, and Alaska belong to two distinct communities. The *northern resident community* ranges from central Vancouver Island to the Gulf of Alaska and likely consists of several subunits which only associate through intermediates (see Dalheim et al., 1997). The *southern resident community* travels the waters off southern Vancouver Island and Puget Sound. The ranges of the two resident communities overlap partially with that of *offshore* killer whales which appear to frequent the waters of the continental slope (Ford et al., 1994). Finally the range of the *transient community* extends from northern California to southeast Alaska and includes the ranges of both resident communities. Resident killer whales have never been observed travelling together with members of the transient community, or with offshore killer whales (Bigg, 1982; Ford et al., 1994).

The vocal behaviour of killer whales consists of three types of vocal signals (Ford, 1989). *Clicks* are short pulses of sound, usually emitted in series, that are used as echolocation signals for orientation and prey capture (Awbrey et al., 1982; Barrett-Lennard et al., 1996). *Whistles* are tonal signals with little or no harmonic content and range in frequency between 6 and 12kHz, although occasionally whistles can be a low as 1.5kHz or as high as 18kHz (Awbrey et al., 1982; Ford and Fisher, 1982; Ford, 1989). Whistles tend to be most common in social contexts (Ford, 1989).There is some evidence for stereotyped whistles in killer whales (H. Jurk, F. Thomsen, pers. comm.).

The majority of killer whale vocalizations fall into the third category of *pulsed* or *burst-pulsed* sounds (Ford and Fisher, 1982). Due to the high pulse repetition frequencies (between 120 and 4500Hz for the calls analysed in this study), pulsed calls have distinct tonal properties. Many pulsed calls contain an overlaid upper frequency component (at 6-8kHz) which is not a harmonic of the pulse repetition frequency. The presence of this upper frequency component suggests that two independent structures function in sound production in killer whales. Ford and Fisher (1982), and Ford (1989) grouped pulsed calls into three categories*. Discrete calls* are highly stereotyped and can easily be assigned to different call types according to their structural properties. 70 to 95% of pulsed calls fall into this category (Ford and Fisher, 1982)*. Variable calls* are not repetitive and cannot be divided into clearly defined call types. Finally, *aberrant calls* are structurally based on a discrete call type, but show some degree of modification. Like whistles, these tend to occur most frequently during social interactions (Ford, 1989).

Members of the northern resident community have a vocal repertoire of 7 to 17 different discrete call types (Ford, 1989). Ford (1989, 1991) showed that captive individuals produced all call types in their group's repertoires. Call repertoires therefore represent true group dialects, and are not merely the sum of the individual signatures of a group's members. Ford (1984, 1989, 1991) also found that certain call types are shared among pods, and that different pods produce consistently different versions, or subtypes, of these shared call types. An acoustic *clan* includes all pods that share at least one call type (Bigg et al., 1990; Ford, 1991). The northern resident community contains three such clans. Matrilineal units of different clans within the same community still frequently associate and interact socially, although they have no call types in common. Strager (1995) has since described similar system of call repertoires from killer whales in the waters off northern Norway, which suggests that the presence of group dialects is not unique to eastern Pacific killer whales, but may be characteristic for the species as a whole.

Although the presence of vocal dialects among resident killer whales is most parsimoniously explained by vocal learning (Ford, 1989, 1991), the ability to modify its vocal behaviour through learning has never been established unequivocally in this species (Janik and Slater, 1997). Bain (1986, 1988) gives a report of a female Icelandic killer whale mimicking the calls of a northern resident female in captivity. A similar incident of vocal mimicry has been described from the Vancouver Aquarium (John Ford, pers. comm.), where a male northern resident killer whale started copying the calls of a southern resident female and subsequently passed them on to two Icelandic juveniles that had never been in contact with the southern resident whale. Ford (1991) also showed that on rare occasions groups in the wild mimic calls of other acoustic clans which are not part of their acoustic repertoire. In a preliminary study, Bowles et al. (1988) recorded the vocal development of a killer whale calf born in captivity, and found evidence suggesting vocal copying as early as 12 days of age. At 1 year of age, its vocal repertoire resembled that of its mother more than that of any other individual in the exhibit. However, the role of vocal learning in establishing this repertoire could not be addressed. An alternative hypothesis for the occurrence of vocal dialects in killer whales therefore could be genetic transmission along maternal lines (Bowles et al., 1988; Janik and Slater, 1997), although it is difficult to explain a genetic mechanism for encoding the complex vocal differences observed among shared call types.

The precise functions of killer whale vocal communication, and of killer whale group dialects in particular, are far from understood. Ford (1991) argues that killer whale calls function in the maintenance of group cohesion and in coordination of group activity. Most pulsed calls have high and low frequency components which are attenuated differentially. A listening whale therefore can obtain precise information on its distance from a caller, regardless of overall source level. Additionally, the upper frequency component is focused by the melon and therefore highly directional (Schevill and Watkins, 1966). For this reason, the relative strength of the upper frequency component communicates the orientation of a calling whale. Having group-specific dialects could serve to make this communication more effective, especially in situations where multiple matrilineal units associate and acoustic interference is a problem (Ford, 1991).

Since members of different communities have never been seen travelling together during 25 years of study, mating may occur preferentially within, or even be restricted to, the community. By signalling the degree of maternal relatedness of individuals, vocal dialects in resident killer whales may play a role in mate selection as a method to increase outbreeding. A similar function has been postulated for songbird dialects (Treisman, 1978; Grant, 1984).

Each member of the northern resident community can be identified from the unique appearance of their dorsal fin and saddle patch (Bigg et al., 1990; Ford et al., 1994). This population has been studied for over 25 years, yielding much information on individual genealogies, life histories, and social interactions (Bigg, 1982; Bigg et al., 1990; Olesiuk et al., 1990). The luxury of a naturally marked population of identifiable individuals, in combination with the complex system of group dialects, makes the northern resident community a model population for the study of patterns of dialect development in killer whales, as well as for testing current hypotheses on the function of vocal dialects, and the nature of gene-culture interaction.

Whereas all previous studies of killer whale vocal dialects have looked at patterns of acoustic variability on the level of the population (Awbrey et al., 1982) or the pod (Ford and Fisher, 1982; Ford, 1984, 1989, 1991; Strager, 1995), my study attempts to describe and quantify dialect variation at the level of the matrilineal unit, the smallest unit of resident killer whale society that can be encountered and recorded alone. The goal of my study is to identify the mechanisms of dialect development in killer whales through quantifying dialect differences both vertically, as change in the vocalizations of groups over time, as well as horizontally as vocal differences between related matrilineal units.

In order to achieve this, a precise measurement of acoustic similarity is needed. Previous studies (Ford, 1991; Strager, 1995) have used the number of shared call types and call subtypes as an indicator of acoustic similarity of the vocal repertoires of different groups. However, since at the level of this study the vocal repertoires of matrilineal units are often identical, a more precise indicator based on the structure of shared call types rather than similarity of vocal repertoire, is called for. In the first chapter, I therefore introduce and test a new method of measuring the similarity of shared call types based on frequency contour extraction and neural network analysis.

In the second chapter, I employ a historical approach to identify the mechanisms by which killer whale dialects evolve, I look at temporal change in the calls of two matrilineal units over a 12 year period. My objective for this chapter is to test whether vocal change can be detected over this period. Furthermore, quantifying the amount of structural change in both groups and comparing it to the acoustic difference between them presents a test for horizontal transmission of structural modifications to the calls. Knowledge of the mechanisms by which vocal change occurs and how it spreads through the population is crucial to interpreting patterns of vocal variation at any point in time.

In Chapter III, I use the acoustic similarity index to compare the vocal signals of the 9 different matrilineal subgroups which make up A-subclan (Ford, 1991) of the northern resident community. The goal of this chapter is to study structural variation of shared call types at the level of the matrilineal unit. I will test whether patterns of acoustic variation are consistent across call types, and interpret the observed patterns using the findings of Chapter II and knowledge about the social histories and genealogy of these groups.

By developing a sensitive index of acoustic similarity, applying this index to identify the mechanisms of dialect development, and using this knowledge to interpret patterns of vocal variation among different social groups, I hope to contribute towards delineating the role of acoustic variation in maintaining the social structure of a wild population of marine mammals. I believe that in the context of the extensive and ongoing research on the behaviour, social dynamics, and population genetics of the northern resident community, this study may help to determine the function of vocal dialects in killer whales, and in animal communication in general.

CHAPTER I: Quantifying Complex Patterns of Acoustic Variation: Use of a Neural Network to Compare Killer Whale Calls

INTRODUCTION

One of the most widespread problems in the study of animal and human vocal communication is describing and quantifying the similarity of acoustic signals. A quantitative measure of acoustic similarity is crucial to any study comparing the vocalizations of different species, social groups, or individuals. Current approaches to this problem fall into two categories*. Statistical approaches* use univariate or multivariate statistics on measurements extracted from acoustic signals to quantify their similarity (e.g., Bailey, 1978; Symmes et al., 1979; Clark et al., 1987; Buck and Tyack, 1993; see Martindale, 1980, and Williams and Slater, 1991 for overviews of statistical methods)*. Perceptual approaches* quantify acoustic similarity through ratings of similarity by human observers (e.g., Tyack, 1986; Sayigh et al., 1990), or by the ability of human or animal subjects to discriminate between classes of signals (e.g., Miller and Nicely, 1955; Loesche et al., 1992).

Statistical methods of quantifying acoustic similarity have the advantage of being objective and repeatable (Martindale, 1980; Clark et al., 1987), making it possible to compare the results from different studies. Biologically, however, such approaches may not be the most meaningful, since they only describe the physical properties of the signals and give no information on how they are perceived by the receiver (see Emlen, 1972; Horn and Falls, 1996).

Perceptual approaches, on the other hand, although often biologically meaningful, have the problem of observer bias. Whereas ratings of similarity by the same observer are probably comparable, ratings made by different observers are often not. In addition, obtaining ratings by human observers or trained animals is a logistic challenge in experiments where the acoustic similarity of multiple samples needs to be assessed in pairwise comparisons, or where sample sizes are large.

In this chapter, I introduce a method using an artificial neural network to quantify the acoustic variation of discrete calls of killer whales. Neural networks classify unknown patterns based on information obtained from a training set of known calls, and have been used successfully in the automated classification of animal vocalizations (e.g., Neumann et al., 1992; Ramani et al., 1993), including killer whale calls (Spong et al., 1993). However, since the performance of a neural network depends on the amount of consistent variation between the different patterns in the training set, I demonstrate that, much like confusion frequencies in psychometrics (e.g., Miller and Nicely, 1955), the discrimination error of a neural network can be used to assess and quantify the similarity of samples of acoustic signals. Artificial neural networks were developed by modelling biological systems of information processing (for overviews of artificial neural networks, see Dasgupta, 1991; Hinton, 1992). This bio-mimetic nature makes neural network analysis promising for comparing and integrating acoustic variation in a biological meaningful way while retaining the objectivity and repeatability of statistical approaches.

To date, most studies have measured the similarity of killer whale dialects at the level of the vocal repertoire (Ford, 1989, 1991; Strager, 1995). In addition, Ford (1984, 1987) provides a quantitative analysis of structural variation in shared call types based on measurements taken of prominent features of the calls. He demonstrated that structural parameters of shared call types show significant differences between pods. Analysis of structural variation at the level of the matrilineal unit has since shown that different matrilineal units have structurally distinct versions of shared call types (D.E. Bain and P. Miller, unpublished data). Finally, individuals are likely to have unique ‘voices’ due to anatomical variation in their sound-producing structures. Killer whale vocal communication therefore exhibits variation on a variety of levels. This graded continuum of acoustic variation provides a challenging field in which to test methods of quantifying the structural similarity of acoustic signals.

Many studies measuring acoustic variation have used frequency contours to describe acoustic signals. Extraction of frequency contours from spectrograms determines the fundamental frequency (or the pulse repetition frequency in pulsed signals) of a vocalization at certain time intervals (usually given by the temporal resolution of the spectrogram). This method has the advantage that, much like a behavioural *gestalt* (Köhler, 1929), the signal is analysed as a unit rather than broken down into disjunct measurements. In addition, biologically irrelevant information, such as background noise, is eliminated from subsequent analyses. The cost for the latter advantage, however, is that any relevant information in the amplitude domain is also lost. Until the development of computer-based methods, frequency contours were usually extracted manually. Most automated procedures used so far (e.g., Buck and Tyack, 1993) have been developed for analysing recordings obtained under controlled circumstances from captive or temporarily isolated animals.

The discrete calls of killer whales are pulsed signals that often exhibit rapid modulation of the pulse repetition rate. Unlike the signals of many birds or other delphinids, the highest amount of energy is not always in the first, second, or third harmonic. The complexity of these calls and the fact that the field recordings used in this study often contained high levels of background noise, meant that extraction algorithms from the literature (e.g., Buck and Tyack, 1993) were not satisfactory. In this chapter I therefore describe a new method of extracting frequency contours that is robust to high levels of background noise and promises to be applicable to acoustic signals from a large number of species.

Similarity of frequency contours has been assessed by a variety of methods. Bailey (1978) used analysis of variance of samples of frequency contours to arrive at a similarity index for bobwhite quail (*Colinus virginianus*) separation calls. Sayigh et al. (1990) quantified similarity of frequency contours of bottlenose dolphin whistles by asking human subjects to judge the similarity of contours. Buck and Tyack (1993) calculated average differences in frequency between contours after 'warping' the time axis to maximize contour correlation. Finally, McCowan (1995) used a combination of cross correlation, principal component analysis, and cluster analysis to quantify contour similarity.

In this chapter, I measure the similarity of frequency contours by assessing the performance of a neural network at classifying unknown contours using information obtained from a known training set. I test the performance of the neural network index on two sets of simulated signals, presenting the neural network with increasingly consistent, but diffuse variability in one case, and highly localized variation in the other. To see how the neural network index rates the similarity of biological signals, I use frequency contours extracted from the calls of 9 matrilineal units of killer whales belonging to A-subclan of the northern resident community (Ford et al.,1994; see Appendix II). For comparison, I measure similarity of the same call samples by asking 3 human subjects to classify unknown calls using information from a known training set.

METHODS

Extraction of frequency contours: the sidewinder algorithm

For extracting frequency contours, suitable calls were digitized from cassette tapes at a sampling rate of 22050Hz including at least 100ms of background noise before the onset of the call. Spectrograms were calculated by fast Fourier Transform (FFT) using the Canary 1.2.1 sound analysis software (Cornell Laboratory of Ornithology) with an FFT size and frame length of 1024 points. Overlap between frames was 87%, and a Hamming window function was used for normalization. These parameters gave a frequency resolution of 21.53Hz, and a temporal resolution of 5.81ms. Contours were extracted using MATLAB 4.2 (The MathWorks Inc.) for the Macintosh with the signal processing toolbox.

The algorithm used in this study assumes that the beginning and the end of the call can be determined visually from the spectrogram. To reduce background noise levels, an average noise spectrum was computed from the part of the spectrogram before the onset of the call, and subtracted from all time bins. To find the pulse repetition frequency at each point in time the autocovariogram $c'_{xx}(m)$ was first estimated for each power spectrum $x(n)$ of the spectrogram using the formula:

$$c'_{xx}(m) = \frac{1}{N-|m|}\sum_{\mathrm{n=0}}^{\mathrm{N-|m|-1}} x(n)x*(n+m)$$ Oppenheim and Schafer (1975) **(1)**

where n is the frequency bin, m equals the offset of the spectrum in frequency bins, and N is the number of frequency bins in the power spectrum. Since the frequencies of any harmonics or sidebands are given by a simple linear relationship, the autocovariogram will show a peak every time m equals a multiple of the pulse repetition frequency and adjacent harmonics or sidebands overlap. Because the power spectrum of the background noise tends to decrease with increasing frequency, and adjacent harmonics or sidebands have similar sound pressure, the second highest maximum (after $m = 0$) in the autocovariogram usually corresponds to the frequency bin containing the pulse repetition frequency. Sometimes this maximum represents the second, and in rare cases the third harmonic. A simple heuristic algorithm which checked for local maxima at 1/2 and 1/3 of the offset of the second highest maximum (Buck and Tyack, 1993), accounted for this.

Figure 1 shows a spectrogram of an N4 call and a frequency contour extracted from it. Figure 2 gives the power spectrum and its covariance sequence at t = 1091ms for the same call. For subsequent analysis, the pulse repetition frequency was determined at 100 equally spaced points throughout the call. Thus calls were essentially standardized for time. However, call length was entered as a separate variable in the analysis to allow discrimination of calls which differed consistently in length, but not in structure.

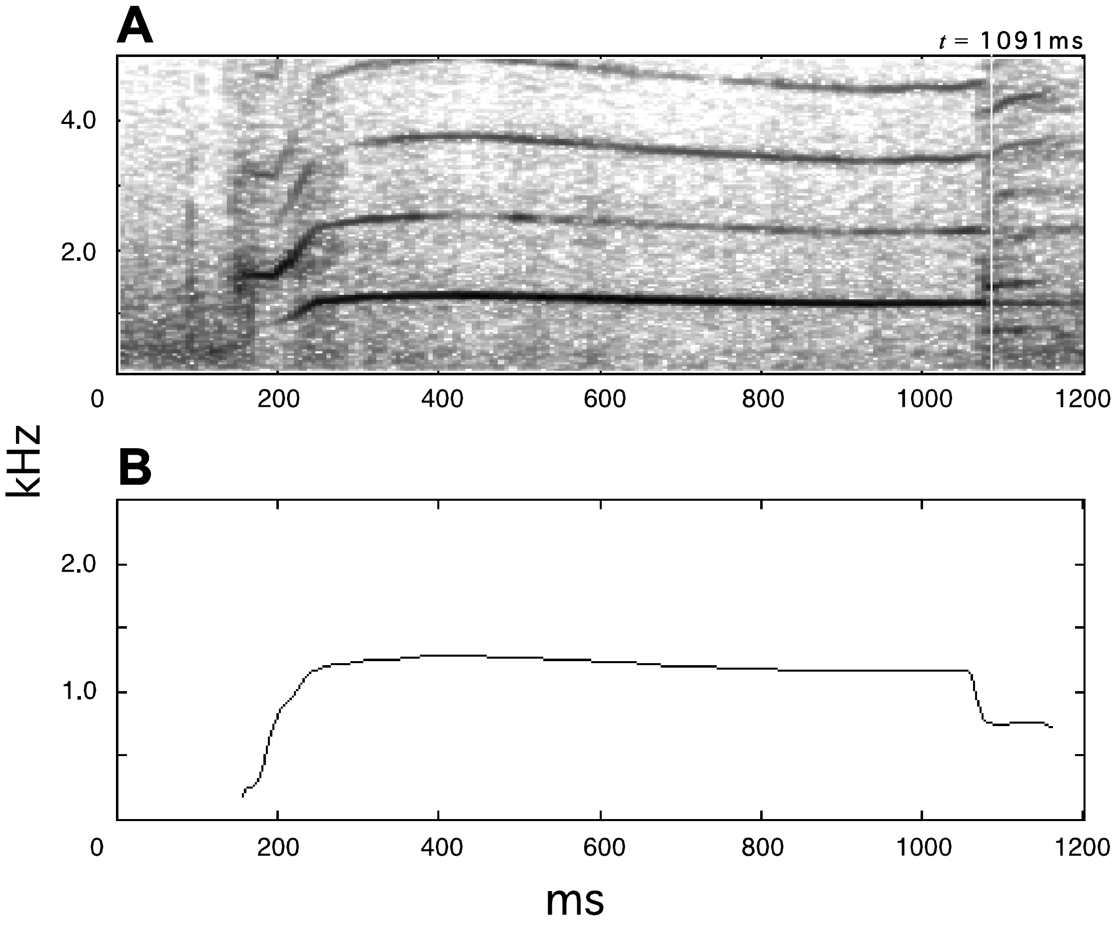


Figure 1: A) Spectrogram of an N4 call. The white line at *t* = 1091ms shows the position of the power spectrum in Figure 2. **B)** Frequency contour extracted from the spectrogram.

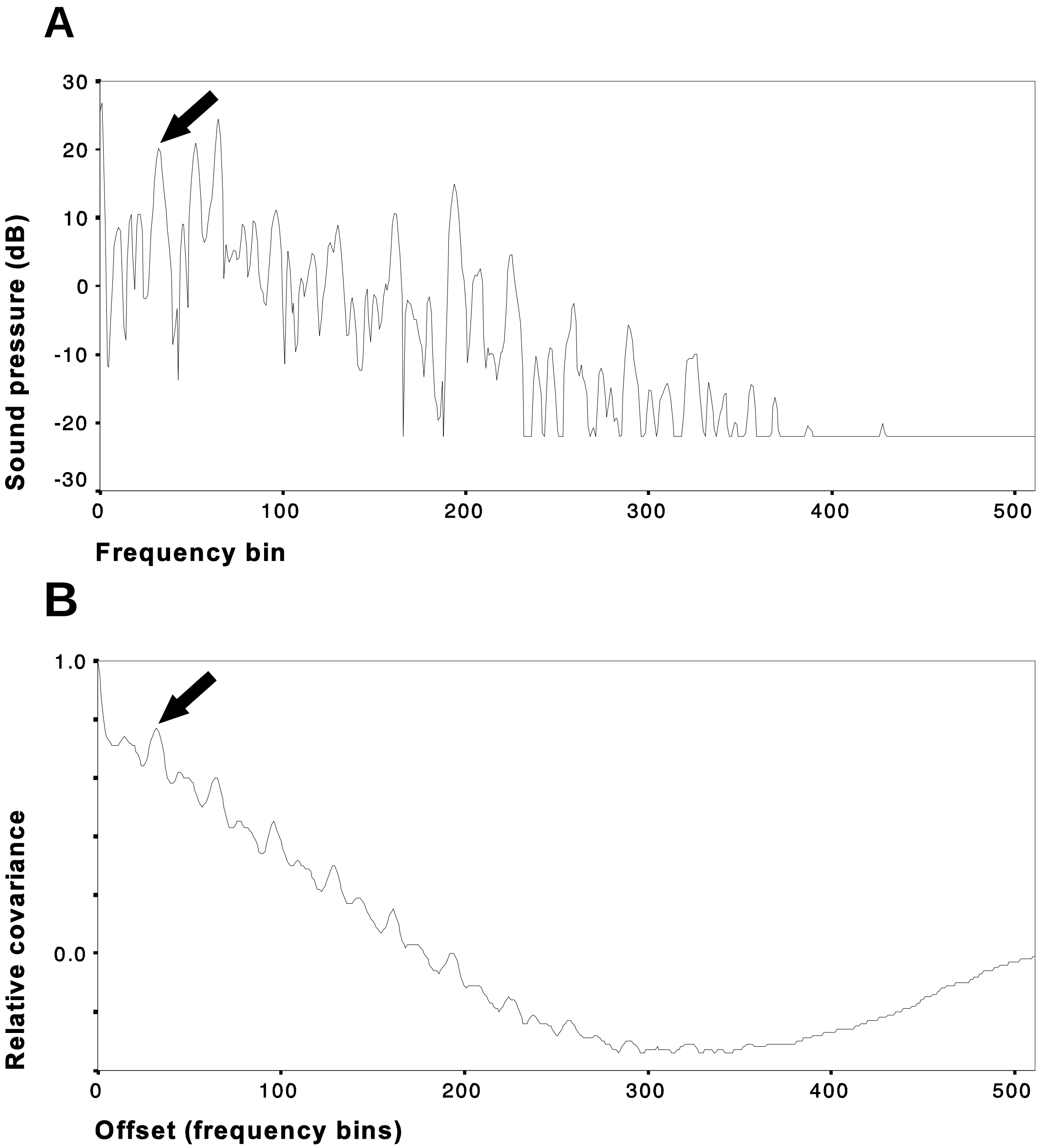


Figure 2: A) Power spectrum of the terminal component of the N4 call in Figure 1 at *t* = 1091ms. Note that the peak sound pressure represents the echo of the main part of the call rather than the pulse repetition frequency of the terminal component (arrow). Frequency resolution is 21.53 Hz per frequency bin. **B)** Autocovariogram of the power spectrum. The arrow indicates the frequency bin containing the pulse repetition frequency**.**

Neural network analysis

For the subsequent analyses, I used a standard backpropagation network (e.g., Rumelhart et al., 1986) with momentum and an adaptive learning rate (Vogl et al., 1988). The algorithms are part of the neural network toolbox of MATLAB 4.2 for the Macintosh. The input size was 101 (100 frequency points plus call length). Since I performed pairwise comparisons, output number was 2.

The number of neurons in the hidden layer (Rumelhart et al., 1986), and the number of training iterations were determined from a set of network design experiments which included comparisons of one call type 1) by the same matrilineal unit from the same 3 recording sessions, 2) by the same matrilineal unit from different recording sessions, 3) by two matrilineal units from the same pod, and 4) by two matrilineal units from different pods. The results suggested that discrimination did not improve detectably when using more than 20 hidden neurons and training for more than 5000 iterations, so that these values were used for subsequent analyses. Neural networks were initialized with random weights, and a small number of neural networks did not significantly improve their performance from the initialized state. Since this failure to train results from the configuration of the weights at initialization rather than a lack of consistent variation in the training sets, such networks were excluded from the analysis by setting a criterion of a decrease of 20% in the training error during the first 150 iterations.

So as to reduce the stochastic component inherent in neural network analysis, I trained as many networks as possible on each comparison between the calls of two groups. To do this, one frequency contour was excluded from the training set. The network was trained on the remaining contours to associate each contour with its respective output ([1 0] or [0 1], according to which group it came from), and the neural network was used to classify the excluded contour. This 'jack-knifing' procedure was repeated until each contour had served as a test contour. For a sample size of n contours from two groups, a total of $2*n$ neural networks were trained on the same problem.

I assessed the performance of the neural network for each test by calculating the discrimination error. This parameter was computed by subtracting the observed output of the neural network from the expected output ([1 0] or [0 1]) and taking the average of the absolute difference. I chose the average discrimination error of all networks trained on one pairwise comparison over the proportion of misclassifications, because the discrimination error not only yields information on whether a classification was correct, but also gives a relative measure of the quality of discrimination.

Demonstrations

The simulated frequency contours for the demonstration experiments consisted of 101 equally spaced points of a sine function between -π and π with an amplitude of 1. Two levels of noise were introduced to the data set. Variation in the structure of the contour was simulated by jittering each contour with random noise with a variance of 0.1. Variation in the frequency domain was simulated by raising or lowering each frequency contour by a constant from a random distribution with a variance of 0.1.

Demonstration 1: The effect of frequency differences

In order to illustrate the effect of overall differences in frequency, the 24 examples of one of the two patterns were increased by multiples of 0.05 (i.e., half of the variance of the random variability in the frequency domain). 48 neural networks were trained for each increment by the method explained above, and the average discrimination error was calculated.

Demonstration 2: The effect of localized structural differences

In order to test whether the neural network is sensitive enough to detect highly localized differences between two patterns, a single point of the simulated contours was increased by multiples of 0.05 in one pattern, but not in the other, and 48 neural networks were trained as above. The average discrimination error was computed as explained above.

Analysis of acoustic variation in the N4 call type

To test the performance of the neural network index on biological data, I used recordings of 9 matrilineal units of killer whales. Matrilineal units consisted of between 2 and 7 individuals (Appendix II), and belong to A-subclan of the northern resident community (Ford, 1989) which inhabits the waters of British Columbia, Canada. The analyses were restricted to recordings in which only one of the matrilineal units was within recording range and was identified visually or photographically (Appendix I). I chose the N4 call type (Ford, 1989, 1991, see Figure 18) for this study, since it is shared by all 9 groups, and because it is one of the most frequently used call types in the groups' repertoires.

Structurally, the N4 calls of A08, A09, A23, A25, and A36 all have relatively low peak frequencies, and a pronounced terminal component at the end of the call (Part 2 of Ford, 1987; see Figure 18). The versions of N4 made by A12 and A30 subpods usually lack the terminal component and have a relatively higher peak frequency. Finally the N4 calls of A11 and A24 subpods (A04 pod of Ford, 1991) tend to be longer than those of any other matrilineal unit and generally end in an upsweep.

N4 calls with adequate signal-to-noise ratios were identified acoustically and visually from recordings, and were digitized using the Canary 1.2.1 sound analysis software. Spectrograms were computed and frequency contours extracted with the sidewinder algorithm. Since the performance of a neural network is highly dependent on the number of examples for each pattern in the training set, sample size for all matrilineal units was standardized to 24, the size of the smallest sample. For each group I included calls from as many independent recording sessions as possible, to present the neural network and the human subjects with calls from a wide range of behavioural contexts, which are known to affect call structure (Ford, 1989). No less than three independent recording sessions were used for any one matrilineal unit (Appendix I). The average discrimination error was generated for all 36 pairwise comparisons of the calls of the 9 matrilineal units.

Classification by human observers

The same 9 samples of 24 calls each were used to determine the classification errors of human observers in pairwise computer-based discrimination tasks. Three female subjects, none of whom had any previous knowledge of killer whale vocal communication, were presented with the discrimination tasks. Subject A was 20 years old and had no musical background. Subject B was 22 years old and had played the flute for 2 years, and Subject C was 20 years old and had played the piano for 13 years.

In each discrimination task, the subject was first presented with a training set of 16 calls belonging to two categories (*a* or *b*) according to the group they came from. The subject could listen to the calls and view their spectrograms, and was then asked to assign a test set of 32 unknown calls to the appropriate category. The classification error gives the proportion of misclassifications among these 32 calls. During the testing, the subject was allowed to return to the training set, but in order to cause her to generalize, was asked not to do so more than 3 times for each discrimination task. Following the experiments, the subjects completed a questionnaire asking whether they classified the calls primarily using acoustic or visual cues.

RESULTS

The sidewinder algorithm proved effective at extracting frequency contours from recordings obtained under a variety of recording conditions. Frequency contours could be obtained from recordings even with high levels of ambient noise if the call was clear and the energy in two or more harmonics exceeded the background noise level. Only recordings containing boat noise with harmonic content, and recordings with a great amount of acoustic reverberation or strong echoes, caused problems in the contour extraction.

Both demonstration experiments show a consistent improvement of neural network discrimination, as the ratio between random variation, applied to both patterns, and consistent variation between the two patterns increases (Figures 3 and 4).

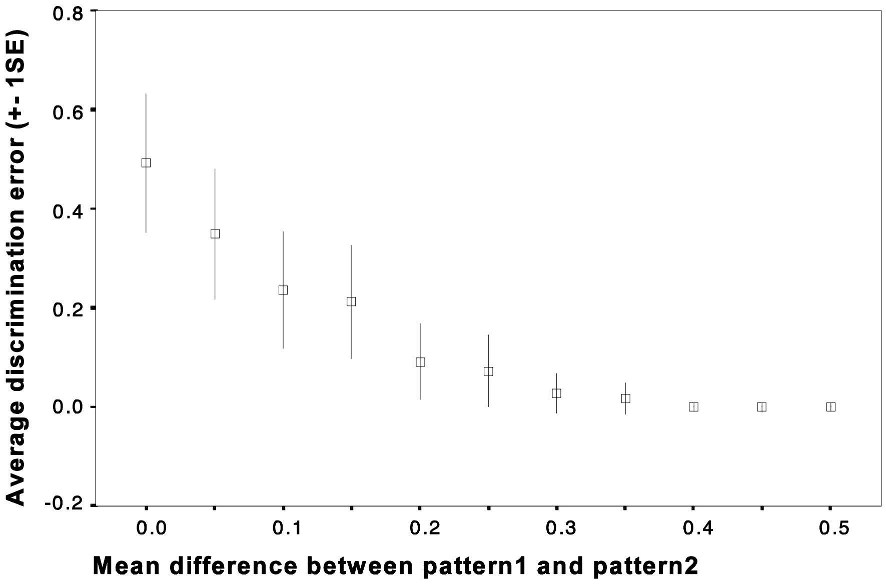


Figure 3: The effect of global differences in contour frequency on neural network discrimination (Demonstration 1).

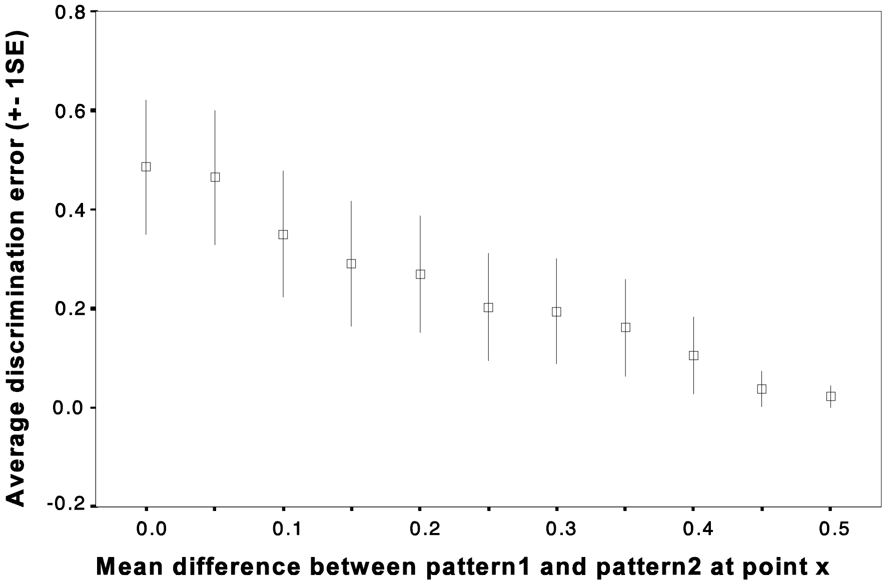


Figure 4: The effect of localized differences in call structure on neural network discrimination (Demonstration 2).

In Demonstration 1 (Figure 3), where the entire pattern was increased in one sample, the average discrimination error drops off rapidly, and reaches near-perfect discrimination at an increase of 0.4 (i.e., 4 times the variance of the background variability). Demonstration 2 (Figure 4), in which only a single point of one pattern was increased, shows that the neural network is able to detect highly localized but consistent differences in contour shape and frequency.

The average discrimination errors of the neural network for the pairwise comparisons of N4 calls ranged from 0.01 (A23 subpod vs. A24 subpod) to 0.48 (A09 subpod vs. A25 subpod; Table I). The average for all discrimination tasks was 0.15. The neural network index grouped the nine matrilineal units into three major clusters according to the similarity of their N4 calls. These are A08-A09-A23-A25-A36, A12-A30, and A11-A24 (Figure 5). These clusters are consistent with structural differences in the calls shown in Figure 18.

Table I: Network performance (average discrimination error) for the pairwise comparisons of N4 calls of the 9 matrilineal units.

	A08	**A09**	**A11**	**A12**	**A23**	**A24**	**A25**	**A30**
A09	0.343							
A11	0.091	0.041						
A12	0.048	0.025	0.080					
A23	0.183	0.194	0.040	0.042				
A24	0.100	0.030	0.285	0.078	0.013			
A25	0.428	0.477	0.039	0.050	0.233	0.033		
A30	0.138	0.061	0.071	0.277	0.086	0.098	0.062	
A36	0.266	0.397	0.065	0.059	0.189	0.059	0.373	0.098

Table II: Classification errors (proportion of misclassifications) of the three subjects for the pairwise discrimination tasks of N4 calls.

	Subject								
	A	0.438							
A09	**B**	0.250							
	C	0.625							
	A	0.125	0.219						
A11	**B**	0.250	0.063						
	C	0.156	0.031						
	A	0.156	0.063	0.063					
A12	**B**	0.094	0.094	0.094					
	C	0.063	0.094	0.031					
	A	0.500	0.250	0.031	0.250				
A23	**B**	0.188	0.469	0.031	0.094				
	C	0.188	0.531	0.000	0.031				
	A	0.250	0.281	0.438	0.281	0.031			
A24	**B**	0.156	0.063	0.375	0.219	0.031			
	C	0.188	0.063	0.281	0.000	0.031			
	A	0.438	0.500	0.031	0.219	0.406	0.156		
A25	**B**	0.438	0.500	0.125	0.094	0.375	0.031		
	C	0.250	0.344	0.125	0.000	0.375	0.000		
	A	0.125	0.125	0.219	0.313	0.094	0.375	0.063	
A30	**B**	0.094	0.125	0.094	0.375	0.000	0.031	0.063	
	C	0.063	0.125	0.000	0.406	0.000	0.000	0.000	
	A	0.344	0.250	0.219	0.344	0.438	0.219	0.500	0.375
A36	**B**	0.094	0.281	0.156	0.156	0.156	0.125	0.313	0.313
	C	0.219	0.188	0.125	0.125	0.281	0.063	0.250	0.281
		A08	**A09**	**A11**	**A12**	**A23**	**A24**	**A25**	**A30**

The results of the classification tasks show that Subjects B and C classified all calls correctly in at least one comparison (Table II). The greatest classification error was higher than random (0.625, A08 vs. A09 by subject C; $p = 0.053$). The average classification error for all discrimination tasks was 0.254, 0.178, and 0.154 for subjects A, B, and C respectively, and a binomial test showed that Subject A had significantly higher classification errors than the other two subjects ($p < 0.001$). The classification errors of the three subjects for any one comparison differed on average by 0.105, and the differences ranged from 0 to 0.375. Subjects A and C said that they used mainly acoustic and some visual cues to do the discrimination. Subject B said she relied mainly on the spectrogram, with some acoustic cues. All three subjects grouped the calls of the nine matrilineal units into three major clusters (Figure 6) which correspond to the clusters generated by the neural network index (Figure 5). However, the results from individual subjects differ in the relationship of matrilineal units within the three clusters, as well as in the positions of the clusters with respect to each other.

Table III gives the correlation matrix of the ratings of acoustic similarity by the three subjects, and by the neural network. All correlations are significant with $p < 0.001$. Two correlation coefficients comparing ratings of different subjects (Subjects A and B; Subjects A and C) are lower than the correlation coefficients comparing human subject ratings and the neural network indices.

Table III: Correlation matrix giving Pearson's coefficient of correlation for the ratings of acoustic similarity by the human subjects and the neural network index. All coefficients are significant with $p < 0.001$.

	Subject A	Subject B	Subject C	Neural Network Index
Classification Error Subject A	1			
Subject B	0.626	1		
Subject C	0.599	0.789	1	
Neural Network Index	0.702	0.775	0.699	1

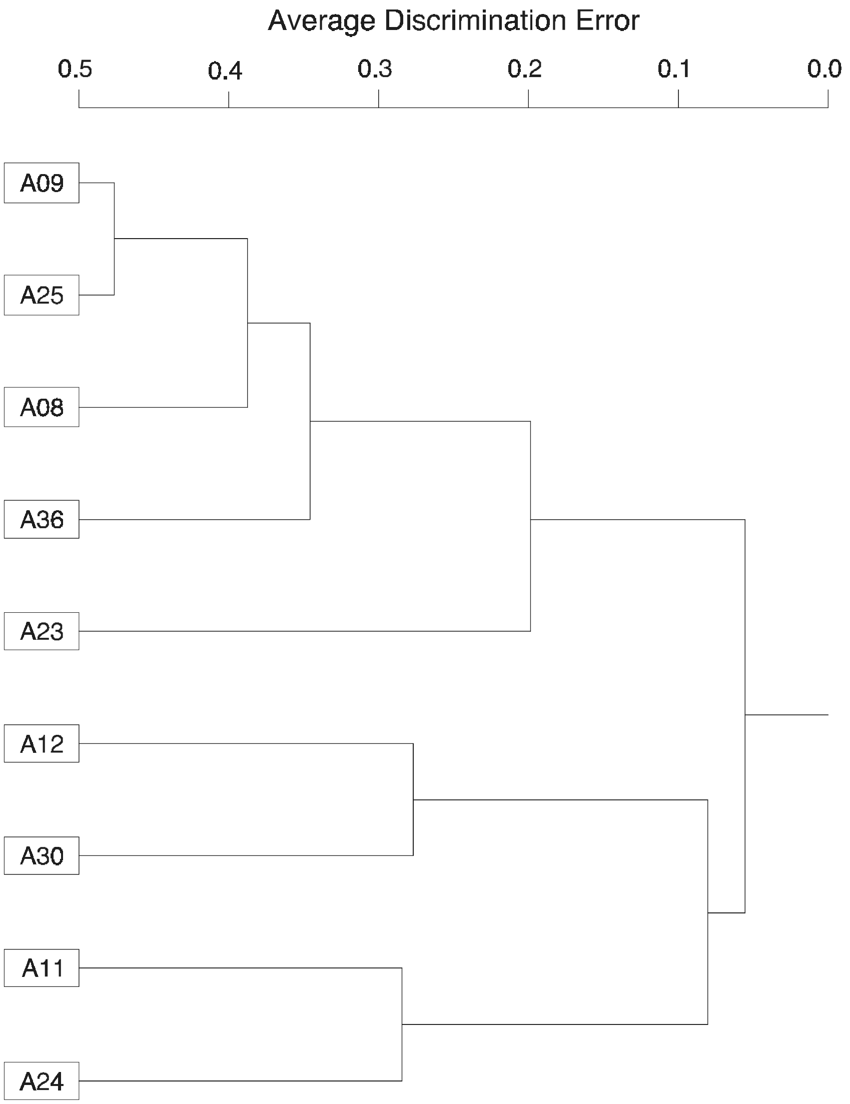


Figure 5: Average linkage dendrogram giving structural similarity of the N4 call type of the 9 matrilineal units of A-subclan based on the neural network index.

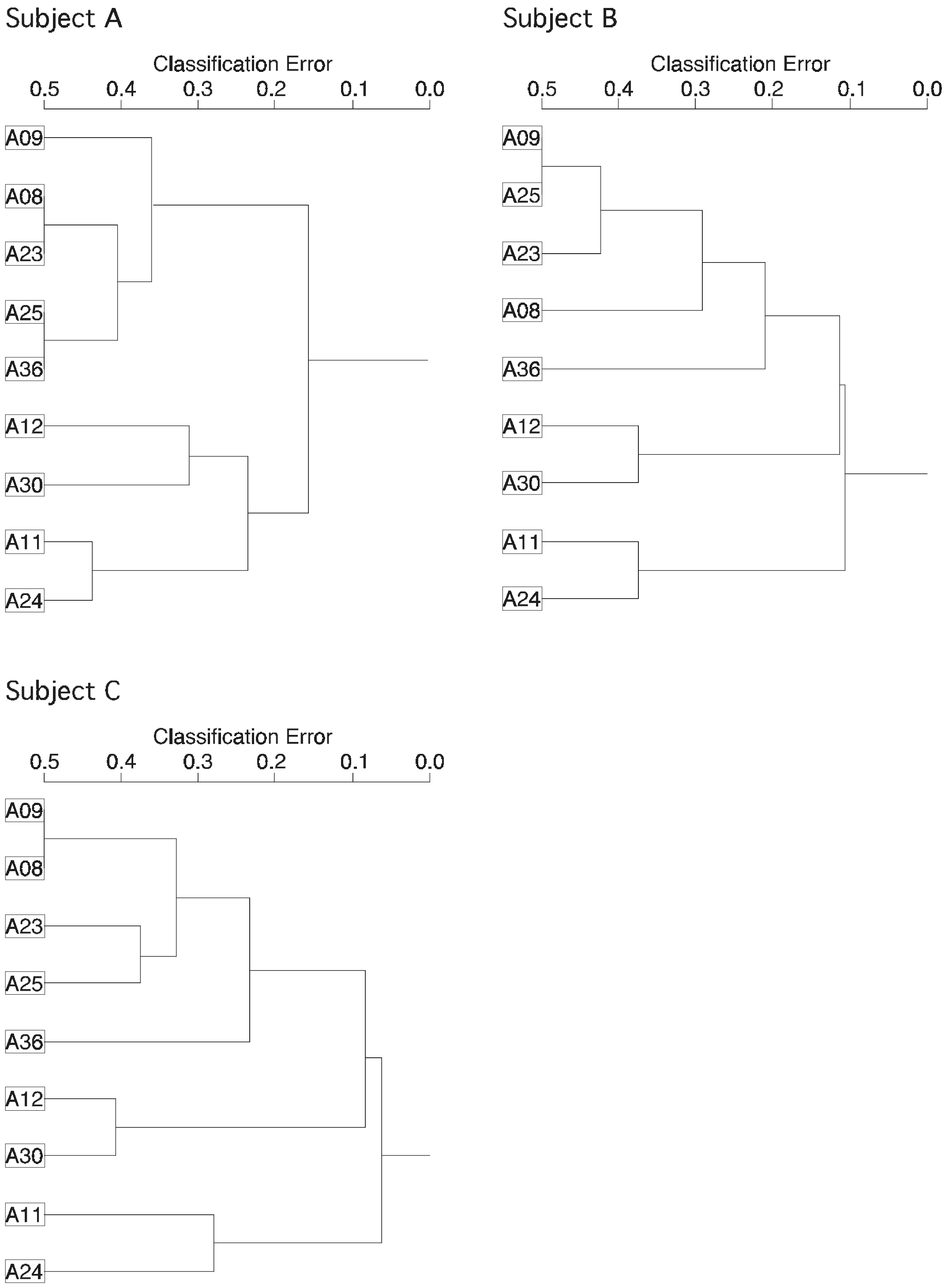


Figure 6: Average linkage dendrograms giving structural similarity of the N4 call type of the 9 matrilineal units of A-subclan based on the classification errors of three human subjects.

DISCUSSION

The contour extraction algorithm based on autocovariance in the frequency domain proved effective for extracting frequency contours from recordings with poor signal-to-noise ratios. Unless the noise itself had harmonic content, it was cancelled out in the autocovariogram, whereas the harmonic signal was amplified. I believe that this algorithm will be useful for extracting frequency contours from noisy recordings of the vocal signals of a wide variety of species, as long as the signal has harmonic content.

The shortcomings of this algorithm are that it cannot be applied to broad-band or pure-tone signals, and that compared to alternative algorithms, it is computationally expensive. Mixed signals, however, can still be analysed by switching to another algorithm (e.g., Buck and Tyack, 1993) if the autocovariogram fails to show harmonic content. Recent developments in computer hardware are likely to further reduce computing time, making real-time frequency contour extraction using this algorithm a possibility.

The advantage of using frequency contours over isolated measurements of the spectrogram lies in the fact that analysis of frequency contours requires no prior knowledge of where to expect the differences in the signals (Bailey, 1978). Subtle and localized differences between two signal patterns are easily missed in conventional analyses by taking measurements of a limited number of structural variables. Unlike discrimination and classification analyses of bioacoustic signals where the input is the waveform (e.g., Neumann et al., 1992), or the spectrogram (e.g., Spong et al., 1993; Erbe, 1997), amplitude information is excluded from the analysis of frequency contours. Although this may be a disadvantage in some studies analysing recordings obtained in controlled environments, it will prove beneficial in others where differences in recording equipment and in the composition of background noise introduces spurious variability into the data. For example, in the study of Spong et al. (1993) it cannot be ruled out that the neural network discriminated along differences in background noise composition rather than individual-specific vocal differences.

The demonstration experiments show that the neural network index responds well both to global variation in frequency, as well as to highly localized variation in contour shape and frequency. The neural network index therefore is able to use structural features such as terminal components (Figure 1, Figure 18), as well as the terminal upsweeps typical of N4 calls of A11 and A24 subpods (see Figure 18) to make its discrimination. Demonstration 2 furthermore shows that the neural network can discriminate between samples of calls which consistently differ in length, but not in structure, since call length was entered into the analysis as a separate variable.

Although the ratings of similarity by the three human subjects agree on a fundamental level, this study suggests that individual human subjects perceive similarity of killer whale calls differently. The ratings of similarity disagree between subjects in the acoustic relationships of matrilineal units within the three clusters, as well as in the position of these clusters with respect to each other. The subject who had never played a musical instrument had significantly higher classification errors than the other two subjects, which may suggest that the amount of musical exposure contributes to the variation among observers (see Halpern et al., 1995; Baribeau et al., 1996; Halpern et al., 1996).

Comparing the ratings of acoustic similarity by the neural network with those of the human subjects showed that both ways of quantifying acoustic variation gave very similar results. The correlation coefficients (Table III) show that the differences between ratings from individual subjects are greater than are subject ratings from the neural network index. Since multiple independent neural networks are trained on the same problem in each comparison, the neural network index will give essentially identical results given the same input data. A neural network based index therefore represents an objective and repeatable means of measuring acoustic similarity, and allows the comparison of results across studies, species, and time.

Like discriminant function analysis (e.g., Job et al., 1995), or analysis of confusion frequencies (e.g., Miller and Nicely, 1955; Loesche et al., 1992), the neural network index of acoustic similarity is based on the premise that similarity and discrimination are inversely related. All three methods rate patterns as similar if the analysis is unable to tell them apart, and conversely consider pattens distinct if the analysis can consistently discriminate between them. This concept of similarity differs from that underlying other methods of analysis which use the geometric distance between two patterns as a measure of their similarity. Examples for the latter are cross correlation (e.g., Clark et al., 1987), and cluster analysis (e.g., McCowan, 1995). Arguably, the first concept of similarity is more applicable to the study of communication, since the information value of a signal is largely determined by how well a receiving animal can distinguish it from competing signals (Beecher, 1989). One difficulty inherent in all measures of acoustic similarity is that animals may not be able to detect all parameters entered in the analysis (see Emlen, 1972), and applying knowledge about the perceptive abilities of the study species when choosing which parameters to include will increase the biological validity of any measure of acoustic similarity.

The training procedure, which involves error back-propagation to discriminate between different patterns, is essentially a self-organizing process and does not depend on strictly linear relationships in the input data. A neural network index will therefore be able to detect and integrate differences between the input patterns that would be missed by most conventional statistical analyses. Research into biological neural systems suggests that these also operate in a non-linear and self-organizing way (Kelso, 1995), which may explain why a neural network based approach is often the best way to model biological signal processing tasks (e.g., Hunt, 1993; Erbe, 1997). The fact that the neural network index of acoustic similarity shows a significant correlation with the association patterns of the matrilineal units in Chapter III suggests that the index rates acoustic similarity in a biologically meaningful way.

An index of acoustic variation based on neural network analysis can be viewed as a hybrid between statistical and perceptive approaches of measuring acoustic similarity. It combines the objectivity and repeatability of a strictly statistical approach with the self-organizing non-linear nature of acoustic perception and biological signal processing, and therefore holds great potential in the study of human and animal communication.

CHAPTER II: Mechanisms and Rates of Vocal Differentiation in Resident Killer Whales

INTRODUCTION

Kroch (1989) and Payne (1996) both point out the importance of a historical approach to the study of vocal dialects. In order to understand patterns of vocal variation in space and among different individuals or social groups, it is essential to identify the mechanisms that generate change, and to document dialect evolution over time. Whereas geographic variation or acoustic differences among individuals and social groups are relatively easy to assess at a single point in time, studying temporal change is a logistic challenge, especially in a long-lived species. Most of our knowledge about the patterns and mechanisms of vocal differentiation with time therefore comes from songbirds, which are relatively short lived, and from humans, where there is a wealth of historical data.

Studies of dialect change in songbirds (e.g., Ince et al., 1980; Payne et al., 1981; Trainer, 1989; Chilton and Lein, 1996; Payne, 1996) have shown varying rates of modification of the vocal signals ranging from detectable change within a single breeding season in yellow-rumped caciques (*Cacicus cela* ; Trainer, 1989) to no detectable structural change over a 20 year period in white-crowned sparrows (*Zonotrichia leucophrys* ; Chilton and Lein, 1996). Although the changes observed in many studies can be explained by random drift (Williams and Slater, 1990), modifications to vocal signals over time may be directional. Lehtonen (1983) documented a directional shift towards song phrases with fewer elements among a population of great tits (*Parus major*) over 34 years which he attributed to increased population density and background noise levels. Gibbs (1990) showed that male medium ground finches (*Geospiza fortis*) singing rare song variants have greater reproductive output. Since juvenile medium ground finches tend to learn the song variant of their fathers, the dialect system contains an element of negative feedback with rare song variants gradually increasing in frequency, while common ones decrease.

Research on temporal change in human languages suggests that the cultural transmission of new linguistic variants follows a sigmoid trajectory. Several studies (e.g., Bailey, 1973; Kroch, 1989; Santorini, 1993) have shown that the frequency of use of new linguistic variants increases slowly in the period immediately after their introduction. Subsequently, the rate of increase rises as the variant becomes more common, and eventually levels off again, as its proportion approaches unity. In humans, dialect change can therefore be modelled by a logistic function (Bailey, 1973; Kroch, 1989). This suggests that the probability of any individual to take over the a new variant primarily depends on its frequency of occurrence in the population.

Vocal change can occur on several distinct levels. In bird song, Marler and Peters (1982), and Lynch (1996) distinguish between *mutational change*, defined as the modification of individual song elements and *recombinational change*, change in the sequence of these elements in the song. Similarly, human languages undergo change on various distinct levels (Bailey, 1973)*. Phonological change* affects the pronunciation of words, and is analogous to mutational change of Lynch (1996)*. Syntactic change* affects the order of words within sentences, and is the linguistic analogue of recombinational change. The third level, *lexical change*, affects the meaning and usage of words.

Killer whale dialects can potentially evolve on two levels. First of all, dialects may evolve through modification of the vocal repertoire, the discrete call types used by a group. Vocal repertoires of killer whales can change through extinction of existing call types, spontaneous generation of new ones, or shifts in the frequency of use of certain discrete calls (Ford, 1991). In addition, the structure of the discrete calls themselves can change, and the fact that different social groups have structurally distinct versions of the same call types (Ford, 1984, 1987, 1989, 1991) is indirect evidence for change at the structural level. Ford’s work (Ford, 1984, 1991) suggests that the vocal repertoires of resident killer whales are extremely stable. The call types produced by pod J01 of the southern resident community remained essentially the same from 1958 to 1986, and the same is true for the frequency of use of different discrete calls. Studies of captive killer whales (Bain, 1986, 1988; Ford, 1989), have shown that individuals retain most if not all of the call types of their social group after more than a decade in captivity.

Although we know that individual call types do not become modified beyond recognition over a 30 year period, so far no study has looked at modifications to the structure of discrete calls with time. In this chapter, I compare the calls made by A12 and A30 subpods of the northern resident community (Bigg et al., 1990; Ford et al., 1994) over a 12 year period. I chose these matrilineal units because of all northern resident matrilineal units, they are the ones encountered most frequently. The composition, genealogies, and demographic changes for both groups are given in Appendix II (Figures A-4 and A-5). The first objective of this analysis is to test for the presence of temporal change in the structure of discrete calls. If the structure of the calls is being modified, a sufficiently sensitive measurement of acoustic similarity comparing samples of calls from the same group should give lower ratings of similarity, the farther the samples are apart in time.

The two matrilineal units examined in this analysis still associate frequently, and any modifications to the structure of call types could be transferred between the two groups by copying. My second objective is to test for the presence of cultural transmission between the two groups. To do this, I determine the rate of vocal differentiation between the groups by comparing their calls and measuring acoustic similarity at various points in time. The effects of any structural modifications to the calls in both groups on the acoustic similarity index should be cumulative, if modification of call structure occurs independently in both groups. In this case, I expect the rate of differentiation between groups to be at least as great as the rate of modification in any one group. If, on the other hand, structural modifications to the calls are transferred between groups, the rate of vocal differentiation should be lower than the rate of modification.

Finally, this study aims to determine which, if any, structural parameters of the calls are being modified. This analysis will test whether modifications to the calls are directional, and whether structural modifications occur in parallel in both groups. Directional change would suggest active modification of the call types, whereas non-directional change would support cultural drift in the structure of calls. Additionally, if structural modifications of the call types are transferred between the groups, structural parameters should show similar trends in the calls of both groups.

METHODS

Underwater recordings were contributed by a number of researchers, and were made using a variety of hydrophones and recording equipment. The recordings covered the period from 1984 to 1997. The analysis was mostly restricted to recording sessions where only one matrilineal unit was within recording range, and was identified visually or photographically by an experienced observer. However, in 8 recording sessions, one of the two matrilineal units and another group belonging to a different acoustic clan and thus not using any of the call types analysed in this study, were within recording range (Appendix I, Tables A-V and A-VI).

Suitable calls were identified acoustically and visually from the recordings and digitized using the Canary 1.2.1 sound analysis software. Sufficient sample sizes were available for the two most commonly used call types, N4 and N9 (Ford, 1991). For the reasons outlined in Chapter I, sample size needed to be standardized, and it was set to 24 for the N4 call type, and 21 for the N9 call types. Calls were selected to maximize the number of independent recording sessions in each sample to include within-group and context-related variability. No sample contained calls from fewer than three independent recording sessions (Appendix I; Tables A-V, and A-VI). Because insufficient N9 calls were available for the A12 subpod from 1986, this sample also includes two calls from 1984 (Table A-V). Spectrograms were computed from the calls, and frequency contours extracted by the method explained in Chapter I. The input for the neural network again consisted of 100 points of the frequency contour and call length as a separate variable.

Test for call modification

To determine whether the calls had been modified over the 12-13 year period, neural networks were trained for all possible year to year comparisons for both groups and both call types (refer to Chapter I for details on the training procedure). Since sample size was 24 for the N4 call type, and 21 for the N9 call type, 48 and 42 neural networks respectively were trained and tested for each year to year comparison. A linear regression model was used to determine the rate of call modification, β_{within}, expressed as the rate of decrease with time of the acoustic similarity index. By generating all possible pairwise comparisons between call samples from all years, s samples were used to generate n comparisons, where:

$$n = \frac{s*(s-1)}{2} \qquad \textbf{(2)}$$

Hence autocorrelation was known to be a problem, but the structure of the autocorrelation was unknown. I therefore assumed that all data points generated with the same sample were correlated, and used the number of samples s (i.e., the minimum number of independent data points), rather than the number of comparisons n, to obtain degrees of freedom for all tests of significance. A one-tailed t-test was used to test whether the acoustic similarity index showed a significant decrease with time. The standard error SE of the slope β_{within} was calculated using the formula:

$$SE_{\beta_{within}} = \sqrt{\frac{RSS_{within}}{RDF_{within}*(\sum x^2)_{within}}} \qquad \text{Weisberg (1985)} \qquad \textbf{(3)}$$

where RSS_{within} is the residual sum of squares of the regression, RDF_{within} are the residual degrees of freedom (i.e., s - 2), and $(\sum x^2)_{within}$ is the sum of squares of X values for the year to year comparisons (Zar, 1996).

Test for horizontal transmission

In order to determine whether the acoustic similarity of the calls of the two matrilineal units had changed over the study period, neural networks were trained to discriminate between the calls of the two groups for all years from which samples were available. Since no samples could be obtained from A12 subpod in 1985, and from A30 subpod in 1986, the call samples from A12 in 1986 were compared to the respective A30 samples in 1985. The rate of acoustic differentiation between the two groups, $\beta_{between}$, was determined by applying a linear regression model to the acoustic similarity indices, and a two-tailed t-test was used to test whether $\beta_{between}$ was significantly different from 0. To see whether the rate of differentiation was significantly lower than the rate of call modification in both groups, I used a one-tailed t-test (Zar, 1996). Again, to correct for possible autocorrelation in the within-group comparisons, the number of samples was used to obtain degrees of freedom. Therefore, the formula for the standard error of the difference between the slopes is:

$$SE_{\beta_{between}-\beta_{within}} = \sqrt{\frac{(s^2_{X*Y})_\beta}{(\Sigma x^2)_{between}} + \frac{(s^2_{X*Y})_\beta}{(\Sigma x^2)_{within}}} \qquad \text{Zar (1996)} \qquad \textbf{(4)}$$

where the pooled residual mean square is calculated as:

$$(s^2_{X*Y})_\beta = \frac{(RSS_{between} + RSS_{within})}{(RDF_{between} + RDF_{within})} \qquad \text{Zar (1996)} \qquad \textbf{(5)}$$

In **(5)**, RDF_{within}, the residual degree of freedom of the within group comparisons, is again obtained from the number of samples (i.e., s-2) rather than from the number of comparisons.

Analysis of call structure

Since the test for call modification did not detect any changes in the N9 call type, this analysis was limited to the N4 call type. Four structural parameters were analysed for temporal change in each group: frequency of the plateau near the end of the call, call length, peak frequency, and position of the frequency peak in the call (Figure 7). These parameters were chosen by training a neural network to discriminate between the two earliest and latest samples from each group. In order to identify the points of the frequency contours that were important to neural network discrimination, the neural network was tested with contours not used in training. One point of the test contour was substituted with the corresponding point from a contour belonging to the other pattern. The contour was tested again, and the effect of the substitution was assessed by subtracting the discrimination error from the test contour without substitution from the resultant discrimination error. One by one, the contribution of each point of the contour to neural network discrimination was examined in this way. Plotting the change in discrimination error with reference to the frequency contour identified the parts of the call that showed the greatest amount of consistent variation between the two samples compared.

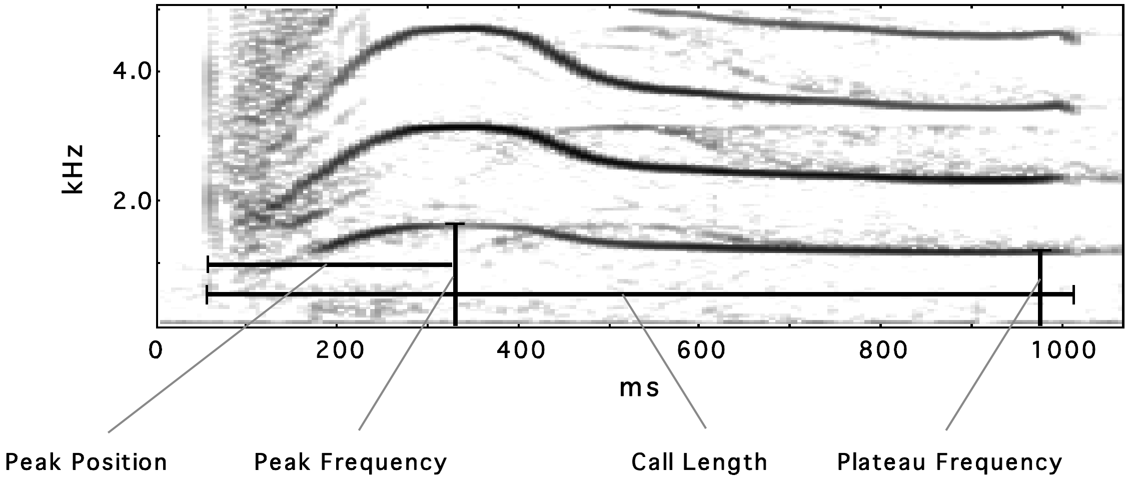


Figure 7: Spectrogram of an N4 call showing the parameters analysed in the comparisons of call structure.

Measurements for the four structural parameters analysed were extracted from the samples of frequency contours. Since it was not necessary to standardize sample size for this analysis, frequency contours not used in the neural network analysis were also included. Mean values and 95% confidence intervals for the four parameters were calculated for each group and each year, and the yearly means were compared by calculating Pearson's coefficient of correlation ($R_{A12\text{-}A30}$; Zar, 1996) to test for any parallel changes to the calls in both groups.

RESULTS

Test for call modification

N4 call type

The acoustic similarity indices for the year to year comparisons of the N4 calls ranged from 0.232 to 0.552 for the A12 subpod, and from 0.210 to 0.522 for the A30 subpod (Tables IV and V; Figure 8A and B). The results show a significant decrease in discrimination error with increasing time between the call samples (A12 subpod: R^2 = 0.435, $\beta_{within\ A12}$ = -0.0219, p = 0.019; A30 subpod: R^2 = 0.299, $\beta_{within\ A30}$ = -0.0150, p = 0.041). This shows that the variation between the samples becomes more consistent with increasing time between them, and is conclusive evidence that both matrilineal units modified the structure of their N4 call type over a period of 12-13 years.

N9 call type

Acoustic similarity indices for the comparisons of the N9 call type ranged from 0.380 to 0.536 for the A12 subpod and from 0.227 to 0.523 for the A30 subpod (Tables VI and VII; Figure 9A and B). Unlike the N4 call type, the results show no relationship between the similarity ratings and the time between the call samples, and the rates of call modification for both groups are not significantly different from zero (A12 subpod: R^2 = 0.003, $\beta_{within\ A12}$ = 0.0009, p = 0.449; A30 subpod: R^2 = 0.004, $\beta_{within\ A30}$ = -0.0015, p = 0.433). The N9 call type, therefore, did not undergo any detectable modification over the period of study.

Table IV: Acoustic similarity indices for the year to year comparisons of N4 calls by A12 subpod (n=24 for each year).

1986	-											
1987	-	-										
1988	-	0.424	-									
1989	-	-	-	-								
1990	-	0.423	-	0.393	-							
1991	-	0.243	-	0.326	-	0.328						
1992	-	0.232	-	0.321	-	0.283	0.528					
1993	-	0.271	-	0.298	-	0.411	0.460	0.328				
1994	-	0.273	-	0.284	-	0.383	0.397	0.347	0.552			
1995	-	0.239	-	0.271	-	0.309	0.447	0.439	0.463	0.452		
1996	-	0.264	-	0.238	-	0.409	0.408	0.338	0.455	0.454	0.408	
1997	-	0.266	-	0.266	-	0.361	0.445	0.368	0.488	0.508	0.516	0.414
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**

Table V: Acoustic similarity indices for the year to year comparisons of N4 calls by A30 subpod (n=24 for each year).

1986	-											
1987	-	-										
1988	0.383	-	-									
1989	0.437	-	-	0.401								
1990	0.381	-	-	0.365	0.410							
1991	0.423	-	-	0.381	0.490	0.316						
1992	0.418	-	-	0.423	0.470	0.404	0.441					
1993	0.416	-	-	0.386	0.508	0.363	0.472	0.512				
1994	0.378	-	-	0.325	0.482	0.339	0.458	0.435	0.522			
1995	0.410	-	-	0.377	0.475	0.375	0.410	0.479	0.479	0.447		
1996	0.236	-	-	0.261	0.342	0.257	0.265	0.313	0.315	0.357	0.371	
1997	0.210	-	-	0.225	0.319	0.254	0.336	0.349	0.327	0.345	0.371	0.439
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**

Table VI: Acoustic similarity indices for the year to year comparisons of N9 calls by A12 subpod (n=21 for each year).

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
1986	-											
1987	-	-										
1988	-	-	-									
1989	-	-	-	-								
1990	-	0.417	-	-	-							
1991	-	0.422	-	-	-	0.421						
1992	-	0.393	-	-	-	0.397	0.459					
1993	-	0.517	-	-	-	0.380	0.370	0.422				
1994	-	0.522	-	-	-	0.396	0.390	0.388	0.480			
1995	-	0.419	-	-	-	0.504	0.525	0.516	0.411	0.463		
1996	-	0.460	-	-	-	0.444	0.424	0.348	0.496	0.479	0.418	
1997	-	0.421	-	-	-	0.414	0.507	0.383	0.450	0.457	0.472	0.536

Table VII: Acoustic similarity indices for the year to year comparisons of N9 calls by A30 subpod (n=21 for each year).

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
1986	-											
1987	-	-										
1988	0.475	-	-									
1989	-	-	-	-								
1990	0.381	-	-	0.436	-							
1991	0.373	-	-	0.414	-	0.442						
1992	0.423	-	-	0.470	-	0.523	0.480					
1993	0.489	-	-	0.505	-	0.473	0.456	0.526				
1994	-	-	-	-	-	-	-	-	-			
1995	0.381	-	-	0.342	-	0.435	0.407	0.367	0.376	-		
1996	0.331	-	-	0.424	-	0.367	0.408	0.492	0.486	-	0.227	
1997	0.454	-	-	0.504	-	0.460	0.404	0.499	0.487	-	0.321	0.422

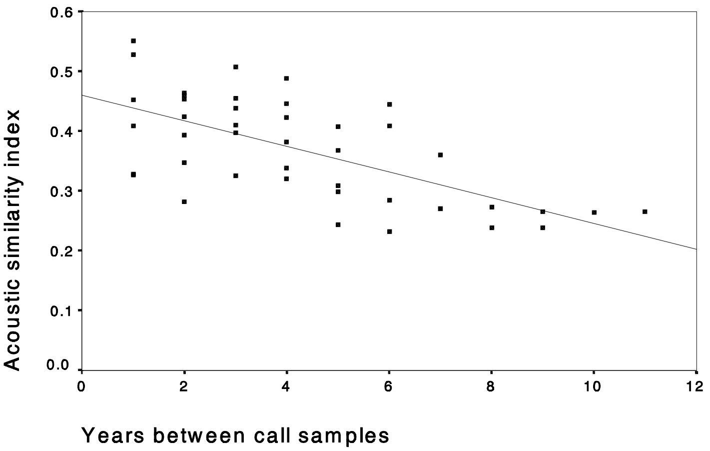
Test for horizontal transmission

N4 call type

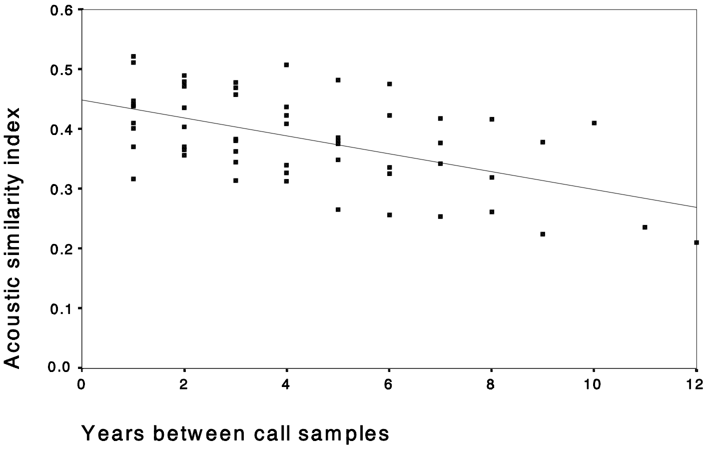
While the results show that both groups modified their N4 call type, Figure 8C suggests that the similarity of the N4 calls of A12 and A30 subpod did not change dramatically between 1985/86 and 1997. Similarity indices for the comparisons between groups range from 0.179 (1996) to 0.371 (1991) with an average of 0.273. The regression of between-group similarity ratings against time gives a slight positive slope ($R^2 = 0.113$, $\beta_{between} = 0.0058$; Figure 8C), suggesting that the calls actually became more similar, but the relationship is nonsignificant ($p = 0.343$). Comparing the rates of call modification of the two groups with the rate of differentiation between them shows that the rate of acoustic differentiation is significantly lower than the rate of modification in A12 subpod ($SE\ \beta_{between}-\beta_{withinA12} = 0.0126$, $p = 0.023$). The significance level for the comparison with A30 subpod's rate of modification in is higher than significance ($SE\ \beta_{between}-\beta_{withinA30} = 0.0125$, $p = 0.057$).

N9 call type

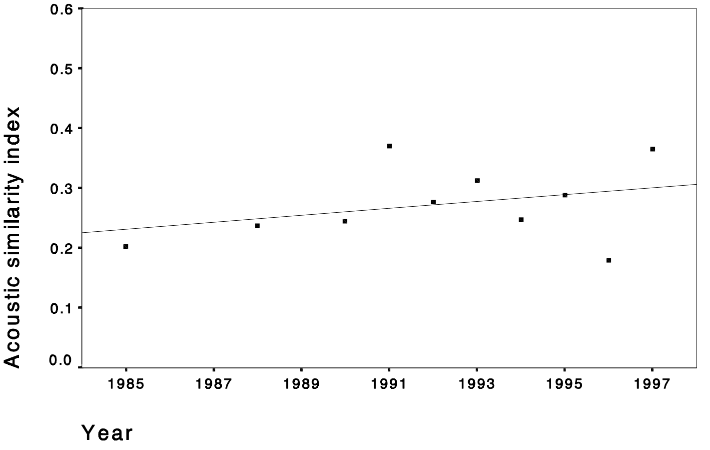
The discrimination errors between groups for the N9 call type range from 0.298 (1996) to 0.460 (1997) with an average of 0.402. As for the N4 call type, the linear regression suggests that the difference between both groups did not change significantly with time ($R^2 = 0.028$, $\beta_{between} = -0.0023$, $p = 0.694$). For this call type, the differences in the rate of call modification in the two groups and the rate of vocal differentiation between them are not significant ($SE\ \beta_{between}-\beta_{withinA12} = 0.0124$, $p = 0.475$; $SE\ \beta_{between}-\beta_{withinA30} = 0.0102$, $p = 0.379$).



A A12 subpod
1986-1997



B A30 subpod
1985-1997



C A12 vs. A30
1985/86-1997

Figure 8: Scatter plots giving the rate of call modification for the N4 call type of A12 subpod (**A**), A30 subpod (**B**), as well as the rate of acoustic differentiation between both groups (**C**).

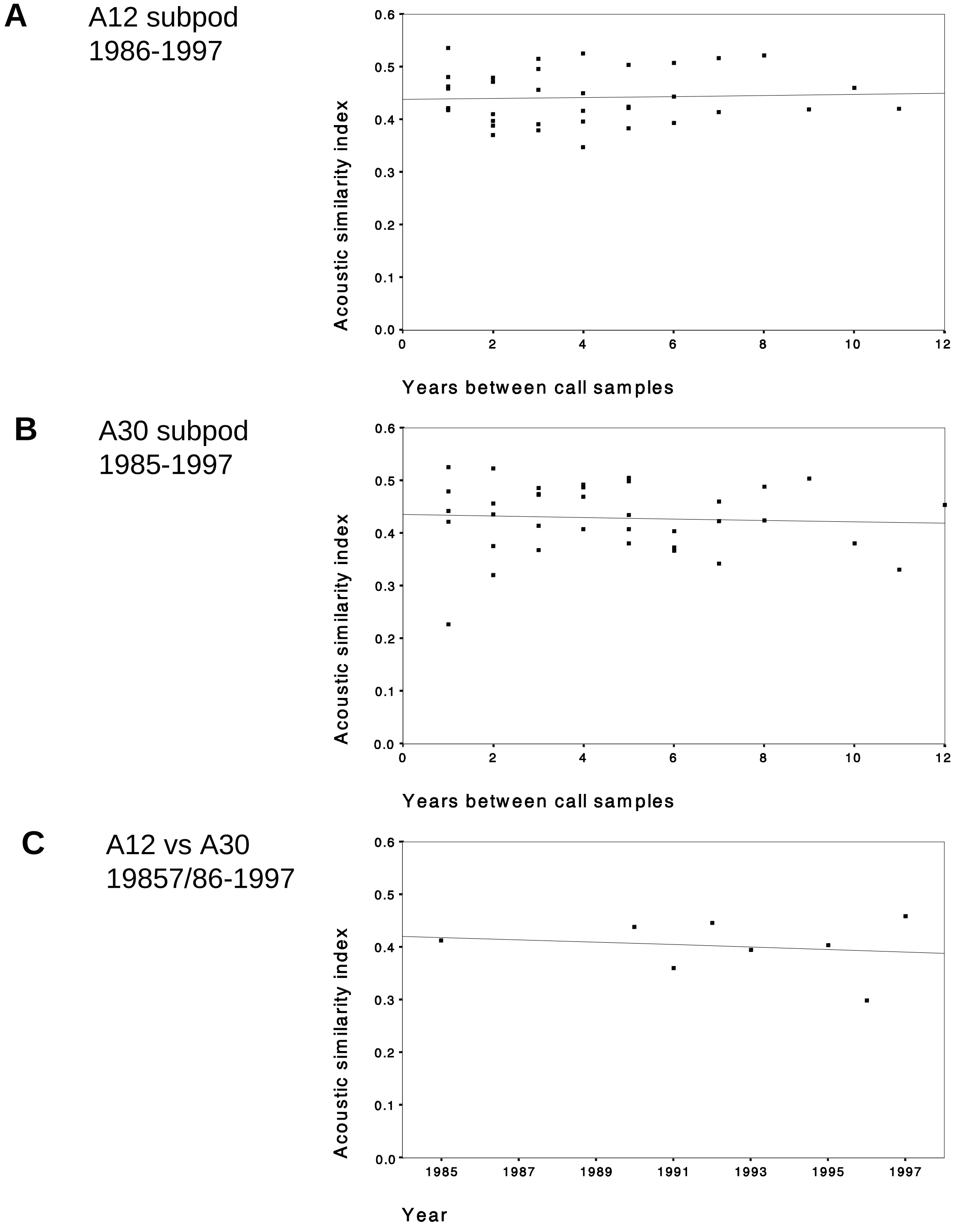


Figure 9: Scatter plots giving the rate of call modification for the N9 call type of A12 subpod (**A**), A30 subpod (**B**), as well as the rate of acoustic differentiation between both groups (**C**).

Analysis of call structure

Mean values and 95% confidence limits for the measurements of plateau frequency, call length, peak frequency, and peak position for both groups (Figures 10-13) show that some parameters of the N4 call type show pronounced changes from one year to the next (e.g., plateau frequency in the A12 subpod 1992-1993; plateau frequency in the A30 subpod from 1990 to 1991 and from 1995 to 1996; peak frequency in the A30 subpod from 1995 to 1996). None of the parameters show a clear directional trend. The measurements from both groups were not significantly correlated for any parameter (Table VIII), although the relationship between the position of the peak frequency in both groups approached significance ($R_{A12\text{-}A30}$ = 0.596; p = 0.069; Figure 13).

Table VIII: Pearson's correlation coefficient and significance levels of the structural changes in the N4 calls of A12 and A30 subpods 1985/86 - 1997.

Parameter	Correlation Coefficient $R_{A12\text{-}A30}$	Significance Level p
Plateau Frequency	0.244	0.497
Call Length	-0.219	0.544
Peak Frequency	0.242	0.501
Peak Position	0.596	0.069

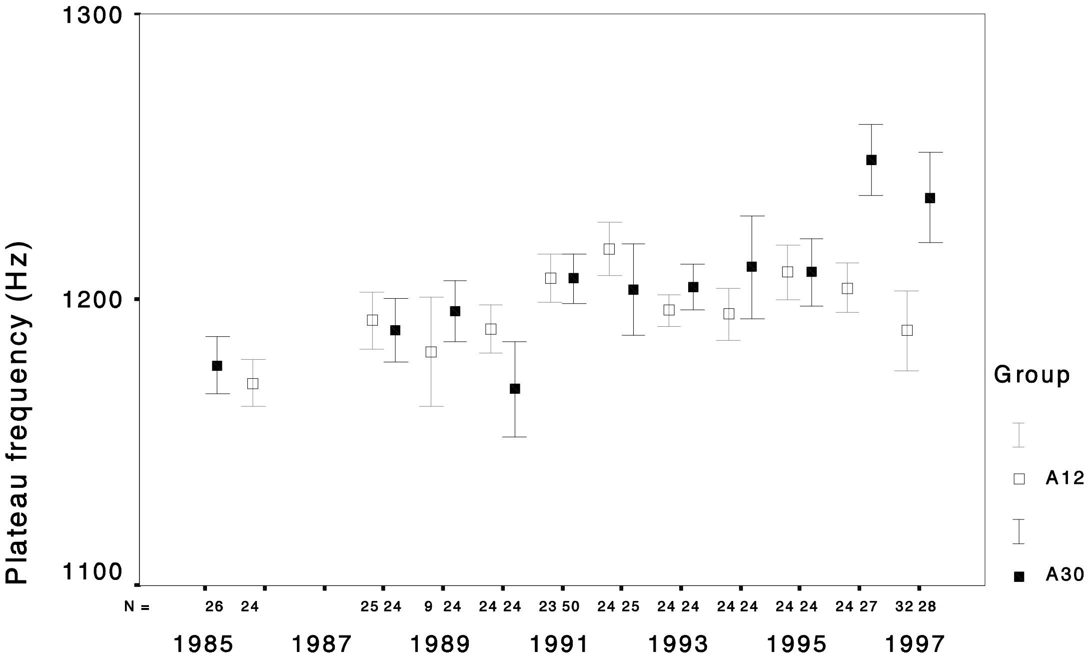


Figure 10: Means and 95% confidence intervals for the plateau frequency of the N4 call type of A12 and A30 subpod from 1985 to 1997.

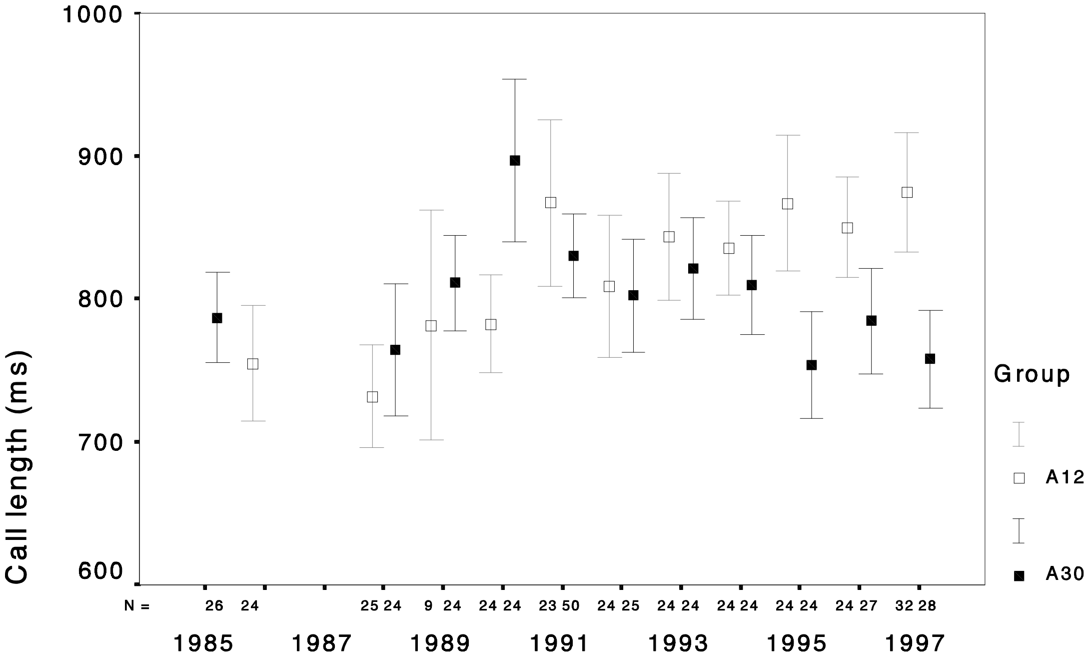


Figure 11: Means and 95% confidence intervals for the length of the N4 call type of A12 and A30 subpod from 1985 to 1997.

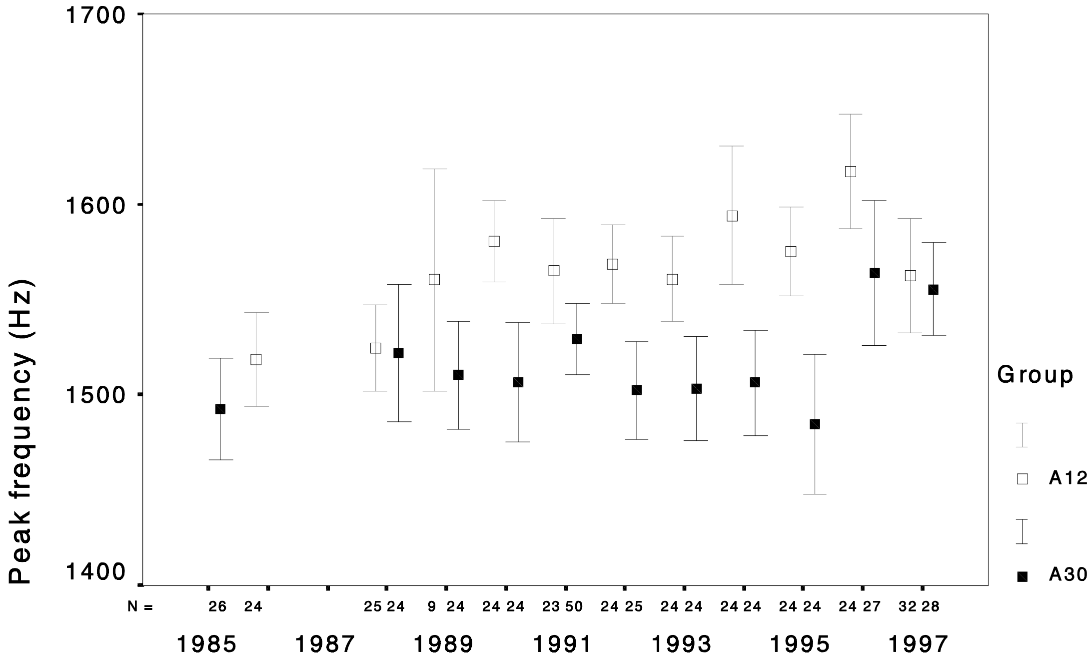


Figure 12: Means and 95% confidence intervals for the peak frequency of the N4 call type of A12 and A30 subpod from 1985 to 1997.

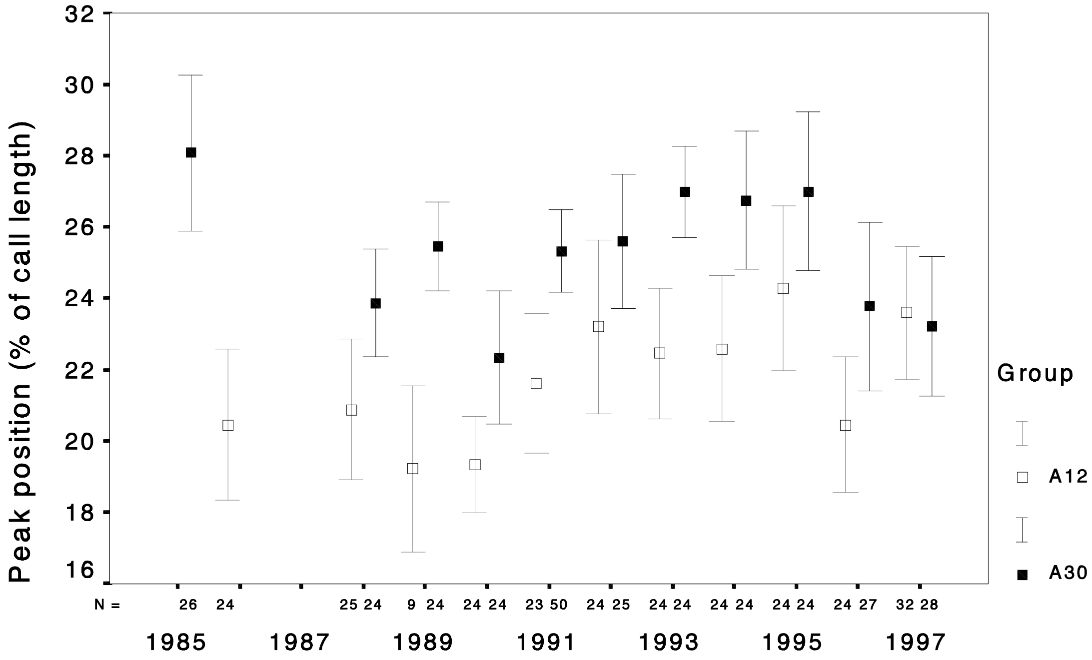


Figure 13: Means and 95% confidence intervals for the peak position of the N4 call type of A12 and A30 subpod from 1985 to 1997.

DISCUSSION

The fact that the acoustic similarity of call samples from the same matrilineal unit decreased with time shows that the discrete calls of killer whales are not static behavioural traits, but are subject to change over time. Killer whale vocal dialects not only evolve on the level of the call repertoire, but, as Ford (1991) suggested, the structure of individual call types undergoes modification as well. This study therefore demonstrates that mutational change in the sense of Lynch (1996), or elemental improvisation in the sense of Marler and Peters (1982), contributes to the evolution of killer whale dialects.

However, the fact that the acoustic similarity of samples of N4 calls decreased consistently both in the A12 and A30 subpod (Figure 8A and B) does not necessarily imply that the structural change is directional. The neural network index of acoustic similarity integrates the amount of variation present over the entire frequency contour, and the increased discrimination can result from directional change in a single parameter, or from the sum of nondirectional changes of multiple parts of the call. The lack of strong directionality in the structural parameters (Figures 10-13) suggests that the latter is the case. The observed pattern is therefore consistent with a theory of structural change through cultural drift (e.g., Mundinger, 1980; Lynch, 1996; Payne, 1996), in which changes to call structure are introduced through random processes and transmitted within the group. Since the mechanism which generates structural change is random, the resultant change lacks strong directionality. However, due to the accumulation of such random modifications, overall variation increases with time.

Although the year to year comparisons for A12 and A30 subpods showed modifications to the N4 call type, the acoustic similarity index for the N9 call type did not show any directional change in either group (Figure 9A and B). This could mean that not all call types accumulate modifications at the same rate and therefore remain more stable than others. Ford (1991) noted that the N3 call type, shared by all members of A-clan, shows very little structural variation among different pods, whereas the structure of others, such as the N8 call type, differs dramatically from one social group to the next. He suggests that the communicative context of different calls may influence their rate of modification. Lynch (1996) similarly used communicative selection to explain the lack of local variability in chaffinch (*Fringilla coelebs*) contact calls in contrast to their songs. He argues that the importance of the calls in social interactions forces individual birds to conform to local call variants. If the N9 call type has a specific communicative function, variability in this call would be disadvantageous. However, the N4 and N9 call type are used quite similarly across different behavioural contexts and have a relatively high index of acoustic association (Ford, 1989) which argues against any profound differences in their communicative function.

This study provides evidence for cultural transmission of call modifications between matrilineal units of killer whales. If the two groups examined in this study had modified their N4 call independently of each other, the rate of acoustic differentiation between the groups should have been at the least as great as the rate of call modification in any one group. The fact that the rate of differentiation between both groups is significantly lower than the rate of modification in the A12 subpod refutes the hypothesis of independent modification, and thus this is evidence for horizontal transmission between both groups. The near-significant correlation between the yearly measurements of peak position for the two groups provides further support for horizontal transmission of modifications to call structure (Table VIII; Figure 13).

The patterns of call modification observed in this study along with the evidence for horizontal transmission are inconsistent with a model of genetic coding for killer whale vocalizations. Changes in group membership, and with it in the genetic composition of the groups, did occur over the 12 year period in both matrilineal units through births and deaths (Figures A-4 and A-5). However, the most pronounced year to year differences in the structural parameters analysed happened between years in which the individual members of the group, and its genetic composition, remained the same. Furthermore, the acoustic similarity indices for the N4 calls of A30 subpod show a downward trend for the years 1990 to 1997 (Table V), a period where no births and deaths occurred within this group (Figure A-5). The change observed therefore is not just the result of changing group membership, but of structural modifications to the calls shared by all group members. The fact that structural modifications to the calls are transmitted between groups requires copying and vocal learning and thus provides additional evidence against a genetic coding of the calls.

The rates of call modification in both groups (Figure 8A and B) suggest that a period of 12 years of separation is sufficient to generate the average acoustic difference of 0.273 observed between the N4 calls of the A12 and A30 subpods. However, these two groups have been observed as functionally independent social units as far back as 1973 (Bigg, 1982). This apparent discrepancy between the date of divergence predicted by the acoustic data, and the observed date can be explained by horizontal transmission between the two groups. If the structural modifications to the calls of one group are not only transmitted within that group, but also from one group to the next, the acoustic difference between the groups will not increase. The two matrilineal units are still seen together frequently (half-weight index of association: 0.542; Table IX) giving ample opportunity for vocal exchange.

Several researchers have proposed to use measures of vocal similarity as a ‘cultural clock’ to reconstruct the cultural evolution of populations of songbirds (e.g., Mundinger, 1980; Payne, 1996) and humans (Cavalli-Sforza and Feldmann 1981; Barbujani, 1991). For killer whales, Ford and Fisher (1982) and Ford (1991) argue that the vocal dialects could serve to determine the timing of group divisions and thus to reconstruct their genealogy. The demonstration that horizontal transmission of structural changes takes place between social groups of killer whales has implications for such reconstructions.

Since modifications to the dialects can be transferred between matrilineal units, these social groups are able to effectively reset and synchronize their cultural clocks. Any time estimates assuming strictly linear divergence of dialects would therefore underestimate the amount of time elapsed since two groups first split up. In an extreme case, the dialects of different social groups could actually converge due to an increase in horizontal transmission among them. Such reticulate patterns of cultural evolution have been proposed by Mundinger (1980) and Payne (1996) for songbird dialects.

The findings in this chapter therefore support the argument of Kroch (1989) and Payne (1996) that cultural evolution is a historical phenomenon and thus must be investigated using historical approaches. Patterns of vocal variation observed at one point in time are the outcome of past modifications and vocal exchange. Only by understanding the mechanisms that drive vocal differentiation, and how they are influenced by demographic factors, can we hope to interpret these patterns. I have shown that a sufficiently sensitive analysis can document acoustic change over a 12 year period in an extremely long-lived species, and I hope that this will encourage other researchers to investigate temporal patterns of acoustic change in different populations of killer whales, as well as in other long-lived species.

CHAPTER III: Patterns of Acoustic Variation Within a Killer Whale Vocal Tradition

INTRODUCTION

Many studies have investigated vocal differences among social groups of animals, and most of these studies have focused on highly territorial species such as birds and humans. Vocal traditions among songbirds tend to be shared between individuals with territories close to each other (e.g., Baptista, 1975; Jenkins, 1977; Payne et al., 1981). The nature of spatial variation between adjacent vocal traditions ranges from abrupt with no shared song elements across dialect boundaries (Baptista, 1975; Thielke, 1992) to graded with various degrees of sharing (Mundinger, 1980; Trainer, 1989). Many species of passerine birds show both types of boundaries within the same dialect system (Mundinger, 1980).

Mundinger (1980) points out the similarity between the structure of dialect variation in songbirds and humans. Human vocal communication exhibits variation in space with abrupt boundaries between different language families, and graded variation within language families, and within individual languages in the form of linguistic dialects

(Greenberg, 1963; Barbujani, 1991). In addition, however, human languages also show differences that are not easily translated into spatial terms, in the form of variation between the language used by different social groups living in the same area (e.g., Krysin, 1977; de-Wolf, 1990), or by different age groups (e.g., Lederer, 1983; Nuessel, 1996).

Territorial species lend themselves to the study of vocal variation because the boundaries defining social groups can be mapped spatially. Therefore, vocal signals from a particular social group can be obtained without the need for visual identification of individuals or groups simply by recording in a certain location. Such geographic approaches to the study of vocal variation have proven successful for some birds (e.g., Marler and Tamura, 1962; Baptista, 1975; Mundinger, 1980; Thielke, 1992; Wright, 1996) and humans (see Barbujani, 1991 for a summary), but they cannot be applied to species in which the home ranges of different social groups overlap to a large degree, or are entirely congruent. Thus most of our knowledge on vocal dialects comes from highly territorial animals, which may have led to biases in our interpretation of the function of vocal variation.

The northern resident community of killer whales provides an ideal study population for investigating group dialects in a non-territorial mammal since all of its members can be identified consistently from natural markings (Bigg, 1982; Bigg et al., 1990). This population has been censussed annually since 1973, and therefore the maternal genealogies of all animals born since then are known. Due to the unique social structure of resident killer whales, genealogical relationships among animals born before 1973 can be inferred with confidence from association patterns (Bigg et al., 1990; Ford et al., 1994; see Appendix II). This wealth of information provides the ‘social map’ necessary to interpret a dialect system delineated by social boundaries rather than geographic borders.

Several researchers have postulated that dialects act as a non-genetic marker of kinship in territorial birds. Treisman (1977, 1978) showed that mechanisms of avoiding conflicts with close kin can confer an advantage on individuals which establish territories next to relatives. Since genetic traits give insufficient resolution as a marker of kinship in highly philopatric species, he suggests that learned behavioural traits, such as vocal repertoires, may serve this function instead. Marler and Tamura (1962) also propose that dialects act as a non-genetic marker of kinship, but that their role is to prevent inbreeding in birds with a high degree of site fidelity. Other researchers, however, disagree with such adaptionist hypotheses and argue that vocal dialects are by-products of demographic events in a population rather than functional markers (see Payne, 1981a; Mundinger, 1982).

Ford (1987, 1991) has shown that different pods of killer whales use structurally different versions of shared call types. In addition, there is evidence for structural variation among different matrilineal units within a pod (D.E. Bain and P. Miller, unpublished data). The goal of this chapter is to examine patterns of such vocal variation at the level of the matrilineal unit, and to interpret these patterns using our knowledge of the social histories of the groups. Specifically, I will examine the relationship between the frequency of association among different matrilineal units, and the similarity of their shared call types.

My findings in Chapter II suggest a relationship between the amount of time two groups spend together and the similarity of their vocal dialects. Temporal changes in the N4 call type were transmitted between matrilineal units. Since the amount of horizontal transmission taking place between two groups depends at least in part on the amount of time they spend in acoustic contact, frequently associating matrilineal units should have more similar calls than groups that rarely travel together. A correlation between association patterns and similarity of shared call types therefore represents additional evidence for horizontal transmission between killer whale matrilineal units.

Hamilton (1964a,b) first proposed that the strength of associations in social animals should reflect their genetic relatedness, and his postulate has been verified for many social species. For killer whales, Bain (1988), Bigg et al. (1990), and Harms (1997), showed that maternal genealogies of individuals are reflected in their association patterns. On a much larger scale, Hoelzel et al. (1998), and Barrett-Lennard (pers. comm.) used mitochondrial DNA to show that killer whale communities, defined as all the individuals known to associate, represent maternal lineages. It is therefore likely that association patterns also reflect maternal genealogies within an acoustic clan. If killer whale vocal dialects act as a non-genetic marker of relatedness, there should be a correlation between the association strength and the acoustic similarity of different social groups.

This study examines the vocalizations of 9 matrilineal units belonging to A-subclan of the northern resident community (Ford and Fisher, 1982; Ford, 1991). Bigg et al. (1990)

assigned these 9 matrilineal units to 3 distinct pods based on their association patterns. These are: A01 pod consisting of matrilineal units A12, A30 and A36, A04 pod with the two matrilineal units A11 and A24, and A05 pod, which contains the matrilineal units A08, A09, A23, and A25. The three pods have since begun to split up with sufficient frequency to allow an analysis on the level of the matrilineal unit. Ford (1991) grouped the nine matrilineal units into a common vocal tradition, *A-subclan*, due to the similarity of their vocal repertoires. The members of A-subclan in turn share several of their call types with the 10 matrilineal units of *B-subclan*. Together they make up *A-clan*, one of three acoustic clans in the northern resident community (Ford and Fisher, 1982; Ford, 1991).

The matrilineal units studied here have vocal repertoires of 13-14 call types or subtypes (Ford, 1987, 1991). Of these repertoires, all groups share 11 call types (N2, N3, N4, N5, N7, N8, N9, N10, N11, N12, and N13, see Ford, 1987). Ford (1987, 1991) further divided the N9 call into 3 subtypes, each assigned to a different pod. In addition to these, one call type is shared by two groups (N1 call type for A01 and A04 pod), and four call types are only used by members of one pod (A01 pod: N27 and N47 call types; A04 pod: N19 call type; A05 pod: N17 call type; Ford, 1987, 1991). Ford (1991) only reported the N13 call from A04 and A05 matrilineal units, however, this call is also used frequently by members of the A36 matrilineal unit, and occasionally by A30 (Deecke, unpublished data).

In addition to these differences in vocal repertoire and call structure, Ford (1991) found significant differences in the frequency with which the different groups use certain call types. Whereas no difference was evident in the usage of the N2, N7, N8 and N11 call type, members of A04 pod used the N4 and N12 call type more often and the N5 and N9 call type less often than members of A01 and A05. Call type N10 occurred more frequently in the repertoire of A05 pod than in that of A01 and A04 pod.

In this chapter, I analyse the association patterns of the 9 matrilineal units to study the strengths of social bonds within A-subclan. I use the neural network index described in Chapter I to quantify the acoustic variation for 4 shared call types. This allows me to refine the acoustic relationships within A-subclan established by Ford (1991) to the level of the matrilineal unit. It also enables me to test whether patterns of acoustic variation are similar for different call types, and whether they are correlated with the frequency of association of the different matrilineal units.

METHODS

Analysis of association patterns

The association patterns of the 9 matrilineal units were determined from a database of sightings of the northern resident community compiled by J. K. B. Ford at the Vancouver Aquarium. The records were contributed by a number of researchers. The association strength for each pair of matrilineal units was determined from the sightings for 1990-1995 by computing their half weight index of association I using the formula:

$$I_{ab} = \frac{x_{ab}}{\frac{1}{2}(n_a + n_b)} \qquad \text{Ginsberg and Young (1992)} \quad \textbf{(6)}$$

Where x_{ab} is the number of sightings of groups A and B together, and n_a and n_b the total number of sightings of A and B respectively. The half weight ratio tends to overestimate the level of association (Cairns and Schwager, 1987; Ginsberg and Young, 1992), but has the advantage of being robust to biases in the encounter frequency of different groups. This was known to be a problem since much of the sighting effort was concentrated in western Johnstone Strait. Some matrilineal units (especially A12, A30, and A36 subpods) enter this area more frequently and spend more time there than do others (Nichol and Shackleton, 1996). In such a situation of differential observability, the half weight index of association best reflects the relative frequency of association, although it is a biased measure of absolute association strength (Cairns and Schwager, 1987).

Analysis of acoustic variation

The underwater recordings used in this study came from several sources and were made using a variety of different recording equipment (Appendix I). Only recording sessions in which one of the 9 matrilineal units was alone within recording range, and was identified visually or through photographs, were included in the analysis. Ideally, I would have liked to restrict this analysis to recording sessions from a single season, since the results of

Chapter II showed that calls are modified with time. However, this was impossible since not all groups were recorded alone every year. Therefore the analysis was centred around the years 1990-1995. Additional recording sessions from earlier or later years were included for groups for which insufficient material was available from this period. For the N4 and N9 call type of A12 and A30 subpods, the 1992 samples were used here.

Suitable calls were identified acoustically and visually from the recordings and digitized using the Canary 1.2.1 sound analysis software. Calls were assigned to one of the call types defined by Ford (1987). Of the 2252 calls digitized, 259 could not be assigned to a call type and were omitted from the analysis. The analysis of acoustic variation was restricted to call types for which more than 15 calls could be obtained from 3 or more groups. For these call types, frequency contours were extracted from spectrograms, and the index of acoustic similarity was determined by the methods given in Chapter I.

To visualize the structure of acoustic variation and association patterns, I generated average linkage dendrograms (Johnson, 1967) from the acoustic similarity indices, as well as from the association data. The pairwise ratings of acoustic similarity for the different call types were compared to the association indices for the groups by computing Pearson's coefficient of correlation ($R_{acoust\text{-}assoc}$; Zar, 1996). To test whether the patterns of acoustic variation are similar for different call types, I computed the correlation coefficient for the similarity ratings of the two call types ($R_{acoust\text{-}acoust}$) for all comparisons for which ratings were available for both call types.

RESULTS

Analysis of association patterns

The database contained 757 sightings involving one or more matrilineal units of A-subclan. The total number of encounters with any one matrilineal unit ranged from 147 (A25 subpod) to 415 (A30 subpod). The indices of association between matrilineal units within A-subclan are very similar to those described by Bigg et al. (1990) for 1978-1987 (Table IX). The values for the half weight index of association range between 0.973 for A11 and A24 subpods, and 0.239 for A09 and A11. The average linkage dendrogram of association groups the 9 matrilineal units into three major clusters: A08-A09-A23-A25, A12-A30-A36, and A11-A24 (see left side of Figure 19), which correspond to A05 pod, A01 pod, and A04 pod respectively of Bigg et al. (1990). However, the frequency of most associations has decreased since their study, and the three A01 matrilineal units are no longer part of a single pod according to the definition of Bigg et al. (1990).

Table IX: Association matrix (half-weight index) for the 9 matrilineal units of A-subclan.

A09	0.725							
A11	0.421	0.239						
A12	0.506	0.401	0.413					
A23	0.766	0.695	0.332	0.470				
A24	0.425	0.252	0.973	0.408	0.324			
A25	0.691	0.607	0.275	0.369	0.782	0.265		
A30	0.333	0.253	0.330	0.542	0.354	0.329	0.270	
A36	0.397	0.379	0.336	0.520	0.391	0.326	0.271	0.370
	A08	**A09**	**A11**	**A12**	**A23**	**A24**	**A25**	**A30**

Analysis of acoustic variation

Sufficient calls could be obtained for the analysis of 4 shared call types: N1, N2, N4, and N9. Within A-subclan, N1 is only used by A11, A12, A24, A30 and A36 subpods (Ford, 1991). However, sample size for the N1 call type of A11 and A24 subpods was too small, so that only 3 matrilineal units were included here. The sample size for the remaining three groups is 18 calls per group. Samples for the N2 call type were available for A08, A12, A30, and A36 subpods. Sample size for this call type is 21 calls per group. The N4 is the only call type for which samples could be obtained from all 9 matrilineal units. Sample size for the N4 call type is 24 calls per group. Finally, the N9 call type was analysed for A12, A23, A25, A30, and A36 subpods with a sample size of 21 calls.

The acoustic similarity index showed a wide range of values. The highest discrimination error of the neural network was 0.508 (N9 call type: A23 vs. A25; Table XIII). In this case the neural network performed no better than random, and did not detect any consistent variation between the calls of both groups. The best discrimination was between the N9 calls of A12 and A25 subpods with a discrimination error of 0.004 (Table XIII), suggesting that the N9 calls of these two groups are very distinct.

N1 call type

The acoustic similarity index rated the N1 calls of A30 and A36 subpods more similar to each other than to those of the A12 subpod (Table X, Figure 15). Structurally, the N1 calls of A12 subpod are significantly longer than those of the other groups (t-test, $p < 0.001$; Deecke, unpublished data; Figure 14), and substitution of frequency contours as described in Chapter II showed, that call length was indeed the most important factor in neural network discrimination. The N1 call type is the only call type for which the acoustic similarity index showed a negative correlation with the association patterns of the groups ($R_{acoust\text{-}assoc} = -0.929$, $p = 0.241$).

Table X: Acoustic similarity matrix for the N1 call type of 3 matrilineal units (n = 18 calls per group).

	A08	**A09**	**A11**	**A12**	**A23**	**A24**	**A25**	**A30**
A09	-							
A11	-	-						
A12	-	-	-					
A23	-	-	-	-				
A24	-	-	-	-	-			
A25	-	-	-	-	-	-		
A30	-	-	-	0.158	-	-	-	
A36	-	-	-	0.127	-	-	-	0.243

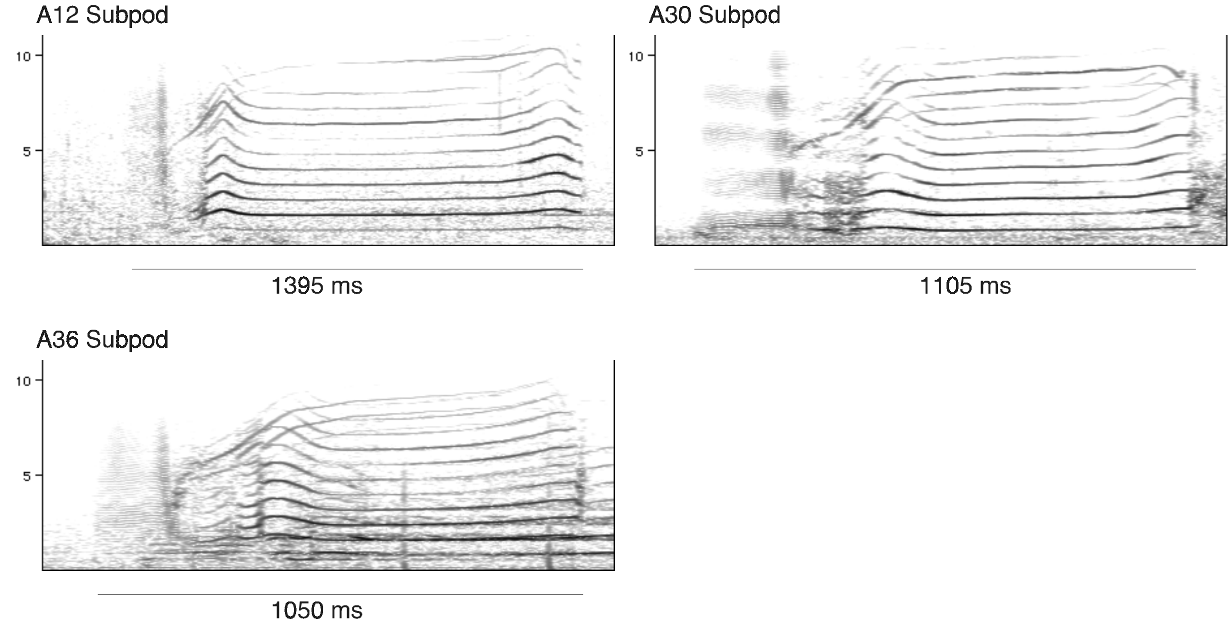
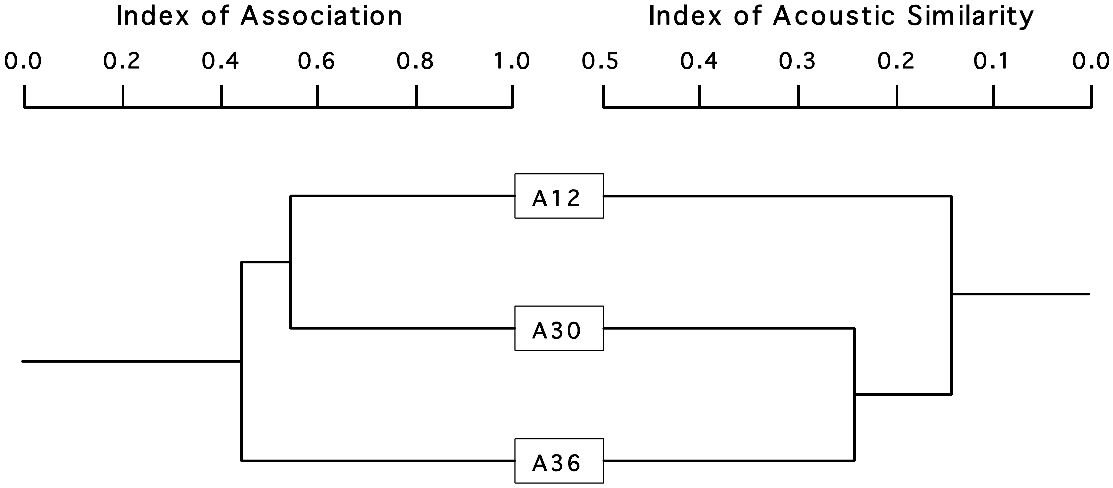


Figure 14: Examples of spectrograms of N1 calls by 3 matrilineal units.



$R_{acoust\text{-}assoc} = -0.929 \quad p = 0.241$

Figure 15: Average linkage dendrograms giving association patterns of 3 matrilineal units based on the half weight index of association (left), and structural similarity of their N1 call type based on the neural network index (right). Sample size is 18 calls per group.

N2 call type

The results for this call type suggest that the N2 calls of A12 and A30 subpods are more similar than those of any other groups examined (Table XI, Figure 17). The dendrogram (Figure 17) furthermore implies that the N2 calls of A36 subpod are more similar to those of A08 subpod, however, Table XI shows this to be an artifact of the average linkage algorithm (Johnson, 1967), and the N2 calls of A36 subpod gave a somewhat higher similarity rating with A30 subpod. Structurally, the N2 calls of A08 tend to be longer than those of A12 and A30, and have a level plateau at the end of the call, while the N2 calls of A36 appear intermediate between those of A12-A30 and A08 (Figure 16). However, this call type is quite variable (see Ford and Fisher, 1982; Ford, 1987, 1989). The acoustic similarity of the N2 call type is not significantly correlated with the association patterns of the four groups ($R_{acoust\text{-}assoc}$ = 0.378, p = 0.460).

Table XI: Acoustic similarity matrix for the N2 call type of 4 matrilineal units (n = 21 calls per group).

	A08	A09	A11	A12	A23	A24	A25	A30
A09	-							
A11	-	-						
A12	0.055	-	-					
A23	-	-	-	-				
A24	-	-	-	-	-			
A25	-	-	-	-	-	-		
A30	0.076	-	-	0.257	-	-	-	
A36	0.105	-	-	0.078	-	-	-	0.113

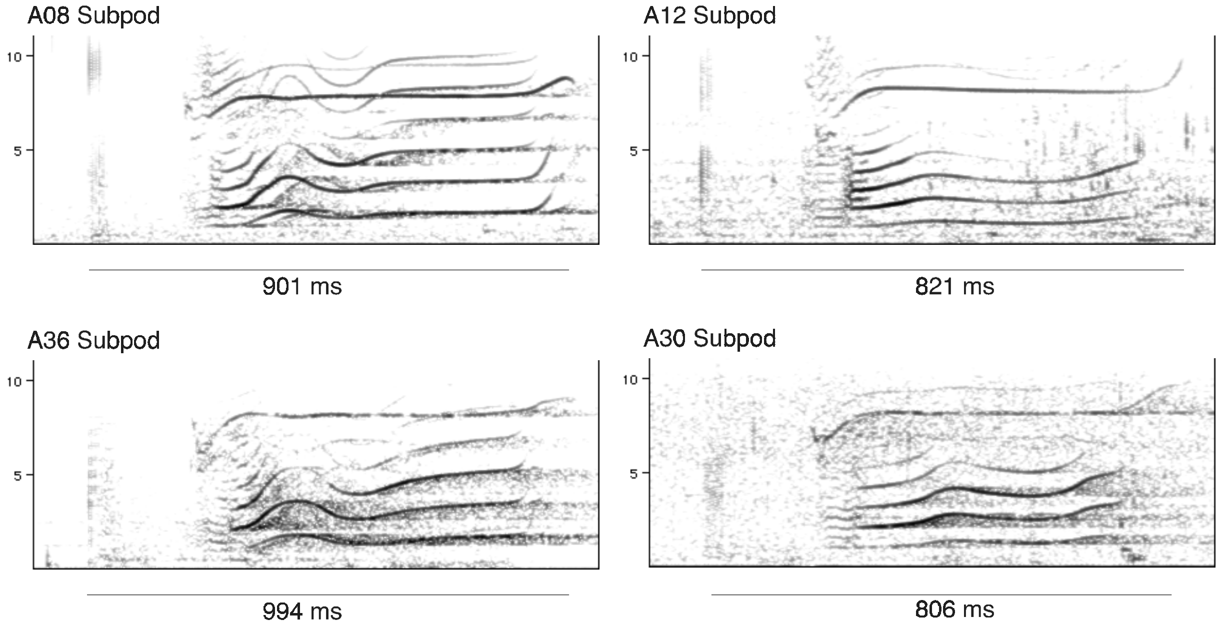
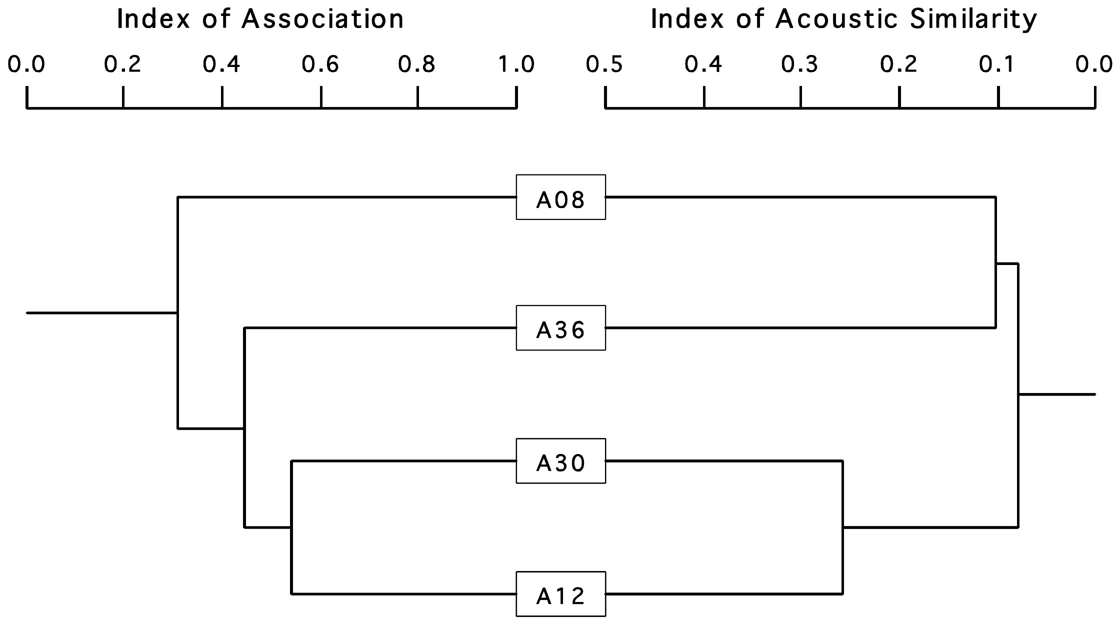


Figure 16: Examples of spectrograms of N2 calls by 4 matrilineal units.



$R_{acoust\text{-}assoc} = 0.378$ $p = 0.460$

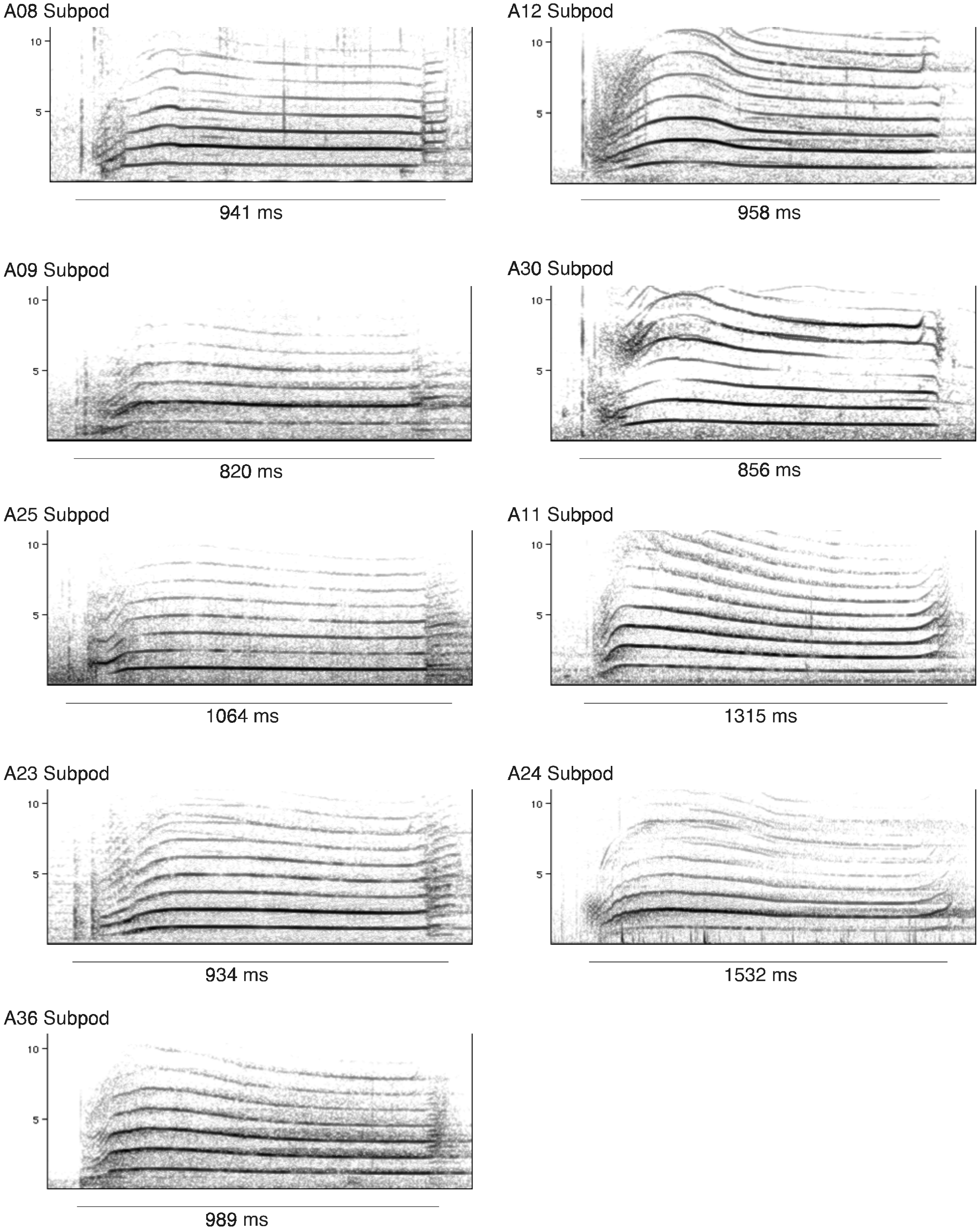
Figure 17: Average linkage dendrograms giving association patterns of 4 matrilineal units based on the half weight index of association (left), and structural similarity of their N2 call type based on the neural network index (right). Sample size is 20 calls per group.

N4 call type

The acoustic similarity indices for the N4 call type (Table XII) group the 9 matrilineal units into three major acoustic clusters. These are: A08-A09-A23-A25-A36, A12-A30, and A11-A24 (Figure 19). These clusters are consistent with structural differences in the calls (Figure 18): the N4 calls of matrilineal units belonging to the first cluster generally have a pronounced terminal component (Part 2 of Ford, 1987), and a relatively low peak frequency. N4 calls of A12 and A30 subpod generally lack the terminal component and have a higher peak frequency. Those of A11 and A24 subpod tend to be longer in duration and generally end in an upsweep. The acoustic similarity ratings for the N4 call type are significantly correlated with the groups' indices of association ($R_{acoust\text{-}assoc} = 0.546$, $p = 0.001$).

Table XII: Acoustic similarity matrix for the N4 call type of 9 matrilineal units (n = 24 calls per group).

A09	0.343							
A11	0.091	0.041						
A12	0.048	0.025	0.080					
A23	0.183	0.194	0.040	0.042				
A24	0.100	0.030	0.285	0.078	0.013			
A25	0.428	0.477	0.039	0.050	0.233	0.033		
A30	0.138	0.061	0.071	0.277	0.086	0.098	0.062	
A36	0.266	0.397	0.065	0.059	0.189	0.059	0.373	0.098
	A08	**A09**	**A11**	**A12**	**A23**	**A24**	**A25**	**A30**


A08 Subpod

941 ms

A12 Subpod

958 ms

A09 Subpod

820 ms

A30 Subpod

856 ms

A25 Subpod

1064 ms

A11 Subpod

1315 ms

A23 Subpod

934 ms

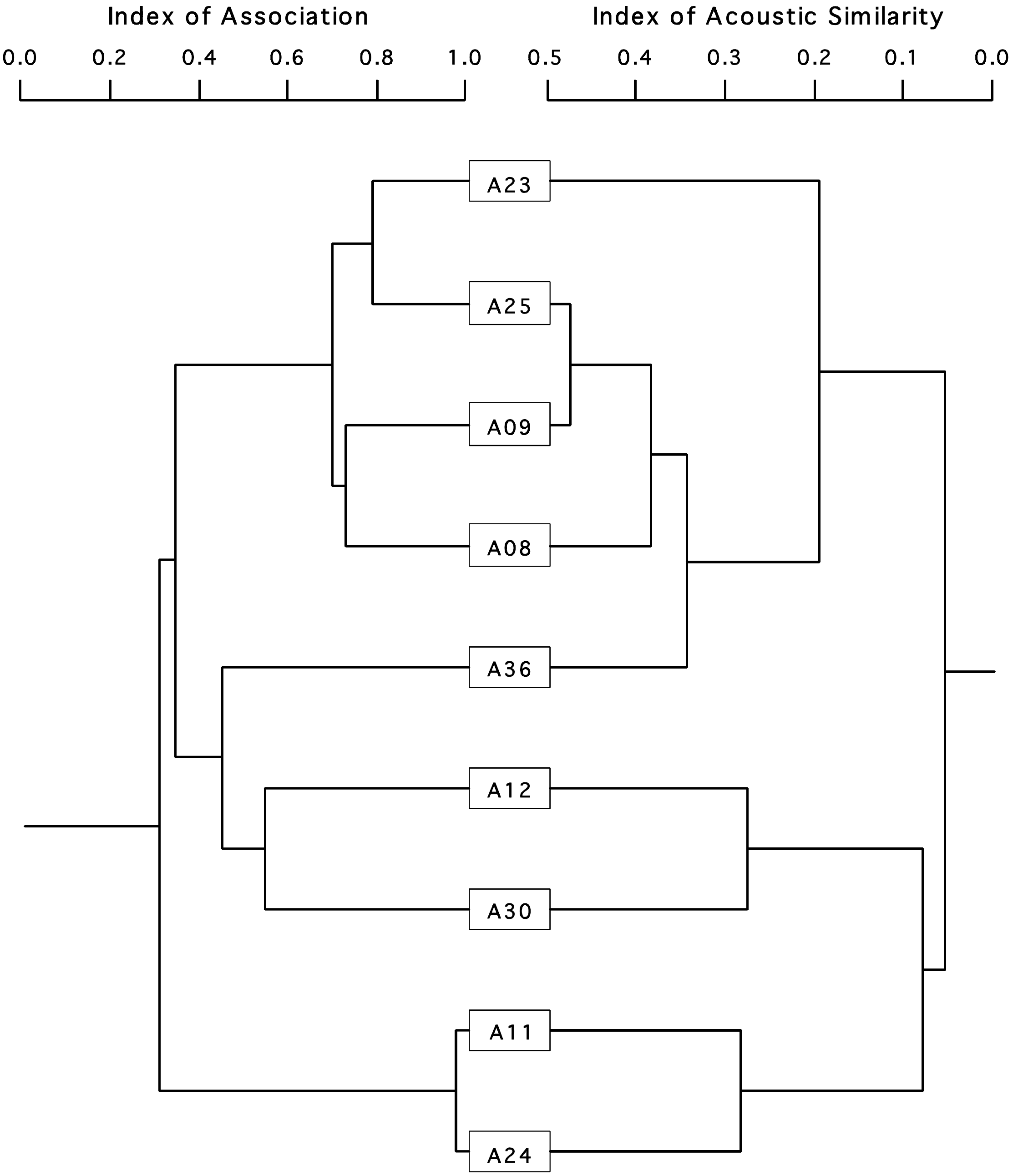
A24 Subpod

1532 ms

A36 Subpod

989 ms

Figure 18: Examples of spectrograms of N4 calls from the 9 matrilineal units of A-subclan.



$R_{acoust\text{-}assoc} = 0.546$ $p = 0.001$

Figure 19: Average linkage dendrograms giving association patterns of the 9 matrilineal units of A-subclan based on the half weight index of association (left), and structural similarity of their N4 call type based on the neural network index (right). Sample size is 24 calls per group.

N9 call type

The acoustic similarity index gave both the highest and the lowest overall rating for comparisons of N9 calls. The versions of N9 from A25 and A23 subpods are extremely similar, as are those from A12 and A30 subpods. The N9 calls of A36 subpod are more similar to A12-A30 than they are to A23-A25 (Table XIII, Figure 21). Structurally, the N9 calls of A23 and A25 subpods (subtype N9iii of Ford, 1987, 1991) end with a pronounced terminal component (Part 4 of Ford, 1987). The versions of A12 and A30 subpods lack this terminal component (subtype N9i of Ford, 1987, 1991). N9 calls from the A36 subpod tend to be higher in frequency and sometimes have a faint terminal component (see Figure 20). The N9 call type gave the highest correlation between the acoustic similarity index and the association patterns ($R_{acoust\text{-}assoc} = 0.786$, $p = 0.007$).

Table XIII: Acoustic similarity matrix for the N9 call type of 5 matrilineal units (n = 21 calls per group).

	A08	A09	A11	A12	A23	A24	A25	A30
A09	-							
A11	-	-						
A12	-	-	-					
A23	-	-	-	0.011				
A24	-	-	-	-	-			
A25	-	-	-	0.004	0.508	-		
A30	-	-	-	0.446	0.006	-	0.005	
A36	-	-	-	0.303	0.005	-	0.017	0.330

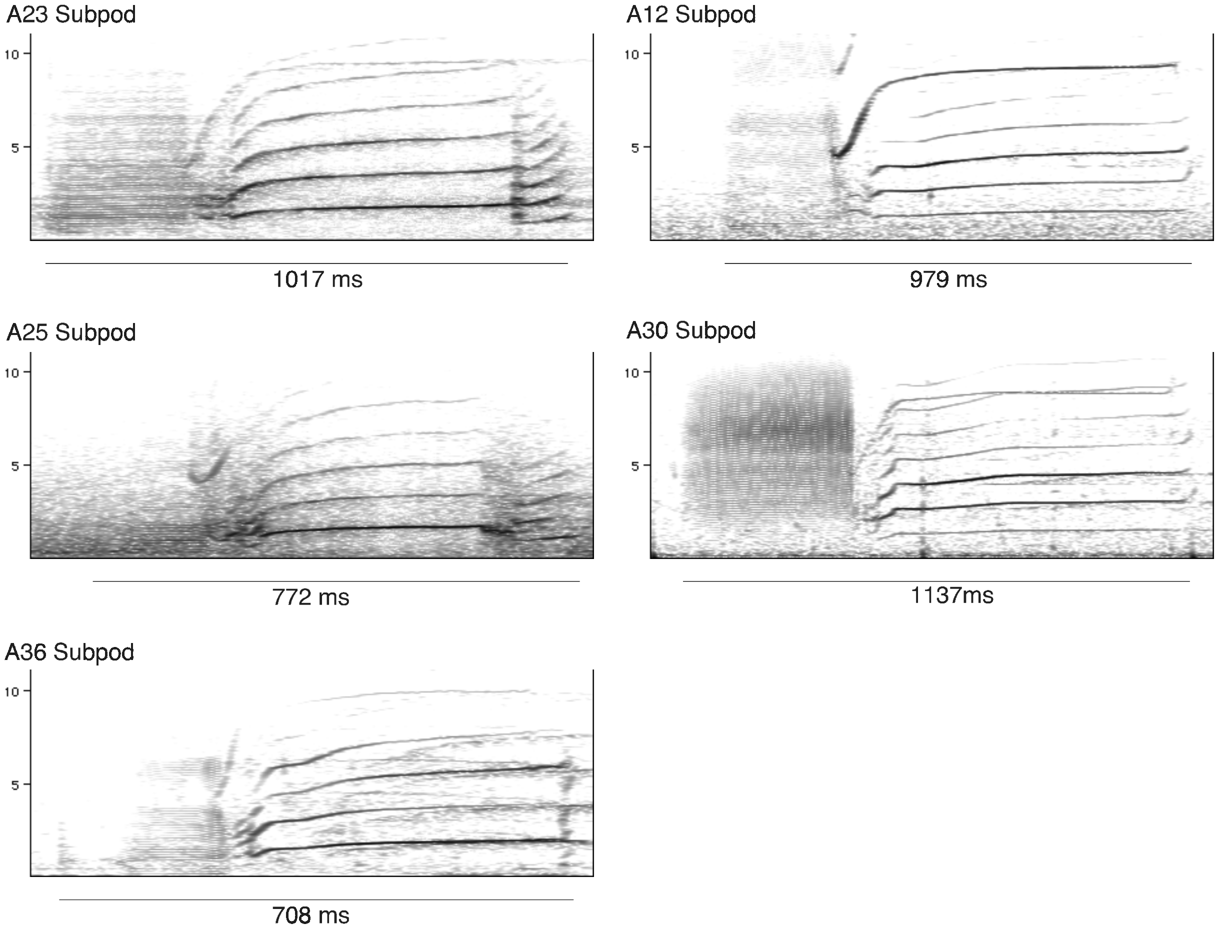
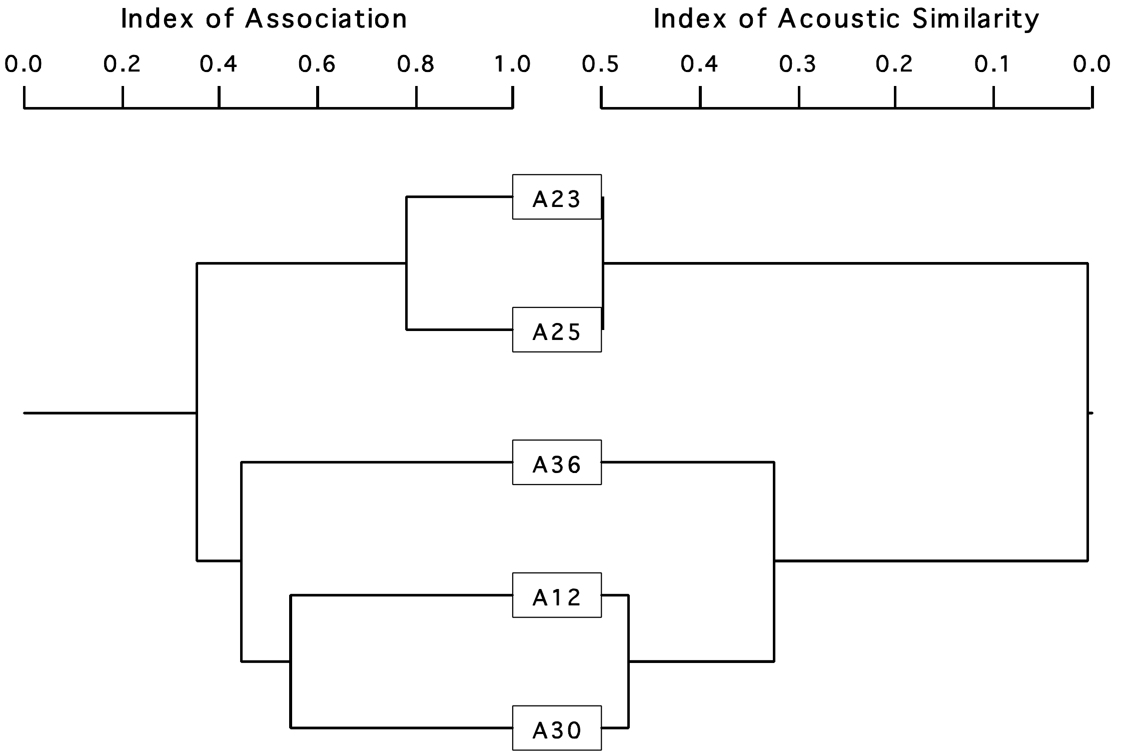


Figure 20: Examples of spectrograms of N9 calls by 5 matrilineal units.



$R_{acoust\text{-}assoc} = 0.786$ $p = 0.007$

Figure 21: Average linkage dendrograms giving association patterns of 5 matrilineal units based on the half weight index of association (left), and structural similarity of their N9 call type based on the neural network index (right). Sample size is 21 calls per group.

Comparison of call types

With the exception of the N1 call type, the ratings of acoustic similarity for different call types are positively correlated (Table XIV). The positive correlation coefficient for the three comparisons of N2 and N9 call type is significant ($R_{acoust-acoust}$ = 1.000, p = 0.005). These findings suggest that patterns of acoustic variation among the matrilineal units of A-subclan are similar for some, but not necessarily all call types.

Table XIV: Correlation matrix for the acoustic similarity ratings of the 4 call types giving Pearson's correlation coefficient ($R_{acoust-acoust}$), significance level (p), and number of comparisons for correlation (N).

		N1	N2	N4	N9
N1	$R_{acoust-acoust}$	1.000			
	p	-			
	N	3			
N2	$R_{acoust-acoust}$	-0.075	1.000		
	p	0.952	-		
	N	3	6		
N4	$R_{acoust-acoust}$	-0.094	0.729	1.000	
	p	0.940	0.100	-	
	N	3	6	36	
N9	$R_{acoust-acoust}$	-0.083	1.000	0.282	1.000
	p	0.947	0.005	0.430	-
	N	3	3	10	10

DISCUSSION

In general, the patterns of acoustic variation within A-subclan found in this study support the existence of the three pods defined by Bigg et al. (1990) from association patterns. For most call types, comparisons of calls from matrilineal units belonging to the same pod gave high ratings of similarity, whereas the ratings for comparisons of groups from different pods were low. The A36 subpod, considered as part of a same pod with A12 and A30 by Bigg et al. (1990) is an exception to this rule. The ratings for the N1 and N9 call type link A36 subpod to A12 and A30 subpods and thus are consistent with the association patterns. The ratings for the N2 call type on the other hand suggest that A36 subpod shows no clear affinity to either A12-A30 or A08 subpod. Finally, for the N4 call type both the neural network index and the similarity ratings by the human subjects in Chapter I suggest that the version made by A36 subpod is actually more similar to that of A05 pod (A08, A09, A23, and A25 subpods, Bigg et al., 1990). Further evidence for an acoustic link of A36 subpod to A05 pod is their frequent use of the N13, a call type assigned to A04 and A05 pod by Ford (1987, 1991). This lack of a consistent pattern of acoustic variation may mean that A36 subpod is only distantly related to A12 and A30 subpod, and only associates with these two subpods due to a lack of a closely related kin group.

Comparing the acoustic similarity ratings for different call types (Table XIV) suggests that acoustic variation within A-subclan follows a similar pattern for certain call types. With the exception of the N1 call type, the ratings for all call types are positively correlated, and the correlation between ratings for the N9 and N2 call types is significant. When looking at A12, A30, and A36 subpods, the three groups for which samples were available for all the call types analysed, the calls of A12 and A30 subpods are more similar to each other than to those of any other group for all but one call type. Again the exception is the N1 call type. Compared to the other call types analysed, the N1 furthermore shows a distinctive distribution, since it is not used by all members of A-subclan. However, it is used by some members of B-subclan (B01, C01, D01, H01, and I01 pods; Ford, 1991), and further research is needed to determine why this call type appears to follow a different pattern of modification.

When interpreting the patterns of acoustic variation found in this study, it is important to keep in mind that the calls of some of the groups come from a period of over 10 years (Appendix I). In Chapter II, I demonstrated that some call types undergo significant modification over such a time span. A low index of acoustic similarity therefore could result from temporal heterogeneity in the call samples from two groups rather than from structural differences in their calls at any point in time, and this leads to biases in the ratings of acoustic similarity. The findings in Chapter II suggest that not all call types are modified at the same rate, and therefore the biases resulting from temporal heterogeneity will be greater for some call types than others. Hence the lower $R_{acoust\text{-}assoc}$ for the N4 call type compared to the N9 call type is consistent with my findings in Chapter II. N9 is a stable call type, and the acoustic similarity ratings for it will not be as biased by temporal heterogeneity in the call samples as those for the more mutable N4.

In spite of this temporal heterogeneity my study found a significant positive correlation between call similarity and the frequency of association for the two call types for which the most extensive data were available. This points to a functional relationship between these two variables generated in three possible ways. First, the correlation could mean that association frequency and acoustic variation both depend on a common factor, such as the time elapsed since the split up of the ancestral group proposed by Ford (1991). Second, frequent association of two groups could be the result of the similarity of their dialects. This would be the case if groups with a similar dialect associate preferentially. Finally, frequent association could be the cause for the similarity of dialects if spending a great amount of time in acoustic contact leads to a convergence of dialect. This last possibility is supported by the findings in Chapter II. The amount of acoustic contact between two groups at least partially determines the amount of horizontal transmission of structural modifications to the calls and thus plays a role in generating and maintaining acoustic similarity.

The positive correlation between acoustic similarity and frequency of association found in this study contrasts with earlier results of Bigg et al. (1990) who compared the association patterns of the pods of the two resident communities to the similarity of their vocal repertoires. At this level, they found no significant relationship between repertoire similarity and frequency of association, and concluded that acoustic clans are not primarily social units, but groupings based on a common genealogical lineage. Similarly, Ford (1984) reports a general consistency between patterns of repertoire similarity at the level of the vocal tradition but not at the level of the community. These contrasting patterns observed at different levels of killer whale social structure can be reconciled by postulating that resident killer whales associate for two distinct reasons. Kin associations, on the one hand, may reflect and enforce genealogical bonds. Non-kin associations, on the other, may reflect social or sexual attraction between members of the different groups.

If killer whales do associate for distinct reasons, then the timing and the scale of a study determines whether or not a correlation between association patterns and dialect similarity will be found. My analysis focusses on nine matrilineal units which are presumably closely related. The main associations among these groups are likely kin associations, and therefore association patterns should correlate with acoustic similarity. In the study of Bigg et al. (1990), however, non-kin associations predominated in the association patterns, especially since most of their data were collected during the summer months, the presumed breeding season of the resident communities (Olesiuk et al., 1990). For this reason, association strengths may no longer reflect genealogy, and with it acoustic similarity.

If the association patterns in resident killer whales do in fact reflect kinship at the level of the matrilineal unit, as they do on the level of the individual (Bain, 1988; Bigg et al., 1990;

Harms, 1997) and the community (Hoelzel et al., 1998; Barrett-Lennard, pers. comm.), this study suggests that the vocal dialects of killer whales act as a non-genetic marker of kinship. Treisman (1977, 1978) argues that in a species with a high degree of philopatry, a purely genetic marker of kinship is too unrefined to identify close relatives during social interactions. He suggests that a learned marker such as the vocal repertoire may serve this function instead. Marler and Tamura (1962) also suggested that vocal dialects reflect kinship but serve as a mechanism of inbreeding avoidance. Resident killer whales, with their apparent absence of juvenile dispersal and small effective population size (Hoelzel et al. 1998), may have a need for a non-genetic marker of kinship in order to avoid competitive interactions with close kin, or to function in mate selection.

It is difficult to reconstruct maternal genealogies within acoustic clans of resident killer whales through genetic analysis because at this level, mitochondrial DNA shows virtually no variation (Barrett-Lennard, pers. comm.). More variable nuclear markers may provide better resolution, however, they are inherited from both parents making them unreliable for reconstructing strictly maternal genealogies. The difficulty in resolving kin relationships within the northern resident community through genetic means supports Treisman's (1977, 1978) point that genetic kinship markers provide insufficient resolution in philopatric species. Therefore, the similarity of shared call types combined with information on the vocal repertoire (Ford and Fisher, 1982; Bigg et al., 1990) and association data is currently the most powerful tool available for reconstructing maternal genealogies of killer whales at the level of the matrilineal unit and the pod.

GENERAL DISCUSSION

The objective of this study was to identify the mechanisms responsible for generating vocal variation among matrilineal units of resident killer whales, and to use this knowledge to interpret patterns of acoustic variation within a killer whale vocal tradition. Previous studies of killer whale dialects have focused on repertoire variation at the level of the pod, and I wanted to extend this research to investigate structural variation at the level of the matrilineal unit. I quantified structural variation using neural network analysis of frequency contours to determine the similarity of samples of calls, and used a historical approach to identify mechanisms responsible for generating variation and for maintaining structural similarity of shared call types. I use these findings combined with association data to interpret patterns of structural variation in call types shared by the 9 matrilineal units of A-subclan, one vocal tradition within the northern resident community.

In the first chapter, I showed that neural network analysis of frequency contours is a useful technique for quantifying patterns of structural variation in the discrete calls of killer whales. Analysis of temporal change suggests that the structure of killer whale calls are modified through structural drift, that is, through the accumulation of non-directional modifications of call structure. Such changes can only be detected by an analysis which assesses and integrates variation of many acoustic parameters and hence are missed by many current approaches. While the results in Chapter I showed that the neural network index evaluates acoustic variation comparably to human subjects, we do not know how similar human acoustic perception is to that of killer whales. In Chapter III however, I found that the acoustic similarity index correlates with a biological parameter, the groups' association patterns, which suggests that it does rate acoustic similarity in a biologically meaningful way.

The results of Chapter II demonstrated that the discrete calls of killer whales are modifiable behavioural traits, and that certain call types are more stable than others. The lack of acoustic divergence between the N4 calls of the two groups, in spite of structural modification of the calls by both groups, is evidence for horizontal cultural transmission on the level of the matrilineal unit. Horizontal transmission between members of the same generation requires vocal learning, and this study therefore provides evidence against the genetic coding of the discrete calls. Bowles et al. (1988) and Janik and Slater (1997) did not rule out genetic coding as a possible mechanism of dialect transmission in killer whales

From the evidence for cultural transmission in Chapter II, I hypothesized that the amount of acoustic contact between the matrilineal units of A-subclan is a good predictor of the structural similarity of call types shared by them. This hypothesis was verified in Chapter III since the patterns of acoustic variation for the two call types analysed most comprehensively gave strong and significant correlations with the groups' association patterns. Observational and genetic evidence suggests that association patterns reflect maternal kinship on the level of the individual and the community, and this may be true on the level of the matrilineal unit as well. Vocal dialects of killer whales may therefore be non-genetic traits which reflect maternal relatedness.

Mundinger (1980) defines a cultural tradition in animals as:

> "*...a learned behavior complex shared by individuals in a population of organisms, with that behaviour complex appearing in the population generation after generation and persisting in the behavioral repertoire of individual organisms following removal from, or of, the immediate learning situation.*"

In addition, he provides two criteria for identifying cultural traditions: 1) cultural transmission of learned behaviours between generations, 2) the presence of different variants of modifiable behaviours in different populations or social groups. Chapter II shows that the discrete calls of killer whales are modifiable, and that vocal differences are transmitted culturally, that is, through copying and vocal learning. Studies of captive killer whales (Bain, 1986, 1988; Ford, 1989, 1991) show that individuals retain their vocal repertoire after being isolated from their social groups, which demonstrates that the behavioural variants persist after removal of the learning situation. Finally, the results of Chapter III support earlier findings by Ford (1984, 1987, 1989, 1991) and Strager (1995) that different social groups of killer whales produce structurally distinct vocal signals, thus satisfying Mundinger's criterion for the presence of different behavioural variants. Hence, the vocal dialects of resident killer whales fulfil all criteria set by Mundinger (1980), and represent true cultural traditions.

Comparing the results in Chapter III with earlier studies by Ford (1984) and Bigg et al. (1990) demonstrates the importance of scale when interpreting patterns of acoustic variation in resident killer whales. Results may differ depending on the level of the social structure at which acoustic variation is analysed. For this reason, one needs to be careful when applying the findings of this study to the individual level, or to the level of the community. While this thesis focusses on the association patterns and patterns of acoustic variation within a single vocal tradition, resident killer whales also associate frequently with individuals belonging to different vocal traditions with whom they share no part of their vocal repertoire (Bigg et al., 1990; Ford, 1991). Killer whales infrequently mimic discrete calls from vocal traditions other than their own, but such mimicked calls have distinct tonal properties from the originals and are easily identified by ear (Ford, 1991). Multiple vocal traditions have persisted in the northern resident community in spite of frequent acoustic contact and the ability for cultural transmission. This suggests that cultural transmission is restricted to the vocal tradition, and is evidence for selective copying in killer whales. Individual animals do not indiscriminately copy from each other, but rather copying occurs only during associations with close matrilineal kin.

Selective copying of vocal patterns has been documented in birds and humans, and whether an individual includes a certain pattern into its vocal repertoire has been shown to depend on a variety of factors. These include the mating success of the tutor using the vocal pattern (Payne, 1985), plumage colour and age of the tutor as well as his date of arrival at the nesting site (Payne and Payne, 1993), frequency of social interactions with the tutor (Payne, 1981b; Kroodsma and Pickert, 1984; Baptista and Petrinovich, 1986) and the frequency of the vocal pattern in the population (Boyd and Richerson, 1985; Kroch, 1989). A bias towards copying the vocalizations of close relatives has been demonstrated in certain songbirds (Gibbs, 1990; Zann, 1990; Mann and Slater, 1995), where juvenile males preferentially copy their father’s song. In bottlenose dolphins, male calves develop a signature whistle similar to that of their mother (Sayigh et al., 1995). A similar bias towards copying from matrilineal kin, albeit present in both sexes, can be used to explain the persistence of distinct vocal traditions among killer whales in spite of frequent acoustic contact between members of different acoustic clans. Bowles et al. (1988) provide additional evidence for selective copying from maternal kin, since in their study a captive calf copied the vocal repertoire of its mother in spite of other individuals in its environment vocalising far more frequently. Unless killer whales possess an additional marker of genetic relatedness at the level of the matrilineal unit, the dialects themselves may serve to determine whether cultural transmission occurs. Documenting and quantifying the relationship between the degree of maternal relatedness and the amount of cultural transmission occurring between individuals and groups will present an important step towards a complete understanding of vocal variation in resident killer whales.

Many studies on vocal dialects so far have focused on the vocal behaviour of songbirds. My study has shown many similarities between the vocal dialects in songbirds and killer whales, but also some fundamental differences. For this reason, definitions of vocal dialects (e.g., Mundinger, 1982), and theories about their function (e.g., Nottebohm, 1975, 1985; Marler and Tamura, 1962) which were developed for songbirds are not always applicable to this species. One of the major differences between the two dialect systems is that killer whale dialects diverge along social boundaries which are not easily translated into spatial terms. In this respect, killer whale dialects are more similar to certain linguistic variation in humans, which serves to delineate social boundaries within an interacting population (e.g., Krysin, 1977; de-Wolf, 1990).

Another fundamental difference is that in many species of songbirds, the song is acquired during a formative period, after which it remains essentially unchanged throughout the animals' life (e.g., Marler, 1970; Payne, 1981b; Slater and Ince, 1982). The colony specific dialects of yellow-rumped caciques are one notable exception to this pattern (Trainer, 1989). The results of Chapter II and the evidence for vocal copying in captivity (Bain, 1986, 1988; Ford pers. comm.) suggests that killer whales are able to modify their vocal behaviour throughout their entire lives. A life-long ability for vocal learning has been documented for several other species of mammals (see Janik and Slater, 1997), and this ability can greatly accelerate the transmission of vocal variants in a population (Trainer, 1989). Due to their lifelong ability to modify their vocal behaviour, social groups of resident killer whales must maintain the structural similarity of call types shared among them through regular acoustic contact and cultural exchange.

My findings suggest that the structural variation of shared call types in resident killer whales is the outcome of two opposing forces. On the one hand, structural modification of call types through cultural drift introduces variation and causes acoustic differentiation. Horizontal transmission, on the other hand, distributes the structural modifications among frequently associating groups, and thus generates acoustic conformity. For some call types, a decrease in the amount of cultural transmission will eventually lead to a divergence of call structure, whereas extensive acoustic contact between two groups may cause structural convergence. The patterns of acoustic variation we observe at any point in time reflect the historical strengths of these two forces acting on the vocalizations of the groups which are being compared.

A similar mechanism of dialect evolution has been proposed for songbirds (see Lemon, 1975; Mundinger, 1980; Catchpole and Slater, 1995; Lynch, 1996) and humans (e.g., Bailey 1973). Two mechanisms generate vocal differences: Cultural drift in the structure of learned vocal signals results from errors in their reproduction and copying, innovation is the spontaneous generation of new vocal patterns, or the active modification of existing ones (Lemon, 1975; Payne, 1996). Cultural transmission distributes this variation throughout the population and hence promotes conformity. Errors in call reproduction and copying, as well as active innovations are passed on from one individual to the next through copying (Mundinger, 1980). In songbirds, cultural transmission can also introduce vocal variation from adjacent populations, or even from different species (Baylis, 1982).

My results can be synthesized into a tentative model for dialect evolution in killer whales. Structural similarity of shared call types reflects genetic relatedness along maternal lines through an indirect relationship, mediated by the amount of cultural exchange among individuals and groups. Similarity is maintained by cultural transmission of structural modifications to the calls, and within a killer whale vocal tradition, the amount of horizontal transmission occurring among social groups is determined by the strength of the bond between them. This is because the frequency of association and hence the amount of acoustic contact between groups reflects this social bond. Additionally, a mechanism of selective copying prevents cultural exchange between unrelated groups, and thus maintains an abrupt dialect boundary between different vocal traditions. This model remains tentative, because it is unclear at which level of maternal relatedness selective copying prevents cultural exchange, and because we do not have a precise understanding of how well association patterns reflect maternal kinship at the level of the matrilineal unit and the pod.

If the correlation between the frequency of association and maternal genetic relatedness is high within a vocal tradition, structural similarity of shared call types acts as a precise marker of maternal kinship, and may therefore function in mate choice or reduction of resource competition with close kin, as outlined by Ford and Fisher (1982) and Ford

(1991). If, on the other hand, the correlation between association patterns and maternal relatedness is low at the level of the matrilineal unit and the pod, the vocal dialects of killer whales are better indicators of the social and cultural history of a group. Wright (1996) suggests that such culturally inherited acoustic traits may act as markers for an entire complex of culturally transmitted behaviours such as food localization and foraging techniques, habitat preferences, or seasonal migratory routes. Resident killer whales feed extensively on Pacific salmon (*Oncorhynchus* spp.; Ford et al., in press), a resource which exhibits a great deal of predictable temporal and spatial variation. Nichol and Shackleton (1996) present some evidence for culturally transmitted behaviour complexes in the form of diet specialization and differential seasonal ranges within the northern resident community. Therefore, social groups of resident killer whales could act as repositories for culturally transmitted information about timing and location of peaks in resource abundance, and the similarity of shared call types could act as an indicator of the similarity of these behaviour complexes among different groups. The results of Chapter II suggest that certain call types are more stable than others. Acoustic variation of mutable call types, such as N4, likely reflects short term social events, whereas more stable call types, such as N9, are better indicators of long term histories of association and possibly maternal kinship. It may well be that killer whale vocal dialects encompass markers of genetic and cultural similarity in the same dialect system.

My findings show that the similarity of shared call types in resident killer whales is maintained by constant horizontal transmission rather than an absence of structural change. This raises interesting questions about dialect evolution in other killer whale populations. The social structure of the transient community also seems to be organized along matrilineal lines, although social bonds within this community appear to be weaker than they are among resident whales. Adult male and female transients are often encountered apart from their mothers (Bigg et al., 1990). Whereas the resident communities of the northeast Pacific exhibit complex systems of vocal dialects, all transient killer whales recorded in Washington State, British Columbia, and southeast Alaska share the same vocal repertoire of 8 call types (Ford, 1984). This homogeneity of the transient dialect either suggests that the discrete call types of transient killer whales are inherently more stable than those of residents, or it can be explained by a great amount of cultural transmission throughout the entire transient community. In the latter case, I would expect all members of the transient community to maintain frequent acoustic contact, either directly or through intermediates in order to allow structural modifications to the discrete calls to spread to all members. Such a high level of cultural transmission could be maintained through seasonal gatherings of large groups allowing for direct acoustic contact, or through frequent and varying association of small groups permitting vocal modifications to spread through indirect transmission.

This study has shed light on mechanisms and patterns of acoustic variation in killer whales on the level of the matrilineal unit. Further research is needed to quantify patterns of acoustic variation among the individuals of a matrilineal unit, and to test whether the mechanisms responsible for generating and maintaining them are the same. New techniques of quantifying acoustic variation, such as the one described in Chapter I, will prove useful here. This study has shown that modifications of the structure of shared call types can be transferred between frequently associating matrilineal units with very similar vocal repertoires. It is left for future research to determine the extent of cultural transmission between more distantly related groups. For example, the members of B-subclan share some call types used by A-subclan. Is there still exchange of structural modifications at this level? Killer whale vocal dialects evolve by modification of the vocal repertoire as well as by modification of call structure, and this study has focused entirely on the structural level. A study taking Ford’s (1984, 1991) work on vocal repertoires to the level of the matrilineal unit and the individual, and taking a detailed look at repertoire stability and call use over time, is needed to test whether cultural transmission acts on the level of the vocal repertoire as it does on the level of call structure. While this study has answered questions about the mechanisms generating vocal change and the patterns of variation they create, much further research is required to fully delineate the influences on vocal dialects in resident killer whales and their role within the context of their unique social organization.

LITERATURE CITED

Awbrey, F., Evans, W., Jehl, J., Thomas, J., and Leatherwood, S. **1982**: Comparison of Ross Sea and Pacific Northwest killer whale vocalizations. *Rep. Int. Whal. Commn.* **32**, 667-670.

Bailey, C.-J. **1973**: *Variation and Linguistic Theory.* Center for Applied Linguistics, Washington DC. 162 pp.

Bailey, K. **1978**: The structure and variation of the separation call of the bobwhite quail (*Colinus virginianus*, Odontophorinae). *Anim. Behav.* **26**, 296-303.

Bain, D.E. **1986**: Acoustic behavior of *Orcinus* : sequences, periodicity, behavioral correlates and an automated technique for call classification. In: B.C. Kirkevold, and J.S. Lockard (eds.): *Behavioral Biology of Killer Whales.* Alan R. Liss, New York, NY. pp. 335-371.

Bain, D.E. **1988**: *An Evaluation of Evolutionary Processes: Studies of Natural Selection, Dispersal, and Cultural Evolution in Killer Whales.* Ph.D dissertation, University of California, Santa Cruz, CA, 256 pp.

Baptista, L. F. **1975**: Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalii*). *Univ. Calif. Publ. Zool.* **105**, 1-52.

Baptista, L. F., and Petrinovich, L. **1986**: Song development in the white-crowned sparrow: social factors and sex differences. *Anim. Behav.* **34**, 1359-1371.

Barbujani, G. **1991**: What do languages tell us about human microevolution? *Trends Ecol. Evol.* **6**, 151-156.

Baribeau, J., Berman, B., Atkin, A., Roth, R.M. **1996**: Musical experience and auditory P300 in a divided attention task. *Brain. Cogn.* **30**, 378-380.

Barrett Lennard, L. G., Ford. J.K.B., and Heise, K.A. **1996**: The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.* **51**, 553-565.

Baylis, J.R. **1982**: Avian vocal mimicry: its function and evolution. In: Kroodsma, D.E., Miller, E.H., and Ouellet, H. (eds): *Acoustic Communication in Birds* Vol. 2. Academic Press, New York, NY. pp. 51-83.

Beecher, M. D. **1989**: Signalling systems for individual recognition: an information theory approach. *Anim. Behav.* **38**, 248-261.

Bel'kovich, V.M., Ivanova, E.E., Yefremkova, O.V., Kozarovitsky, L.B., and Kharitonov, S.P. **1991**: Searching and hunting behaviour in the bottlenose dolphin *(Tursiops truncatus*) in the Black Sea. In: K. Pryor, and K.S. Norris, (eds.): *Dolphin Societies: Discoveries and Puzzles.* University of California Press, Berkeley, CA. pp. 38-77.

Bigg, M.A. **1982**: An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. Int. Whaling Comm.* **32**, 655-666.

Bigg, M.A., Olesiuk, P.F., and Ellis, G.M. **1990**: Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whaling Comm. Spec. Issue No.* **12**, 383-405.

Bowles, A.E., Young, W.G., and Asper, E.D. **1988**: Ontogeny of stereotyped calling of a killer whale calf, *Orcinus orca*, during her first year. *Rit Fisk.* **11**, 251-275.

Boyd, R., and Richerson, P.J. **1985**: *Culture and the Evolutionary Process.* University of Chicago Press, Chicago, IL. 331 pp.

Buck, J.R., and Tyack, P.L. **1993**: A quantitative measure of similarity for *Tursiops truncatus* signature whistles. *J. Acoust. Soc. Am.* **94**, 2497-2506.

Cairns, S.J., and Schwager, S.J. **1987**: A comparison of association indices. *Anim. Behav.* **35**, 1454-1469.

Caldwell, M.C., and Caldwell, D.K. **1965**: Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). *Nature* **207**, 434-435.

Catchpole, C., and Slater, P. J. B. **1995**: *Bird Song: Biological Themes and Variations.* Cambridge University Press, Cambridge, UK. 248 pp.

Cavalli-Sforza, L. L. **1997**: Genes, Peoples and Languages. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 7719-7724.

Cavalli-Sforza, L. L., and Feldman, M.W. **1981**: *Cultural Transmission and Evolution: A Quantitative Approach.* Princeton University Press, Princeton, NJ. 388 pp.

Chilton, G., and Lein, M. R. **1996**: Long-term changes in songs and song dialect boundaries of Puget Sound white-crowned sparrows. *Condor* **98**, 567-580.

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.

Conner, D.A. **1982**: Dialects versus geographic variation in mammalian vocalization. *Anim. Behav.* **30**, 297-298.

Crowley, P.H., Provencher, L., Sloane, S., Dugatkin, L.A., Sophn, B., Rogers, L., Alfieri, M. **1996**: Evolving cooperation: The role of individual recognition. *Biosystems* **37**, 49-66.

Dahlheim, M.E., Ellifrit, D.K., Swenson, J.D. **1997**: *Killer Whales of Southeast Alaska: A Catalogue of Photo-Identified Individuals.* U.S. National Marine Fisheries Service, Seattle, WA. 79 pp.

Dasgupta, C. **1991**: Neural networks: An overview. *J. Indian Inst. Sci.* **71**, 491-502.

de-Wolf, G-D. **1990**: Social and regional differences in grammatical usage in Canadian English: Ottawa and Vancouver. *Amer. Sp.* **65**, 3-32.

Emlen, S.T. **1972**: An experimental analysis of the parameters eliciting species recognition. *Behaviour* **41**, 130-171.

Erbe, C. **1997**: *Masked Hearing Thresholds of Beluga Whale* (Delphinapterus leucas) *Vocalizations in Icebreaker Noise.* Ph.D. Dissertation University of British Columbia, Vancouver, BC. 215 pp.

Ford, J.K.B. **1984**: *Call Traditions and Vocal Dialects of Killer Whales* (Orcinus orca) *in British Columbia.* Ph.D. Dissertation University of British Columbia, Vancouver. 435 pp.

Ford, J.K.B. **1987**: A Catalogue of underwater calls produced by killer whales *(Orcinus orca*) in British Columbia. *Can. Data Rep. Fish. Aquat. Sci. No.* **633**. 161 pp.

Ford, J.K.B. **1989**: Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia, Canada. *Can. J. Zool.* **67**, 727-745.

Ford, J.K.B. **1991**: Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia, Canada. *Can. J. Zool.* **69**, 1454-1483.

Ford, J.K.B., and Fisher, H.D. **1982**: Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Rep. Int. Whaling Comm.* **32**, 671-679.

Ford, J.K.B., Ellis, G.M., and Balcomb, K.C. **1994**: *Killer Whales - The Natural History and Genealogy of* Orcinus orca *in British Columbia and Washington State.* UBC Press, Vancouver, BC. 102 pp.

Ford, J.K.B., Ellis, G.M., Morton A.B., Palm, R.S., and Balcomb, K.C., **in press**: Diet specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* in press.

Gibbs, L.H. **1990**: Cultural evolution of male song types in Darwin's medium ground finches, *Geospiza fortis. Anim. Behav.* **39**, 253-263.

Ginsberg, J.R., and Young, T.P. **1992**: Measuring associations between individuals or groups in behavioural studies. *Anim. Behav.* **44**, 377-379.

Gouzoules,H., and Gouzoules, S. **1990**: Matrilineal signatures in the recruitment screams of pigtail macaques, *Macaca nemestrina. Behaviour* **115**, 327-347.

Grant, B.R. **1984**: The significance of song variation in a population of Darwin's finches. Behaviour **89**, 90-116.

Greenberg, J.H. **1963**: The languages of Africa. International Journal of American *Linguistics* **29**, 1-177.

Halpern, A.R., Bartlett, J.C., Dowling, W.J. **1995**: Aging and experience in the recognition of musical transpositions. *Psychol. Aging* **10**, 325-342.

Halpern, A.R., Kwak, S., Bartlett J.C., Dowling, W.J. **1996**: Effects of aging and musical experience on the representation of tonal hierarchies. *Psychol. Aging* **11**, 235-246.

Hamilton, W.D. **1964a**: The genetic evolution of social behaviour I. *J. Theor. Biol.* **7**, 1-16.

Hamilton, W.D. **1964b**: The genetic evolution of social behaviour II. *J. Theor. Biol.* **7**, 17-52.

Harms, E. **1997**: *Association Patterns and Pod Cohesion in Northern Resident Killer Whales* (Orcinus orca). M. Sc. thesis, University of British Columbia, Vancouver, BC. 53 pp.

Hinton, G.E. **1992**: How neural networks learn from experience. *Sci. Am.* **268**, 145-151.

Hoelzel, A.R., Dahlheim, M., and Stern, S.J. **1998**: Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. *Journal of Heredity* **89**, 121-128.

Hoese, H.D. **1971**: Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy* **52**, 222-223.

Horn, A.G., and Falls, J.B. **1996**: Categorization and the design of signals: the case of song repertoires. In: Kroodsma, D.E., and Miller, E.H. (eds.): *Ecology and Evolution of Acoustic Communication in Birds.* Comstock Publishing Associates, Ithaca NY. pp. 121-135.

Hunt, E. **1993**: A proposal for computer modelling of animal linguistic comprehension. In: Roitblat, H.L., Herman, L.M., and Nachtigall, P.E. (eds.): *Language and Communication: Comparative Perspectives.* Lawrence Erlbaum Associates, Hillsdale, NJ. pp. 85-94.

Ince, S.A., Slater, P.J.B., and Weisman, C. **1980**: Changes with time in the song of chaffinches. *Condor* **82**, 285-290.

Insley, S.J. **1992**: Mother-offspring separation and acoustic stereotypy - A comparison of call morphology in two species of pinnipeds. *Behaviour* **120**, 103-122.

Janik, V.M., and Slater, P.J.B. **1997** Vocal learning in mammals. *Adv. Study Behav.* **26**, 59-99.

Jenkins, P.F. **1977**: Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav.* **25**, 50-78.

Job, D.A., Boness, D.J., and Francis, J.M. **1995**: Individual variation in nursing vocalizations of Hawaiian monk seal pups, *Monachus schauinslandi* (Phocidae, Pinnipedia), and lack of maternal recognition. *Can. J. Zool.* **73**, 975-983.

Johnson, S.C. **1967**: Hierarchical clustering schemes. *Psychometri.* **32**, 241-54.

Kelso, J. A. S. **1995**: *Dynamic Patterns: The Self-organization of Brain and Behavior.* MIT Press, Cambridge, MA. 334 pp.

Köhler, W. **1929**: *Gestalt Psychology.* Horace Liveright, New York, NY. 369 pp.

Kroch, A.S. **1989**: Reflexes of grammar in patterns of language change. *Lang. Var. Change* **1**, 199-244.

Kroodsma, D.E., and Baylis, J.R. **1982**: A world survey of evidence for vocal learning in birds. in: Kroodsma, D.E., Miller, E.H., and Ouellet, H. (eds): *Acoustic Communication in Birds* Vol. 2. Academic Press, New York, NY. 311-337.

Kroodsma, D.E., and Pickert, R. **1984**: Sensitive phases for song learning: effects of social interactions and individual variation. *Anim. Behav.* **32**, 389-394.

Krysin, L.P. **1977**: On social differences in the use of linguistic variants. *Int. J. Soc. L.* **13**, 53-70.

Lederer, R. **1983**: Prep school slanguage. *Verbatim* **9**, 1-3.

Lehtonen, L. **1983**: The changing song patterns of great tits, *Parus major. Ornis fenn.* **60**, 16-21.

Lemon, R.E. **1975**: How birds develop song dialects. *Condor* **77**, 385-406.

Loesche, P., Beecher, M.D., and Stoddard, P.K. **1992**: Perception of cliff swallow calls by birds *Hirundo pyrrhonota* and *Sturnus vulgaris* and humans *Homo sapiens. J. Comp. Psychol.* **106**, 239-247.

Lougheed, S.C., and Handford, P. **1992**: Vocal dialects and the structure of geographic variation in morphological and allozymic characters in the rufous-collared sparrow, *Zonotrichia capensis. Evolution* **46**, 1443-1456.

Lynch, A. 1996 Population memetics of bird song. In: Kroodsma, D.E., and Miller, E.H. (eds.): *Ecology and Evolution of Acoustic Communication in Birds.* Comstock Publishing Associates, Ithaca NY. pp. 181-197.

Mann, N.I., and Slater, P.J.B. **1995**: Song tutor choice by zebra finches in aviaries. *Anim. Behav.* **49**, 811-820.

Marler, P. **1970**: A comparative approach to vocal learning: Song development in white-crowned sparrows. *J. Comp. Physiol. Psychol.* **71**, 1-25.

Marler, P., and Peters, S. **1982**: Subsong and plastic song: their role in the vocal learning process. In: Kroodsma, D.E., and Miller, E.H. (eds.): *Acoustic Communication in Birds* Vol. 2. Academic Press, New York, NY. pp. 25-50.

Marler, P., and Tamura, M. **1962**: Song ‘dialects' in three populations of white-crowned sparrows. *Condor* **64**, 368-377.

Martindale, S. **1980**: On the multivariate analysis of avian vocalizations. *J. Theor. Biol.* **83**, 107-110.

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.

Miller, G.A., and Nicely, P.E. **1955**: An analysis of perceptual confusions among some English consonants. *J. Acoust. Soc. Am.* **27**, 338-352.

Mitani, J.C., Hasegawa, T., Gros Louis, J., Marler P., Byrne, R. **1992**: Dialects in wild chimpanzees. *Am. J. Primatol.* **27**, 233-243.

Mundinger, P.C. **1980**: Animal cultures and a general theory of cultural evolution. *Ethol. Sociobiol.* **1**, 183-223.

Mundinger, P.C. **1982**: Microgeographic and macrogeographic variation in birds. In: Kroodsma, D.E., Miller, E.H., and Ouellet, H. (eds): *Acoustic Communication in Birds* Vol. 2. Academic Press, New York, NY 147-208.

Mundinger, P.C. **1995**: Behaviour-genetic analysis of canary song: Inter-strain differences in sensory learning, and epigenetic rules. *Anim. Behav.* **50**, 1491-1511.

Nelson, D.A., Marler, P. **1994**: Selection-based learning in bird song development. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 10498-10501.

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. *Biol. Cybern.* **66**, 485-469.

Nichol, L.M., and Shackleton, D.M. **1996**: Seasonal movements and foraging behaviour of northern resident killer wales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. *Can. J. Zool.* **74**, 983-991.

Nottebohm, F. **1975**: Continental patterns of song variability in *Zonotrichia capensis:* some possible ecological correlates. *Am. Nat.* **109**, 605-624.

Nottebohm, F. **1976**: Phonation in the Orange-winged Amazon parrot, *Amazona amazonica. J. Comp. Physiol.* **108**, 157-170.

Nottebohm, F. **1985**: Sound transmission, signal salience and song dialects. *Behav. Brain Sc.* **8**, 112-113.

Nuessel, F. **1996**: Intergenerational language differences: some observations on the notion of 'gerontolect'. *Geolinguistics* **22**, 28-31.

Olesiuk, P.F., Bigg, M.A., and Ellis, G.M. **1990**: Life history and population dynamics of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whaling Comm. Spec. Issue* **12**, 209-243.

Oppenheim, A.V., and Schafer, R.W. **1975**: *Digital Signal Processing.* Prentice Hall, Englewod Cliffs, NJ. 585 pp.

Payne, R.B. **1981**: Population structure and social behavior: Models for testing the ecological significance of song dialects in birds. In: R.D. Alexander and D.W. Tinkle (eds.): *Natural Selection and Behavior.* Chiron Press, New York, NY. pp. 108-120.

Payne, R.B. **1981**: Song learning and social interaction in indigo buntings. *Anim. Behav.* **29**, 688-697.

Payne, R.B. **1985**: Behavioral continuity and change in local song populations of Village Indigobirds, *Vidua chalybeata. Z. Tierpsychol.* **70**, 1-44.

Payne, R.B. **1996**: Song traditions in indigo buntings; origin, improvisation, dispersal, and extinction in cultural evolution. In: Kroodsma, D.E., and Miller, E.H. (eds.): *Ecology and Evolution of Acoustic Communication in Birds.* Comstock Publishing Associates, Ithaca NY. pp. 198-220.

Payne, R.B., and Payne, K. **1977**: Social organization and mating success in local song populations of Village Indigobirds (*Vidua chalybeata*). *Z. Tierpsychol.* **45**, 113-173.

Payne, R.B., and Payne, L.L. **1993**: Song copying and cultural transmission in indigo buntings. *Anim. Behav.* **46**: 1045-1065.

Payne, R.B., Thompson, W.L., Fiala, K.L., and Sweany, L.L. **1981**: Local song traditions in indigo buntings: cultural transmission of behaviour patterns across generations. *Behaviour* **77**, 199-221.

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 WCNN* **1**, 304-307.

Rasmuson, T.M. and Barclay, R.M.R. **1992**: Individual variation in the isolation calls of new-born big brown bats (*Eptesicus fuscus*): Is variation genetic? *Can. J. Zool.* **70**, 698-702.

Rumelhart, D.E., Hinton, G.E., and Williams, R.J. **1986**: Learning internal representation by error propagation. In: Rumelhart, D.E., and McLelland J. (eds.): *Parallel Data Processing* Vol.1. MIT Press, Cambridge MA. pp. 318- 362.

Santorini, B. **1993**: The rate of phrase structure change in the history of Yiddish. *Lang. Var. Change* **5**, 257-283.

Sayigh, L.S. **1992**: *Development and Functions of signature whistles of free-ranging bottlenose dolphins*, Tursiops truncatus. Ph.D. dissertation, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution WHOI 92-37. 344 pp.

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. *Behav. Ecol. Sociobiol.* **26**, 247-260.

Sayigh, L.S., Tyack, P.L., Wells, R.S., Scott, M.D., and Irvine, A.B. **1995**: Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus. Behav. Ecol. Sociobiol.* **36**, 171-177.

Schevill, W.E., and Watkins, W.A. **1966**: Sound structure and directionality in *Orcinus* (killer whale). *Zoologica* **51**, 70-76.

Slater, P.J.B. **1989**: Bird song learning: causes and consequences. *Ethol. Ecol. Evol.* **1**, 19-46.

Slater, P.J.B., and Ince, S.A. **1982**: Song development in chaffinches: what is learned and when? *Ibis* **124**, 21-26.

Snow, D.W. **1968**: The singing assemblies of little hermits. *Living Bird* **7**, 47-55.

Spong, P., Symonds, H., Gaetz, W.C., Jantzen, K., and Weinberg, H. **1993**: *A neural network method for recognition of individual* Orcinus orca *based on their acoustic behaviour: Phase 1.* Paper presented at Oceans 1993, Conference of the IEEE, Victoria, BC. 4 pp.

Strager, H. **1995**: Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Can. J. Zool.* **73**, 1037-1047.

Symmes, D., Newman, J.D., Talmage-Riggs, G., and Katz Lieblich, A. **1979**: Individuality and stability of isolation peeps in squirrel monkeys. *Anim. Behav.* **27**, 1142-1152.

Thielke, G **1992**: Stabilität und Änderungen von Dialekten und Dialektgrenzen beim Gartenbaumläufer (*Certhia brachydactyla*). *J. Orn.* **133**, 43-59.

Trainer, J.M. **1989**: Cultural evolution in song dialects of yellow-rumped caciques in Panama. *Ethology* **80**, 190-204.

Treisman, M. **1977**: The evolutionary restriction of aggression within a species. *J. Math. Psychol.* **16**, 167-203.

Treisman, M. **1978**: Bird song dialect, repertoire size, and kin association. *Anim. Behav.* **26**, 814-817.

Tyack, P.L. **1986**: Whistle repertoires of two bottlenose dolphins, (*Tursiops truncatus*): mimicry of signature whistles? *Behav. Ecol. Sociobiol.* **18**, 251- 257.

Vogl, T.P., Mangis, J.K., Ziegler, A.K., and Alkon, D.L. **1988**: Accelerating the convergence of the backpropagation method. *Biol. Cybern.* **59**, 257-263.

Weilgart, L. and Whitehead, H. **1997**: Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40**, 277-285.

Weisberg, S. **1985**: *Applied Linear Regression* 2nd ed. Wiley, New York, NY. 324 pp.

Wenrick Boughman, J. **1997**: Greater spear-nosed bats give group-distinctive calls. *Behav. Ecol. Sociobiol.* **40**, 61-70.

Wiley, R.H. **1971**: Song groups in a singing assembly of Little Hermits. *Condor* **73**, 28-35.

Williams, J.M., and Slater, P.J.B. **1990**: Modelling bird song dialects: the influence of repertoire size and numbers of neighbours. *J. Theor. Biol.* **145**, 487-496.

Williams, J.M., and Slater, P.J.B. **1991**: Computer analysis of bird sounds: a guide to current methods. Bioacoustics **3**, 121-128.

Wright, T.F. **1996**: Regional dialects in the contact call of a parrot. *Proc. Roy. Soc. B:* **263**, 867-872.

Zann, R. **1990**: Song and call learning in wild zebra finches in south-east Australia. *Anim. Behav.* **40**, 811-828.

Zar J. C. **1996**: *Biostatistical Analysis.* Prentice Hall, Upper Saddle River NJ. 662 pp.

APPENDIX I: List of Recording Sessions Used

Table A-I: Recording sessions for A08 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
01 Aug 1985	D.E. Bain	-	5	2	-	
13 Oct 1986	D.E. Bain	-	-	2	-	
20 Jul 1995	D. Briggs	-	4	3	-	
27 Jul 1995	D. Briggs	-	6	4	-	
05 Jun 1997	J.K.B. Ford	-	1	13	-	
26 Aug 1997	F. Thomsen	-	5	-	-	

Table A-II: Recording sessions for A09 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
17 Sep 1991	OrcaLab	-	-	6	-	
27 Sep 1991	OrcaLab	-	-	6	-	
05 Oct 1991	OrcaLab	-	-	6	-	
06 Oct 1991	OrcaLab	-	-	6	-	

Table A-III: Recording sessions for A23 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
04 Nov 1993	OrcaLab	-	-	9	4	
21 Oct 1994	OrcaLab	-	-	1	-	
16 Jul 1995	D. Briggs	-	-	-	9	
20 Jul 1995	OrcaLab	-	-	14	5	
35209	G.M. Ellis	-	-	-	3	

Table A-IV: Recording sessions for A25 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
26 Jul 1984	D.E. Bain	-	-	5	1	
20 Jul 1985	OrcaLab	-	-	2	1	
09 Sep 1986	OrcaLab	-	-	-	9	
09 Jul 1990	OrcaLab	-	-	17	4	
20 Jul 1995	D. Briggs	-	-	-	4	
08 Jul 1996	D. Briggs	-	-	-	2	

Table A-V: Recording sessions for A12 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
28 Aug 1984	D.E. Bain	-	-	-	2	
14 Jul 1986	OrcaLab	-	-	3	1	
05 Aug 1986	OrcaLab	-	1	6	9	
07 Aug 1986	OrcaLab	-	3	15	9	
19 Aug 1988	OrcaLab	-	-	9	-	
06 Sep 1988	OrcaLab	-	-	2	-	I31 subpod also in recording range
15 Sep 1988	OrcaLab	-	-	10	-	
22 Sep 1988	OrcaLab	-	-	3	-	
02 Jul 1990	OrcaLab	-	-	5	-	
03 Jul 1990	OrcaLab	-	-	5	5	
04 Jul 1990	OrcaLab	-	-	5	4	
15 Jul 1990	OrcaLab	-	-	4	1	
12 Oct 1990	OrcaLab	-	-	5	11	
04 Aug 1991	OrcaLab	-	2	3	2	
26 Aug 1991	OrcaLab	-	2	13	4	
25 Oct 1991	OrcaLab	6	2	8	15	
14 Oct 1992	OrcaLab	-	-	7	10	
13 Jul 1992	OrcaLab	1	-	5	3	
03 Aug 1992	OrcaLab	3	-	8	8	
21 Sep 1992	OrcaLab	-	-	4	-	
30 Jul 1993	OrcaLab	-	-	8	7	
18 Aug 1993	OrcaLab	-	-	7	7	
23 Aug 1993	OrcaLab	-	-	9	7	
14 Jul 1994	OrcaLab	-	-	7	2	
15 Oct 1994	OrcaLab	-	1	9	6	
17 Oct 1994	OrcaLab	-	1	8	13	
08 Sep 1995	J.K.B. Ford	4	-	4	4	0953-1421hrs.
08 Sep 1995	OrcaLab	1	-	5	4	1500-2010hrs.
12 Sep 1995	OrcaLab	-	-	6	3	I11 subpod also in recording range
21 Sep 1995	OrcaLab	1	2	2	3	
28 Sep 1995	OrcaLab	1	1	3	3	
08 Oct 1995	OrcaLab	1	-	4	-	
10 Oct 1995	OrcaLab	-	2	-	4	
30 Jul 1996	OrcaLab	-	-	7	10	I15 subpod also in recording range
09 Sep 1996	OrcaLab	-	-	2	2	I11 subpod also in recording range
12 Nov 1996	OrcaLab	-	-	8	9	
13 Nov 1996	OrcaLab	-	-	7	-	
15 Jul 1997	F. Thomsen	-	3	4	7	
18 Jul 1997	F. Thomsen	-	-	1	3	
23 Jul 1997	OrcaLab	-	-	4	1	
23 Jul 1997	F. Thomsen	-	-	4	-	
27 Jul 1997	F. Thomsen	-	-	3	3	
28 Jul 1997	F. Thomsen	-	1	1	1	
01 Aug 1997	F. Thomsen	-	-	3	6	
26 Sep 1997	OrcaLab	-	-	4	-	

Table A-VI: Recording sessions for A30 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
25 Jun 1985	A. Morton	-	1	6	4	
07 Jul 1985	D.E. Bain	-	4	7	11	
13 Jul 1985	D.E. Bain	-	1	10	3	
24 Jul 1985	D.E. Bain	-	-	1	3	
12 Jul 1988	OrcaLab	-	-	7	5	
15 Jul 1988	OrcaLab	-	-	5	-	
15 Sep 1988	OrcaLab	-	-	8	8	
22 Oct 1988	OrcaLab	-	-	4	8	I31 subpod also in recording range
21 Jun 1989	OrcaLab	-	-	5	-	
25 Jun 1989	OrcaLab	-	-	6	-	
20 Jul 1989	OrcaLab	-	-	3	-	
11 Oct 1989	OrcaLab	-	-	5	-	
02 Nov 1989	OrcaLab	-	-	5	-	
13 Jun 1990	OrcaLab	-	-	8	5	
18 Jun 1990	OrcaLab	-	-	5	2	
23 Jul 1990	OrcaLab	-	-	7	7	
30 Aug 1990	OrcaLab	-	-	4	7	I11, I15 subpods also in recording range
33386	OrcaLab	1	-	1	-	
15 Jul 1991	OrcaLab	-	-	2	3	
19 Aug 1991	OrcaLab	1	-	2	1	
23 Aug 1991	OrcaLab	5	3	11	6	
24 Aug 1991	OrcaLab	2	-	2	9	
30 Aug 1991	OrcaLab	2	-	6	2	
04 Sep 1992	OrcaLab	2	-	2	5	
06 Sep 1992	OrcaLab	5	-	5	6	
03 Oct 1992	OrcaLab	-	-	6	5	
23 Oct 1992	OrcaLab	-	-	11	5	
26 Jun 1993	OrcaLab	-	-	8	5	
11 Aug 1993	OrcaLab	-	-	4	8	
19 Sep 1993	OrcaLab	-	-	5	2	
16 Oct 1993	OrcaLab	-	-	3	1	
13 Nov 1993	OrcaLab	-	-	4	5	
19 Jul 1994	OrcaLab	-	3	10	-	
06 Aug 1994	OrcaLab	-	1	1	-	
26 Oct 1994	OrcaLab	-	-	13	-	
28 Jun 1995	OrcaLab	-	1	4	10	
30 Jun 1995	OrcaLab	-	1	4	3	
02 Jul 1995	OrcaLab	-	-	4	-	
10 Jul 1995	OrcaLab	-	1	4	4	
09 Aug 1995	OrcaLab	-	-	4	1	
13 Aug 1995	OrcaLab	-	-	-	1	
03 Nov 1995	OrcaLab	-	-	1	1	
04 Nov 1995	OrcaLab	-	1	3	1	
17 Jul 1996	OrcaLab	-	-	9	7	
18 Jul 1996	OrcaLab	-	-	8	8	
03 Aug 1996	OrcaLab	-	-	7	6	
13 Jul 1997	F. Thomsen	-	-	1	1	
16 Jul 1997	F. Thomsen	-	-	1	-	
17 Jul 1997	F. Thomsen	-	2	9	3	
18 Jul 1997	OrcaLab	-	-	-	5	
23 Jul 1997	F. Thomsen	-	1	-	2	
31 Jul 1997	F. Thomsen	-	-	4	2	
02 Aug 1997	OrcaLab	-	-	-	4	
08 Aug 1997	F. Thomsen	-	1	6	1	I15 subpod also in recording range
09 Aug 1997	F. Thomsen	-	-	3	3	I15 subpod also in recording range

Table A-VII: Recording sessions for A36 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
26 Jul 1985	D.E. Bain	-	4	-	-	
25 Jul 1991	OrcaLab	1	-	3	2	
20 Sep 1991	OrcaLab	-	-	2	-	
22 Sep 1991	OrcaLab	3	2	1	1	
30 Sep 1991	OrcaLab	6	-	18	4	
01 Jun 1992	J.K.B. Ford	5	-	-	-	
05 Jul 1994	J.K.B. Ford	-	1	-	-	
11 Aug 1994	V.B. Deecke	3	1	-	14	
11 Sep 1996	F. Thomsen	-	7	-	-	
27 Aug 1997	F. Thomsen	-	1	-	-	
07 Sep 1997	F. Thomsen	-	6	-	-	

Table A-VIII: Recording sessions for A11 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
20 Jul 1985	D.E. Bain	-	-	4	-	
08 Aug 1987	D. Briggs	-	-	14	-	
14 Aug 1987	D. Briggs	-	-	6	-	

Table A-IX: Recording sessions for A24 subpod

Date	Recorded by	N1	N2	N4	N9	Comments
17 Sep 1985	A. Morton	-	-	1	-	
?? May 1992	S. Wischniowski	-	-	6	-	
?? May 1993	S. Wischniowski	-	-	7	-	
14 Aug 1995	D. Briggs	-	-	10	-	

APPENDIX II: Composition and Genealogies of the Matrilineal Units of A-Subclan

modified from Bigg et al. (1990); Ford et al. (1994)

Legend for Figures A1-A7:

┋ ┋	Animal born before 1973, genealogy and age inferred from association patterns
†	Dead or missing in 1997
c	Removed by live capture
?	Sex undetermined

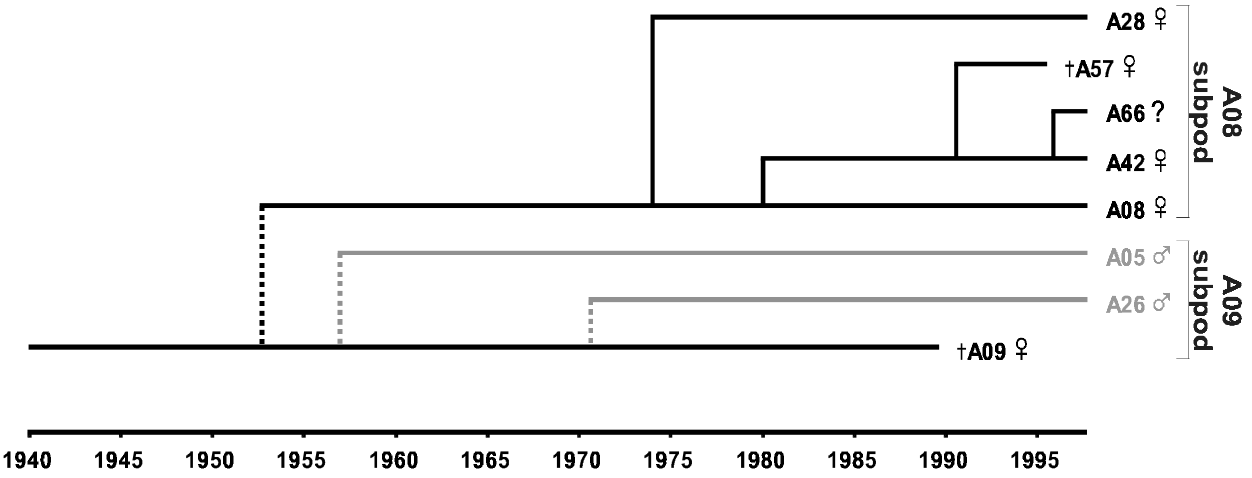


Figure A-1: Composition and genealogies of A08 and A09 subpods.

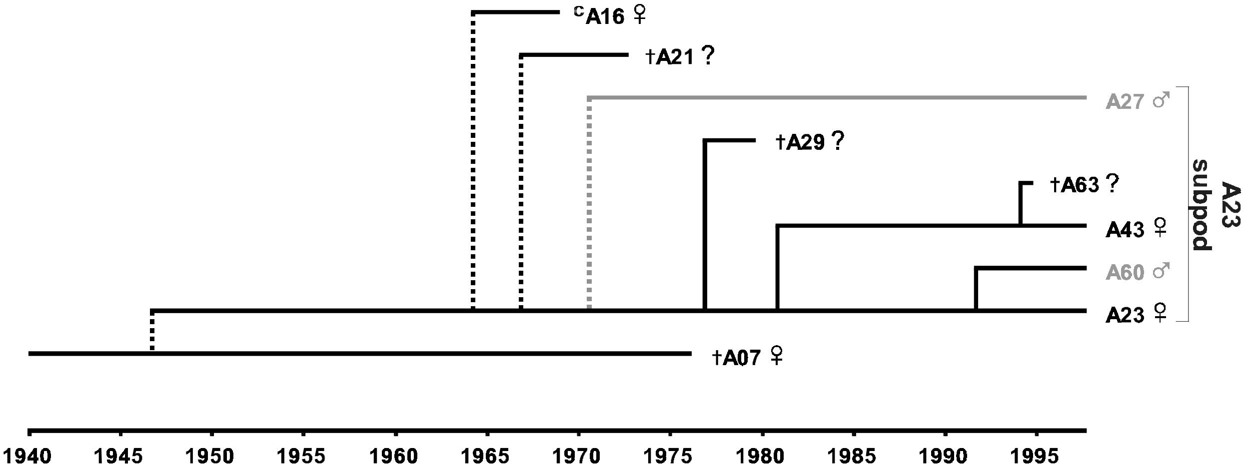


Figure A-2: Composition and genealogy of A23 subpod.

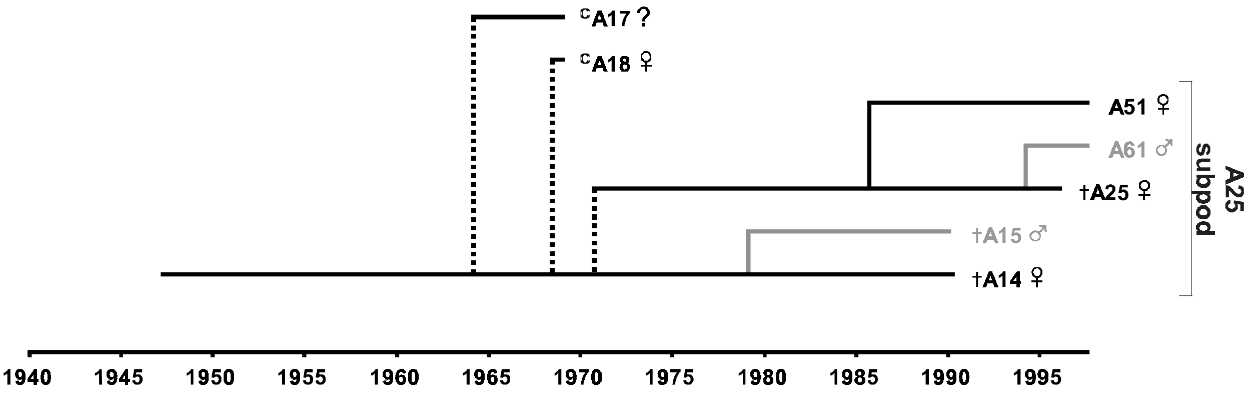


Figure A-3: Composition and genealogy of A25 subpod.

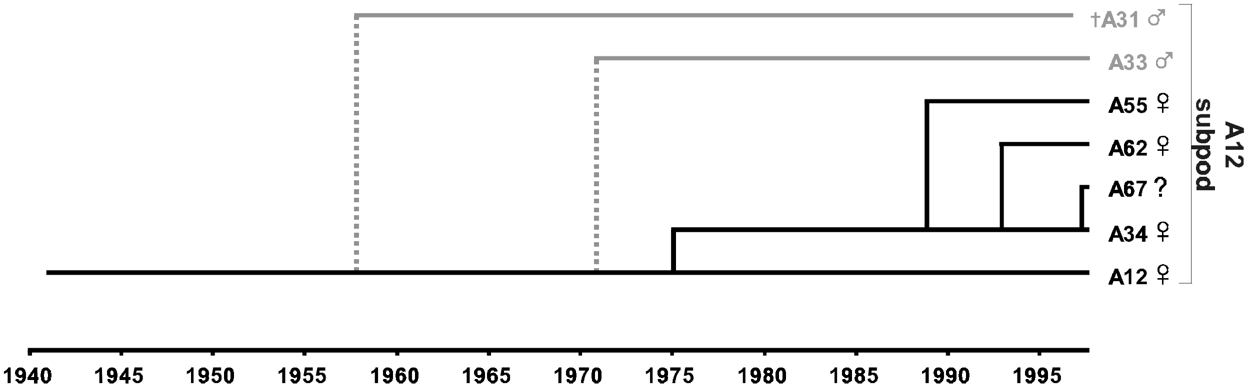


Figure A-4: Composition and genealogy of A12 subpod.

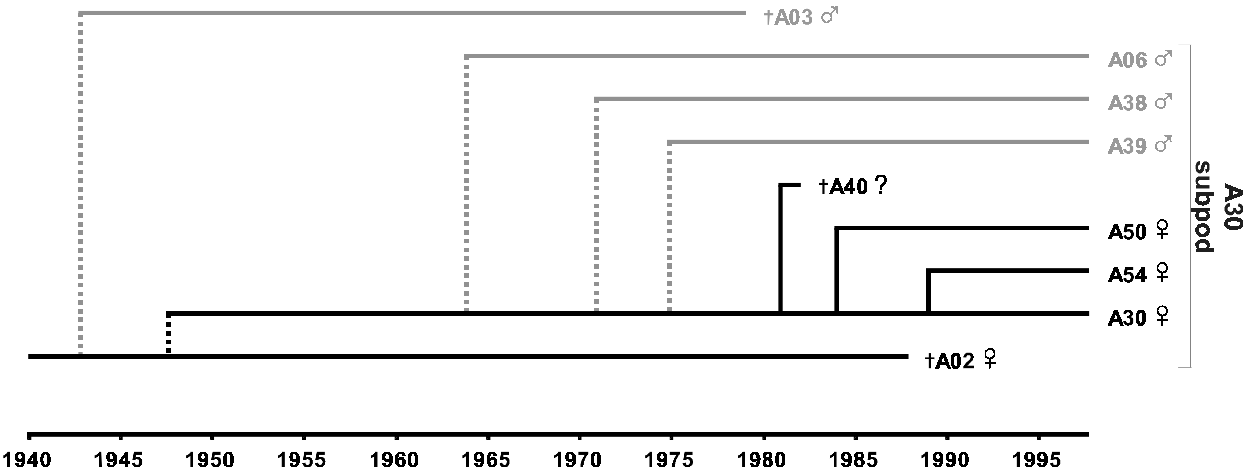


Figure A-5: Composition and genealogy of A30 subpod.

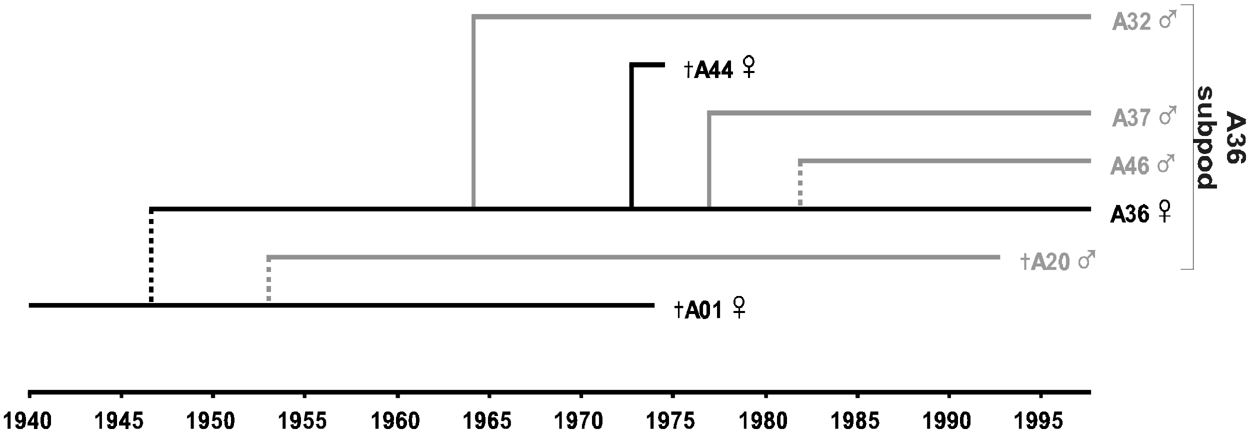


Figure A-6: Composition and genealogy of A36 subpod.

Figure A-7: Composition and genealogies of A11 and A24 subpods.

APPENDIX III: MATLAB 4.2 Algorithms for Frequency Contour Extraction and Neural Network Analysis

1) Function Sidewinder

```
function X = sidewinder(X, tempres, freqres)
[height,duration] = size(X);
z = (1:height).*freqres;
x = (1:duration).*tempres;
spgram = pcolor(x,z,X)'; axis([1 x(duration) 0 z(250)]);
colormap((hot)); shading flat
drawnow
like = input('Is the call to your liking (y/n)?   ','s');
if like == 'n',
        close(gcf),
        y = [ ], break,
end
disp('Click on the beginning of the call')
[start, whatever] = ginput(1);
start = round(start/tempres);
disp('Click on the end of the call')
[stop, whatever] = ginput(1);
stop = round(stop/tempres);
X = silence2(X,start);
y = ones(1,duration);
floor = min(min(X));
timebin = start;
oldetyme = 0;
while timebin <= duration
        spectrum = X(1:height,timebin);
        bottom = find(spectrum > floor);
        if ~isempty(bottom);
                last = bottom(length(bottom));
        else
                last = 5;
        end
        autoco = xcov(spectrum);
        autoco = autoco(round(length(autoco)/2):length(autoco));
        y(timebin) = chamois(autoco,2, last);
        Y(:,timebin) = autoco;
        timebin = timebin+1;
        time = round((timebin-start)/(5*(duration-start)) * 100)*5;
        if oldetyme ~= time
                disp([sprintf('%3.0f', time),'%'])
                oldetyme = time;
```

```
        end
end
y(stop:duration) = ones(size(stop:duration)).*y(stop);
z = (1:height).*freqres
x = (1:duration).*tempres;
spgram = pcolor(x,z,X)'; axis([1 x(duration) 0 2*max(y(start:stop)*freqres)]);
colormap((hot)); shading flat
hold on
contour = plot(x(start:stop),y(start:stop)*freqres,'b-');
drawnow
y = y*freqres;
call = y(start:stop);
y(1:100) = spline(1:length(call),call,1:length(call)/100:length(call));
y(101) = (stop - start)*tempres;
y = y(1:101);
plot(y(1:100));
disp(sprintf('The call is %1.0f ms long', y(101)))
disp('  ')
X = y;
```

2) Function Chamois

```
function X = chamois(X, first, last)
if first == 0
   counter = last-2;
   while counter > 1
      slope = X(counter+1:last);
      foot = X(counter);
      if any(slope < foot)
         localmin = counter;
         counter = 0;
      end
      counter = counter-1;
   end
   last = localmin;
   first = 2;
end
counter = first;
while counter <= last
   slope = X(1:counter-1);
   foot = X(counter);
   if any(slope < foot)
      localmin = counter;
      [k,localmax] = max(X(localmin:last));
      localmax = localmax + localmin;
      counter = length(X);
   end
   counter = counter+1;
end
X = localmax;
```

3) Function Netindex

```
continue = 'y';
pattern1 = input('name the first pattern (eg: a12-n1):  ', 's');
pattern2 = input('name the second pattern:  ', 's');
pID1 = [1 0]';
pID2 = [0 1]';
[filename path] = uigetfile(‘*’, ‘choose a batch file’);
[filelength,filenumber] = size(neurowaffle);
minerr = 0.625*filenumber;
disp(sprintf('Your neurowaffle contains %1.0f inputs',filenumber))
hidden = input('How many hidden neurons will it be today?   ');
result = zeros(6:2);
clear output batch filename identifier
i = 1;
while i <= filenumber
    clear TR W1 W2 b1 b2 epochs
    testfile = neurowaffle(:,i);
    testout = syrup(:,i);
    if i == 1
        trainfile = neurowaffle(:,[i+1:filenumber]);
        trainout = syrup(:,[i+1:filenumber]);
    elseif i == filenumber
        trainfile = neurowaffle(:,[1:filenumber-1]);
        trainout = syrup(:,[1:filenumber-1]);
    else
        trainfile = neurowaffle(:,[1:i-1 i+1:filenumber]);
        trainout = syrup(:,[1:i-1 i+1:filenumber]);
    end
    trainsuccess = 0;
    while trainsuccess == 0
    initsuccess = 0;
        while initsuccess ==0
            clear TR W1 W2 b1 b2 epochs tp
            [W1, b1, W2, b2] = initff(trainfile, hidden,'logsig',trainout,'logsig');
            tp = [NaN 1];
            [W1,b1,W2,b2,epochs, TR] = trainbpx(W1,b1,'logsig',W2,b2,'logsig',trainfile,trainout,tp);
            if TR(1,1) < minerr
                disp('Network initialised just fine!')
                disp('  ')
                initsuccess = 1,
            else
                disp('Trouble initialising, will try again')
                disp('  ')
            end
          end
        tp = [25 150];
        [W1,b1,W2,b2,epochs, TR] = trainbpx(W1,b1,'logsig',W2,b2,'logsig',trainfile,trainout,tp);
        checker = TR(1,150)/TR(1,1);
        if checker < 0.8
            trainsuccess = 1;
```

```
            disp('Network trains just fine!')
            disp('  ')
        else
            disp('Trouble training, will try again')
            disp('  ')
        end
      end
    tp = [500 4850 0.00001];
    [W1,b1,W2,b2,epochs, TR] = trainbpx(W1,b1,'logsig', W2,b2,'logsig',trainfile,trainout,tp);
    [a b] = size(TR);
    lasterr = TR(1,b);
    out = simuff(testfile,W1,b1,'logsig', W2,b2,'logsig');
    if testout == pID1
        testpattern = pattern1;
    elseif testout == pID2
        testpattern = pattern2;
    end
    if out(1) > out(2)
        outpattern = pattern1;
    else
        outpattern = pattern2;
    end
    disp(sprintf('The results of network %1.0f out of %1.0f are:', i, filenumber))
    disp('  ')
    disp(['Input:  ' testpattern])
    disp('  ')
    disp(['Output:  ' outpattern])
    disp(sprintf('%1.5f %1.5f',out))
    disp('  ')
    [a b] = size(TR);
    lasterr = TR(1,b);
    discerr = mean(abs(out-testout));
    disp(sprintf('Discrimination error: %1.5f', discerr))
    disp('  ')
    results(1:2,i) = testout;
    results(3:4,i) = out;
    results(5:6,i) = [discerr; lasterr];
    i=i+1;
end
results(1:4,filenumber+1) = [NaN NaN NaN NaN]';
results(5,filenumber+1) = mean(results(5,1:filenumber));
results(6,filenumber+1) = mean(results(6,1:filenumber));
disp(['The average discrimination error for ' pattern1 ' vs ' pattern2 ' is:']);
disp(sprintf('%1.5f', results(5,filenumber+1)))
hidden = num2str(hidden);
eval(['save ' [pattern1 pattern2 '.' hidden] ' results'  ' -ascii']);
```